The introduction of woodland field layer species into secondary woodlands.

by

Joanna Lynne Francis

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With happy memories of walks with Digby
in Hampshire's ancient woodlands.

Abstract.

The enhancement of field layers in newly created woodlands by the introduction of field layer species is the subject of the work presented in this thesis. Particular emphasis is placed on species associated with ancient woodlands, which, due to their poor colonising abilities and lack of competitiveness, are frequently absent from new, isolated plantations. Both the development of practical techniques for such introductions, and their ecological implications are considered.

Results of detailed monitoring of field trials for the large-scale introduction of field layer species into young plantations are presented and discussed. The results demonstrate the feasibility and success of field layer introductions into the new woodlands. They also indicate which species are more successfully introduced as seeds and which as young plants. Species groups, distinguished by their regenerative strategies, are identified.

An experiment for the introduction of ancient woodland field layer species as plants into woodlands of different ages is described. The timing of introductions, the necessity for ground pre-treatments, and the choice and method of species introductions are considered. The results of species survival and performance are discussed in relation to environmental factors and competition. The introduction of species as plants is generally successful even outside ancient woodland habitats, and survival rates are high. Pre-treatment with herbicide is unnecessary in woodlands where shade levels are substantial. In open areas, herbicide pre-treatment reduces competing vegetation and enhances the survival and performance of the field layer species.

The autecological details of 30 field layer species, are collated, compared and discussed. This information, together with results from the experimental work, literature and field observations, is incorporated into a decision support system. This can be used as future guidance for the enhancement of field layers in new woodlands and young plantations by the addition of woodland field layer species.



Plate.1 *An enhanced woodland field layer in a young plantation at Milton Keynes.*

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1. Introduction.

1.1 The ecological characteristics of Britain's natural woodlands.

Britain's woodland history began after the last glaciation ended, and by 7000BC, after a period of stable climatic conditions, our islands were almost continuously wooded. Having developed over the centuries, the woodland communities that exist now are extremely varied, with an enormous complexity both of species and structure. Using the characterisation of age, Peterken (1977a) classified different types of woodland:

i. Primary Woodland. This consists of remnants of the original "primaeval forest" or "wildwood" of the first continuous forest cover. Only 1%, which is represented by a few greatly modified fragments, remains. Such primary woodland is found on steep slopes, scarps or deep valleys, *i.e.* inaccessible land, or that unsuitable for agricultural use.

ii. Secondary Woodland. This occupies sites which have not been continuously wooded through the historical period. It is either the product of natural succession, or planting on land which was at some time unwooded.

Despite man's intervention in the management of secondary woodland, some is of considerable age and is termed **ancient secondary woodland.** This is defined, by Peterken, as that which existed prior to 1600 and which has been continuously wooded since then. All remaining woodland is classed as **recent secondary woodland.** Peterken (1977a) notes that "ancient woodland therefore comprises both primary woodland, and secondary woods originating before the threshold".

Whilst it is possible to prove the status of ancient woodlands using pollen analysis, cartographic, archeological and documentary evidence (Rackham 1980), natural ecological features can also indicate age. Martin & Pigott (1975), and Stevens (1975), have studied the soils of primary woodlands, and have found them to have distinct characteristics. In general, the soil attributes of ancient woods remain quite close to natural, since they have been undisturbed by cultivation and major vegetational changes

and are little affected by minor disturbances, such as animal activity and the growth, decay and fall of trees (Peterken 1981a).

Another important characteristic of ancient woodlands is the associated field layer, which is influenced by the continuity of a wood and its management history. Peterken (1981a) states that "it is possible that the herbaceous communities of ancient woods have descended without much alteration from those of the primaeval, natural woodlands which once occupied the same ground." In 1974, he introduced the concept of assessing the age and value of an ancient wooded site using indicator species.

The field layer species selected as ancient woodland indicators by Peterken (1974) are those that:

a. **are especially associated with woodland conditions.** These are defined as:

i. "species which can tolerate the shade of a closed woodland canopy,

ii. others which in some way require woodland conditions",

b. **exhibit a poor colonizing ability.** The existence of these species depends on the continuity of woodland on particular sites.

Such species are found mainly in long-established woodlands, many of which are ancient coppices, where some are able to survive the deep shade as vegetative units, flowering profusely when the light phase occurs after coppicing. Surveys of their presence or absence within any individual wood can indicate its age and continuity. Just as plant communities vary, species used as indicators change from region to region, so specific lists are compiled for different areas. The English Nature South Region ancient woodland vascular plant list is given in Appendix A. Examples of typical indicators in this region are *Anemone nemorosa** (Wood Anemone), *Lamiastrum galeobdolon* (*L. galeobdolon* ssp. *montanum*, Yellow Archangel), *Luzula pilosa* (Hairy Wood Rush), *Oxalis acetosella* (Wood Sorrel) and *Primula vulgaris* (Primrose). Ancient woodland field layer species are characterised particularly by their tolerance of shade, non-competitiveness and poor colonising abilities. With features such as poor seed set in

*Nomenclature follows Stace (1991).

deep shade, production of few, heavy seeds and often vegetative propagation, they may be reluctant even to invade an extension to an existing ancient wood. Woodruffe-Peacock (1918) observed the methods of entry of plant species into a fox-covert that had been planted in 1797. He concluded that the majority of true woodland species which colonised the covert were either carried into the wood on clothes, or dropped by birds, stating that " the modes of carriage are as various as the visitors to a covert are frequent or rare", and thereby showed that other agencies were necessary for colonisation. Peterken (1981b) studied the distribution of *A. nemorosa* in Central Lincolnshire. He found it to be an excellent ancient woodland indicator, with 95 out of 101 sites in which it was recorded being ancient woods, remnant hedgerows or adjacent secondary woodlands. Whilst this species has a limited capacity to colonise recent woods which are adjacent to ancient ones, the soils of these usually encourage the growth of competive vegetation against which it is unable to survive. It is suggested that since *A. nemorosa*'s strategy for growth and survival developed while the country was continuously wooded, it now has very little or no capacity for dispersal over any distance into a new territory (Peterken 1981b). Many other field layer species which have developed simultaneously may well have similarly limited colonisation abilities. In 1988, Webster & Kirby studied the species composition of an ancient woodland and a recent adjacent wood (planted between 1889 and 1898) in Essex. They found that the ancient woodland had a richer field layer, consisting of more ancient woodland indicator species and observed that only a few of these had colonised slowly into the recent woodland. In 1925, in an overview of Norfolk woodlands, Beevor commented that no bluebells grew in the planted woodlands which were about 100 years old, and hence these plantations "failed in charm".

1.2 The case for *new* woodland enhancement.

The "inertia of vegetation" (Rackham 1980) means that when a new wood forms, whether by accident or design, it does not suddenly acquire a full woodland field layer. Characteristically, a recent secondary woodland, typically with disturbed and, possibly, quite fertile soil, will have a poor, rough, and rather uninteresting field layer. This may consist of species such as nettles, brambles, ivy, coarse grass species and others, which

either have the ability to colonise new sites, or which may persist on the site from its former land use. Newly planted woodlands, or rather *plantations*, initiated by farmers, urban planners and others, may therefore take many hundreds of years to become as diverse as ancient woodlands, especially in obtaining a full complement of interesting and attractive field layer species.

In 1918, Woodruffe-Peacock wrote of species' colonisation into woods that "seeds are **ever arriving** from near at hand or more distant localities". However, 49 per cent of England's ancient secondary woodland was lost between 1930 and 1984 (NCC 1989), and the remaining areas are much reduced and isolated. Further, Peterken & Game (1984) claim that "the barriers to future accumulation of species in recent woods will be even greater, because the populations of woodland species in hedges and unwooded habitats have been greatly reduced by agricultural intensification". Studies on some isolated woods indicate that even those of great age do not possess field layers as diverse as those in ancient woodlands. Hayley Wood, Cambridgeshire, (Rackham 1975) is almost certainly ancient, and probably of primary woodland status with its particular tree and shrub communities, soil and field layer species. It has always been managed under a coppice system, as have two nearby woods, Papworth Wood and Overhall Grove, which are secondary woods of 800 and 400 years in age. This is perhaps an age old example of habitat re-creation and, indeed, one in which, due to the age of the younger stands, one would have assumed work to be complete. Despite the length of time that these secondary woodlands have had to develop, studies have shown that "the isolation of these woods has proved a complete barrier to colonisation by many woodland species to one or both of these sites" (Peterken 1977a). A few field layer species had colonised fairly recently, *e.g. A. nemorosa*, and were still spreading. The continued presence of *Urtica dioica* (Common Nettle), *Poa trivialis* (Rough Meadow Grass), and *Galium aparine* (Cleavers) in the field layer indicated that the sites had been cultivated and inhabited in the past. A study carried out in Swedish plantations (Bråkenhielm 1977) indicated that some woodland species, such as *L. pilosa*, *O. acetosella*, and *Viola riviniana* (Common Violet), soon became established after a crop was cleaned or thinned. However, it is suggested (Hill 1979a) that the differences in climate, and in the availability of the diverse local flora nearby the forest plots probably allowed this rapid colonisation.

As a legacy of recent land use in Britain, the next few hundred years may see quite different and even slower species colonisation of woodland field layer species into new woodlands, particularly those which are isolated. This may result in the plantations that are developing now never having comparable field layer communities to those in existing ancient woodlands. As woodland habitats become increasingly discontinuous, many woodland species in Western Europe may now have rather uncertain futures, unless they have some means of moderately long-range dispersal, whereas "five thousand years ago this would have been an unnecessary luxury" (Webb 1966). Indeed, with their characteristically slow dispersal, poor colonising ability and relatively small individual populations, which are subject to large fluctuations in density, the ancient woodland species have even been described by Peterken (1977b) as 'extinction-prone' (Terborgh 1974). Buckley (1989) writes of the poor colonists, which are unlikely to invade a new wood by themselves, often being the more attractive and interesting field layer species. For enhancement in ancient woodland re-creation schemes, he states that "contrary to the normal ethics of habitat creation, which discriminate against the widespread dispersal of less common species, *they would have to be put there*".

1.3 A review of schemes for creating woodland habitats.

Intensive agricultural practices, developments in commercial forestry and the mushrooming of new towns have all led to the dramatic reduction and fragmentation of natural habitats in recent years. As people become increasingly aware of this rapid decline in the diversity of the countryside and concern for the environment escalates, many are supportive of habitat creation schemes. Whilst the preservation of natural and semi-natural plant and animal communities should never cease, habitat loss can be compensated for to a limited extent, and the environment thus improved. For some years, parks and gardens departments and landscapers have been influenced by natural habitats in their planting schemes, but the concept of re-creating such habitats in their entirety is very new.

The aim of habitat creation exercises is generally "to establish semi-natural vegetation communities which in some way resemble the semi-natural original, although not

necessarily to re-create their full diversity" (Buckley 1989). The objectives of those concerned will vary widely and hence generate much debate as to the simplicity or complexity of the work. It is important that such schemes should be encouraged, but it should be stressed that attempts at replacement habitat creation are only poor substitutes for the loss of ecologically important sites. Developers and consultants have a tendency to use habitat creation in order to permit habitat destruction (Anon 1989), and this should be very carefully controlled. Further, some believe that conservation should nurture and manage existing resources, rather than substituting them with poor replicas. Indeed, Sutherland & Gibson (1988) are emphatic that "man-made habitats are no substitute for the real thing". Many people now realise, however, that even properly conserved and protected resources may be threatened in the future. So, as the science of habitat creation, or restoration ecology, develops, and suitable technologies with which to respond to environmental problems become refined, there is a growing awareness that such knowledge can be used appropriately to good effect. Berger (1990) makes the extremely valid observation that "Our task is to see that restoration is used properly -to repair past damage, not to legitimize new disruption".

To date, opportunities for habitat reconstruction in Britain have been rather limited, but much more scope now exists since countryside policies are beginning to change. The withdrawal of large areas of agricultural land, less intensive farming and forestry practices, and new possibilities in cities and on rural urban fringes should all lead to important new challenges for alternative land use. The different techniques of habitat reconstruction are summarised by Buckley (1989), as "habitat transplantation, habitat enhancement or diversification and habitat creation". The employment of these techniques to restore habitats, with particular reference to woodland, is reviewed below.

1.3.1 **Habitat transplantation.**

When habitat transplantation is practised, an original, existing habitat is moved from its present site to a new one. Prigmore (1987) writes that this method of reconstruction may be employed when

i. the flora and fauna of a particular site are threatened by development,
ii. areas of reclamation or re-creation are to be re-vegetated with locally-growing species,
iii. data are to be generated for experimental purposes,
iv. publicity for a scheme is needed,
and v. earthworks and spoilheaps require stabilisation.

An example of the transplantation of a woodland habitat is the work of Down & Morton (1979a, 1979b and 1980) in relation to the proposed destruction of North Darenth Wood, Kent. This study was initiated when permission was requested to quarry the ancient woodland site, which was a Site of Special Scientific Interest. The company involved undertook to create, by transplanting or other means, a *new* woodland, if permission for the quarry was granted. The overall strategy of the research was to characterise the plant species of the existing wood, to study how suitable plant material might be removed from it, and, finally, to consider the re-establishment of both coppice, standard trees, and the field layer into a new site. Standards and coppice stools from a nearby wood were transplanted, along with forest seedlings and commercially grown trees. Except in the case of the latter, which failed, this achieved a considerable amount of success, since the transplanted specimens survived, although with some indications of transplanting stress. However, it was five years (at which time the project had lapsed as planning permission had not been granted) until a sufficient degree of shade existed for the introduction of field layer species. These had been removed from a wood near North Darenth, and replanted into a nursery area where they established and increased very successfully. They were not, however, transplanted to the *new* wood. Down & Morton (1989) found that whilst it was "technically and biologically .... practicable to transplant both canopy trees and a variety of ground flora, by simple methods, and achieve establishment rates close to one hundred percent without requiring any lengthy preparation or unusual machinery .... many questions were left unanswered."

Another example of habitat transplantation is furnished by work around Stanstead Airport in the early 1980's. In 1981, prior to the expansion of the airport, the site was surveyed, and whilst "no high value wildlife sites were found, ... several of medium interest, and others of more local importance were identified" (Anderson 1989). These

habitats were varied, and included ancient woodland remnants, hedges, a fen and patches of species-rich grassland. At the planning inquiry, the British Airports Authority committed itself to incorporating some habitats into the development, transplanting others, and promised a substantial landscaping scheme. Small sections of woodland were relocated in 1987 by excavating shrubs and small trees, (post-coppicing), and removing them to a 'wildlife area'. This subsequently had top soil from beneath existing hedges spread onto it. Species survival was good, although it was initially reduced prior to the exclusion of rabbits and deer. Field layer species, which were either introduced with the soil, or which were transplanted, established successfully, as did transplanted grassland turves. The landscape design, produced with reference to the local flora of Essex, has since developed well, having been guided by ecological principles.

At Biggins Wood, Kent, Buckley (1987) was given a working brief by Eurotunnel "to collect the ground flora for propagation and eventual return to a new site". He carried out botanical surveys of the existing site, collected plants and seeds throughout the growing season, and investigated their propagation characteristics. Two methods of habitat reconstruction were considered: the movement of soil containing seeds and roots in order to re-locate the field layer, and the introduction of seeds or nursery-grown plants into the receptor site. Whilst much further work is necessary, interesting aspects have emerged, such as the poor germination of shade-tolerant herbs. This intimates the potential difficulties for establishing a woodland field layer by seeding alone. It was also concluded that any soil removed for relocation should be to a depth of at least 10cm from each of the main woodland stand types. Realising the importance of some form of over-head canopy to sustain a woodland field layer, practical solutions to overcome the initial lack of canopy were also contemplated.

1.3.2 **Habitat enhancement and/or diversification.**

Habitat enhancement occurs when attempts are made to maximise the ecological potential of existing but degraded or impoverished habitats. Amongst many examples, species-poor grasslands have been improved with the addition of wild flower species, (Wells *et al.* 1981), field margins have become increasingly diverse as a result of the

reduction of pesticide spraying, and woodland rides and glades have been successfully managed to encourage light-demanding edge species, and hence insects and birds (Anderson & Carter 1987). Areas of unmanaged and neglected secondary woodland can be enhanced by additional planting with native tree and shrub species.

1.3.3 Habitat creation.

Schemes of habitat creation are attempts at the complete reconstruction of natural ecological habitats. Actual *replication*, the precise and accurate reconstruction of a particular habitat, is very rarely possible, and so the ecological approach is, more usually, to attempt to *imitate* native plant communities that are adapted to the site conditions and are suitable for its proposed use (Cole 1982).

Work on the creation of grassland habitats has been very successful, with researchers in both Britain and Holland creating species-rich grasslands on new sites. An example of such a scheme is the pioneering work by Wells *et al.* (1981), who developed a suitable seed mixture, accompanied by management plans, for the creation of wildflower meadows. Similarly, in Warrington, Cheshire, the landscaping team created diverse, attractive and low-maintenance grassland habitats within the new town (Greenwood & Moffatt 1982).

Opportunities for habitat creation often occur in areas of greatest habitat loss. The environs of our new towns, the development of which has frequently destroyed or fragmented, existing semi-natural habitats, are subsequently (and somewhat ironically) sites for habitat reconstruction. With landscaping schemes becoming more varied and increasingly natural, it is the aim of the planners to enhance the surroundings of the inhabitants. Many types of habitat, as well as grasslands, have been imitated, and so re-created by urban landscape designers. A small acid bog was formed in an alkaline environment in the centre of Wolverhampton, (I.C. Trueman, pers. comm,); coastal lagoons were created by the RSPB at Minsmere, Suffolk, to encourage water birds (Hill 1989); and sand dunes were made out of the brick rubble from house demolition in the Hague, which, after being planted with suitable species, are now said to be

indistinguishable from the real dunes to which they are linked (Bos & Mol 1979). Whilst no natural habitat is easily reconstructed, these examples indicate that work is progressing, with much experience being gained by the consultants involved in such schemes.

Woodland habitats are much more difficult to create, and the reason for this is the very species complexity and structural diversity that makes them so appealing. However, their inclusion in urban habitat creation schemes is very necessary, and Tregay (1979) makes the important observation that "whereas traditional urban parkland has been designed mainly to be *looked at*, urban woodlands are also landscapes to become *involved in*, and can offer many of the experiences presently confined to the countryside." Recognising the importance of amenity woodland for a variety of other reasons, such as visual appearance, conservation, structure and education, landscape designers endeavour either to incorporate existing woodlands into urban environments, or to create new woodland areas.

Whilst the latter is a relatively new concept in Britain, as early as the 1930's, landscapers in Holland planted Bos Park, a 900ha recreational woodland, outside Amsterdam. This innovative work is certainly one of the first examples of urban habitat creation. In the Bos, native tree species were planted, and, with careful management, an extensive system of footpaths, bridleways and cycleways has been developed, enabling visitors to explore the woods (Tregay 1979). However, the early attempts at urban woodland creation tended to follow established forestry practices, with little attention being given to the understorey or field layers. Hence, they have resulted in rather uninteresting *plantations*, which lack structural diversity (G. Dawe, pers. comm.). Similarly, during the 1940's, large numbers of herbaceous plants were introduced into woodlands four miles away from central Amsterdam, creating discrete compartments beneath the canopy. These plantings were extremely intense, and, like the woodlands, rather artificial, but they were the beginnings of important urban habitat creation, and have since been considered critically, and so improved upon.

In the town of Delft, a unique experiment was carried out on a site of 4.5 ha between large blocks of flats. The town planners hoped to "achieve the integration of man in

nature within an urban environment" (Bos & Mol 1979). Their objective was to combine public awareness of and interest in nature with site planning for use by various groups of people. The topography made by building excavations was merely accentuated, with some areas dug deeper and others piled up, thereby creating a very informal land shape. Initially, only a few, necessary paths were laid out, others being created by the inhabitants themselves as they traversed the site. Shrubs and native trees were planted, where appropriate, and a mixture of cereals, clover and poppies were sown beneath, to reduce rampant weed growth. Within two years, an acceptable wild garden developed and, though not *ecologically-based*, it was successful in that it appealed to the residents, who had been involved in the initial planning procedures. Indeed, a report by the Netherlands Institute for Preventative Medicine found that the new design was attractive to both children and adults, and made better use of the area than more conventionally planned open spaces. They even recommended that the experiment should be used in other towns. The Dutch certainly have a clear perception of the requirement for new habitats, and now approach the creation of new woodlands with management plans of up to 120 years. Natural planting continues, with approaches developing to diversify structure and enhance naturalness, such as incorporating existing landscapes into creation schemes.

In Sweden, the importance of urban habitat creation is also recognised. Areas of new, natural landscapes may either be planted, or a housing development may be built into existing woodland, as has occurred near Stockholm (Tregay & Ertzgaard 1980). In the 1970's at Helsingborg, south Sweden, a 2 ha area of woodland was created using rough, resilient, and fairly unkempt vegetation, to provide a tough and hard-wearing play area. As in Holland, this is utilised more and perceived better by local residents than nearby ornamental landscapes. The Swedish recognise that when many of their housing developments expanded (from 1950 onwards), insufficient attention was given to open space, and that some nature-like constructions were rather too neat and tidy in their establishment period. So, in 1980, a research team of landscape architects, with widely varying backgrounds, was set up at the Swedish University of Agricultural Sciences, to assess nature-like open spaces (Gustavsson 1982). They have started more than one hundred experimental sites within sixty different areas of Sweden, of which six have been selected for total evaluation. The researchers are aiming to evaluate all aspects of

natural planting, from what degree of naturalness is suitable where, to which species should be planted, and at which stage they should be introduced.

Whilst urban habitat creation is a much newer concept in Britain, planners and landscapers can draw upon the experiences of those abroad and employ their techniques. In 1970, Land Use Consultants became involved in the Stoke-on-Trent Land Reclamation Programme. This required large scale forestry planting, for which the company developed non-commercial forestry planting patterns (Eardley 1973). Their objective was to create informal parkland or forest areas similar to the Bos Park in Amsterdam or London's Hampstead Heath. Realising that natural woodland development is a series of successional stages, but not having the time to wait for this, they developed a method of planting which would be continuous, give variety, develop quick cover and encourage wildlife. They designed two forestry planting patterns, one as a framework and the other mainly for accenting and barriers. Transplants and forestry whips were planted and showed success in the early stages. The expectations are that the various mixes, which include twenty native species, will ultimately develop into a very natural forest park of genuine ecological value.

The two most publicised examples of widescale urban woodland creation in Britain, at Milton Keynes, Buckinghamshire and Warrington, Cheshire, were initiated in the early 1970's. The master plan for Milton Keynes New Town was published in 1968, soon after the site for the new city had been designated, and was designed specifically "to permit flexibility and encourage change with growth" (Youngman 1977). With the city centre located on the highest ground, the surrounding area was for housing developments and road systems. The city's form was determined by the road pattern, and so the treatment of the land bordering the *grid* roads was crucial to its image. It was decided that Milton Keynes should be a *city of trees*, and the master plan showed a tree-lined road system, whereby traffic was screened from houses, and *vice versa*. Policies were drawn up, which detailed the purposes of both the grid road reservations, and the *linear parks*, which run along water courses. Proposals were included which ranged from the creation of a favourable image for the new city, through the protection of housing and industrial areas from the glare, noise and visual intrusion of traffic, to the creation of corridors for wildlife (Milton Keynes Master Plan). With only three large woods plus

a few neglected copses in existence and these objectives in mind, a bold tree planting strategy was carried out between 1975 and 1980, with ten thousand trees planted per year in both grid road reservations and numerous other situations. Major sections of the city were allocated groups of species chosen for their visual distinctiveness rather than precise ecological correctness, but with a good proportion of native species within them to encourage wildlife development (Southard 1977). With various management plans, including the introduction of both understory and field layer species, once tree canopies had matured sufficiently (see Chapter 2), these urban woodlands are slowly developing, and already providing harbour for a wealth of insects, birds and animals.

The other example of widescale urban woodland habitat creation is in Warrington New Town, where in 1974, landscape architects began to consider the development of three residential areas on the site of a former Royal Ordnance Factory (Scott *et al.* 1986). Knowing that early Dutch and Swedish work lacked diversity of habitat, structure, age and spatial character, they recognised that successful schemes depended upon "skilled management programmes to create ecological and spatial diversity" (Tregay 1986). With this in mind, they created Birchwood District, a new landscape on 400ha of despoiled land, which was planned, designed, and managed on ecological principles. Oakwood, one of the residential areas, was designed as a web of woodland belts linked to the existing woods on the margins of the area. It was arranged to enclose *cells* for residential developments, schools, playing fields and other land uses (Tregay & Moffatt 1980). The earliest woodland belts were established three years before the first housing completions, and played a major role in creating a green environment for the first residents. Plantings used species of trees and shrubs indigenous to the region, which reflected the local soil conditions and the existing landscape features (Greenwood & Moffatt 1982). Whilst problems were encountered, such as nurse species being too vigorous in places, and some planting mixtures being too complicated, the scheme has generally been successful. A pleasant and subtle landscape has been produced, with maintenance costs dramatically reduced in comparison with conventional horticultural areas. However, the Warrington Landscape team realise that "some bold management decisions are necessary" to create more spatial variety, and clarity within mixed-species plantations (Tregay 1986). With reference to his work in Warrington, Tregay notes that there is a clear distinction between the management of most designed urban landscapes

and that of nature-like vegetation, and stresses the importance of the use of different management regimes to create diversity. Whilst the role of the habitat designer is not diminished, as it is he who creates the main structure and composition of the new landscape, Tregay emphasises the "dynamic qualities of plantations", and hence the importance of their subsequent management.

Cole (1982) writing with reference to the William Curtis Ecological Park, also sees management techniques as important, especially in relation to the size of a woodland block. Changes in the management of any one section of a woodland will be dependent on its size and the amount of public access with which it has to cope. For example, whereas large blocks can have discrete units designated within them to specifically encourage the growth of a field layer, small blocks of woodland could only be so managed if isolated, or with very limited public access.

In 1987, the Countryside Commission published a policy document which suggested that national forestry targets should be updated in terms of both the quantity and quality of trees being planted. To achieve the new objectives, two new multi-purpose forestry initiatives were proposed: the New National Forest and Community Forests. The particular aim of the New National Forest was to demonstrate multi-purpose forestry, encompassing "agricultural diversification, timber production, landscape improvement, ecological and cultural enhancement, economic and enterprise development, and public recreation" (Gilder 1991). The target forest area was 150 square miles, half to be planted with trees, and the rest to remain as open farmland and villages. By 1991, the site which had been chosen for the new forest was in the Midlands, covering parts of Derbyshire, Leicestershire, Staffordshire and Warwickshire. The Commission intends that 20,000ha of land will be planted within a period of 30-50 years.

The Countryside Commission and the Forestry Commission are jointly supervising the proposed Community Forests. Three sites were designated in 1987, with a further 11 announced in 1991 (Gilder 1991). The aim of these forests is to provide a major recreation resource and to enhance the environment in areas close to large urban developments. Whilst both the New National Forest and the Community Forests are in their infancy, the scope for woodland creation in the selected areas is clear. It is to be

hoped that the ambitious nature of the proposals does not prevent the ideas being put into practice.

1.4 Woodland creation in a changing agricultural scene.

It is recognised that any increase in the country's woodland cover is beneficial, enhancing landscape diversity, producing complex reservoirs of plants and their associated wildlife, and possibly increasing home-grown timber stocks. Whilst the urban environment clearly offers many opportunities for woodland reconstruction, the recent policy of removing land from agricultural use to reduce current overproduction gives another chance for tree planting and hence woodland habitat creation. Various schemes have been proposed by agencies such as the Countryside and Forestry Commissions, and in 1987 the Ministry of Agriculture announced proposals for a **Farm Woodland Scheme** to be introduced in 1988 for an initial period of three years. With an objective of planting up to 36,000ha, the aims of the Scheme were to divert land from agricultural production, to create environmental and recreational benefits, to contribute to farm incomes and rural employment, and to encourage greater interest in timber production from farms (Insley 1988). The scheme offered farmers annual payments over a number of years to help bridge the gap between the planting of trees and the first income from the thinning of timber. Farmers who planted broadleaved species, or mixtures in which they predominated, received much higher rates, as the importance of diversity within a wood, not merely the amount of tree cover, was recognised. Existing farm woodlands have often been unmanaged, resulting in poor quality timber, but many are on fertile, lowland soils and, if managed correctly, should allow farmers to grow valuable, high quality wood. In addition to timber production, objectives such as landscape, conservation, game, shelter and minor products, can be considered (Hibberd 1989). By planting trees, the farmer can not only diversify his business, and improve the appearance, and often the capital value of his land, but also can contribute greatly to the farm's conservation and sporting value.

Despite initial optimism, the uptake of the Farm Woodland Scheme was rather slow, with only 11,200ha, about a third of the original target, planted by 1991. Various

studies, *e.g.* that of Clarke & Johnson, which is summarised in The Forestry Commission Research Information Note 225 (1992), have shown a reluctance by farmers in some regions to consider trees as long-term crops and to plant trees on productive agricultural land. Further, the premiums paid for tree planting were considered insufficient by many farmers, since they were lower than the short-term Set Aside payments. The scheme was therefore reviewed, and in 1992 the **Farm Woodland Premium Scheme** was introduced. This is an updated version of the original scheme, which has been made more acceptable to farmers by being more economically viable. No longer are the grants merely for planting trees, as annual payments for continued woodland management are also available. To date, there have been applications for tree planting on 1,969ha of farm land.

Major changes in the government's Set-Aside Scheme, have recently made it compulsory for every farmer to put 15% of land into Set-Aside. At present, the E.E.C. is reluctant to allow trees to be planted on this land, but it is hoped that this view will change in the near future. If it does, this will increase the opportunities for land to be released from intensive agricultural use, and for natural habitats to be created.

1.5 Field layer introductions: the way forward.

There are obvious benefits for farmers, and those involved in urban schemes, planting trees, and this should be encouraged. The actual *creation of a woodland*, however, presents a far more daunting task. Decades of intensive land use will probably result in a poor species diversity within new woodlands, and unless this is to be acceptable, limited, and carefully monitored and recorded, field layer introductions may well be beneficial. There is surely a case for attempting this, as otherwise the diversity of our woodland habitats may decline, and subsequently be lost.

In some urban habitat creation schemes, the tree and shrub layers have grown sufficiently to reduce the light intensity on the woodland floor, and the introduction of field layer species has been attempted. By the early 1980's, the tree establishment techniques used in Milton Keynes had lead to successful canopy development within the

new plantations. A *bare earth* policy, consisting of regular herbicide treatments, had been employed for a few years to encourage tree growth by reducing competition from weeds. This also created a favourable situation for the introduction of woodland field layer species, which was begun on an experimental basis in 1981, and then expanded into a large-scale field trial in 1987. Reported in detail in Chapter 2, the scheme has been generally successful, and has lead subsequently to the widespread introduction of woodland field layer species throughout the city's young plantations (Street & Mond 1992). Tregay (1985) reported that eight years after the initial tree and shrub plantings in Warrington, the development of a canopy in many plantations had reduced the light to less than 10%, and had produced a layer of leaf litter. With these seemingly ideal conditions, 14 species of woodland plants, including *Hyacinthoides non-scripta* (Bluebell), *P.vulgaris* and *Silene dioica* (Red Campion), were introduced into various sites. Although many are still alive and some of the woodland edge species have spread, others are only surviving and are perhaps unsuitably sited. Cohn & Packham (1991), working in urban plantations in Wolverhampton, have carried out experimental work involving the use of wood chip mulches and leaf litter. They have reported good results, particularly with the establishment of species such as *L. galeobdolon*, which is adapted to tolerate such conditions. Whilst this approach may be possible for small areas, it is considered that such a method may be both too expensive and labour intensive to apply to large scale schemes.

With recognition of the need for further work in this field, the project reported in this thesis was specifically set up in 1989 to study the introduction of ancient woodland field layer species into secondary woodland. Administered by the Forestry Research Co-ordination Committee, it was one of 12 projects funded by an N.E.R.C. Special Topic Programme on Farm Forestry. It was closely associated with the Farm Woodland Scheme, and amongst the topics has considered methods for introducing field layer species into new farm woodlands. However, whilst those farmers who have planted trees may consider their new woodlands for timber products and game, the scope for the introduction of field layer species into farm woods is not yet known. It is clear that in the urban situation, many new woodlands have been and are being planted, and in some cases have reached an ideal stage for field layer introductions. The need for these has been described, and one aim of this project was therefore to study the physical

possibility of making successful field layer introductions into new woodlands.

A significant proportion of the field work reported in this thesis took place in Milton Keynes, a true urban woodland situation. Here, the large-scale field trial implemented in 1987 presented ideal opportunities to investigate both the survival and establishment of some 25 woodland field layer species that had been introduced into the young plantations. Additionally, patterns of species establishment and spread were studied. Other experimental work was situated in Berkshire, and has included the introduction of field layer species into a new plantation, a farm woodland, young and mature forest plots, and an ancient copse. This study has specifically considered ecological aspects of the introduction of ancient woodland species, with their associated problems of propagation, colonisation, and exacting light requirements. Experimental objectives, which encompassed the timing of introductions, the necessity for ground pre-treatments, method of introduction, and species choice were all investigated. The ecological implications of the behaviour of such plants in areas outside their natural habitat were considered, in an attempt to elucidate the tight links of such species with ancient woodlands yet virtual absence from recent ones. The study has also encorporated germination tests on a wide range of woodland field layer species, and an investigation of the dispersal capacities of species from an ancient woodland into an adjacent plantation. Additionally, an extensive reference source of the growth characteristics and strategies of woodland field layer species has been compiled. The information gathered from the experimental work, field observations and literature sources has been used to create a decision support system for the enhancement of recent woodlands with field layer species.

The thesis is set out as follows:

Chapter 1 describes the ecological characteristics of Britain's natural woodlands, and those of the associated field layer species. With reference to the loss of natural habitats during this century, a case for new woodland enhancement is proposed. Recent schemes for creating woodland habitats are reviewed, and the opportunities for woodland creation within agriculture are considered. Finally, with details of recent attempts at field layer introduction, the purpose and content of this project are described.

Chapter 2 describes the enhancement of newly planted woodlands in Milton Keynes. In 1987, an experiment was implemented by the Institute of Terrestrial Ecology, Monks Wood, to study practical methods for the large scale introduction of woodland herbaceous species into newly planted woodlands. Twenty five field layer species were introduced by sowing and planting methods into replicated experimental plots over six sites. Monitored by I.T.E. in 1987 and 1988, the experiment was encompassed into this research from 1990. The sites have subsequently been monitored in detail, and data are presented and discussed.

Chapter 3 is an analysis of the performance and distribution of woodland field layer species, during their establishment within young plantations. Within the I.T.E. experimental sites in Milton Keynes, the establishment of 10 field layer species was monitored in more detail. Data were collected for environmental factors, such as light, canopy cover, soil type, and competition levels. These were analysed and related to the performance and distribution of the introduced species. The pattern of the development of a field layer within a young plantation is discussed.

Chapter 4 describes the experimental introduction of ancient woodland field layer species into woodlands of different ages. A new experiment was implemented in Berkshire to encompass the main practical objectives within the project. Plants of six ancient woodland field layer species were introduced into woodlands of different ages, ranging from a new plantation to an ancient copse. Results of the monitoring in 1991 and 1992 are presented, and are related to environmental data such as light levels, soil type and competition. The importance of the timing of field layer introductions, the

necessity for ground pre-treatments to reduce competition, the choice of species, and the method of introduction are discussed.

Chapter 5 addresses the autecology of woodland field layer species. With a comprehensive literature survey, field observations, and experimental work, particular characteristics and growth strategies were gathered for 30 South Region woodland field layer species. Such information about species autecology was collated to aid their successful introduction into new areas.

Chapter 6 develops a procedure for the introduction of field layer species into new woodlands. The information gathered about the introduction of ancient woodland field layer and other woodland herbaceous species into secondary woodland from experimental work, field studies and literature surveys was compiled to aid both urban habitat managers and farmers. From the information, recommended procedures for field layer introduction are suggested. A preliminary attempt has been made to develop a decision support system for the enhancement of new woodlands.

Chapter 7 contains a summary and a general discussion of the results of the 3-year research programme. Practical aspects of field layer enhancement and the ecology of woodland field layer species are summarised. The benefits and ethics of field layer enhancement, and further considerations and future developments are discussed.

2. The enhancement of newly planted woodlands in Milton Keynes.

2.1 Introduction

The Milton Keynes Master Plan (1968) designated a vast tree-planting scheme in order to create a "city of trees" (Higson 1977). Planting began in 1974, and by 1980 many plantations had been completed and were beginning to establish. It was recognised by the managers of city parks, roadsides and recreation areas, that there were opportunities for the introduction of wildflower species into the plantations to hasten their development into woodlands. However, since only very limited field layer introductions had occurred elsewhere at that stage and knowledge of such work was poor, the Development Corporation sought advice from ecologists at the Institute of Terrestrial Ecology, Monks Wood. Thus, in 1981, Dr L. Boorman was awarded a contract to study the introduction of ground flora species into new woodlands within the city.

The initial study began in 1981, when a small-scale experiment was set up in nine different areas in Milton Keynes. Species such as *P. vulgaris*, *Geum urbanum* (Wood Avens), *H. non-scripta*, and *Arctium minus ssp. pubens* (Lesser Burdock) were either sown or planted into plots which had received various pre-treatments. The germination of seeds and the growth, subsequent establishment and flowering of plants were monitored, and by 1986 it was clear that both methods of introduction were significantly successful. Study of canopy densities and the related light intensities indicated that the light intensity at ground level should be between 10-40% of full daylight in order for woodland species to survive and establish, yet be low enough to reduce competition from non-woodland colonisers. The other interesting result from these small-scale experiments was the considerable variation in success of different species at different sites. Species success or failure was not easily predictable in any particular area, and so it was suggested that species mixtures should be used (Boorman 1990).

Following the success of the first experiment, it was decided to increase the scale of the work, both in terms of the area covered and the number of species used. In 1987, a field

trial was implemented at six young plantation sites in Milton Keynes, with the particular aim of providing practical methods for the large-scale introduction of herbaceous plant species into planted woodland. This field trial was designed to investigate the suitability of woodland field layer species for introduction, the methods of species introduction *i.e.* whether by seed or young plants, and the densities of that introduction. The species chosen for introduction were all representatives of the flora of local ancient woodlands, without being rare or very limited in their distribution. The experiment was started in March 1987 by Dr Boorman, ITE, and was incorporated into the research reported in this thesis in 1989. The results of monitoring this experiment form a major component of the work reported in this thesis.

One of the most essential pieces of information missing from the large field trial, was data on the initial establishment rates for the woodland field layer species that were introduced as seed into the young plantations. This is because the monitoring of the sown plots in 1987 and 1988 was not sufficiently quantitative to calculate reliable germination rates. Without such information, it proved difficult to interpret the density data gathered in 1990 and 1991, because it would have been desirable to compare the recorded densities with established (germinated) densities rather than sown densities. In order to obtain some information that could be related to this main experiment, it was decided to monitor one of the sites in Milton Keynes that was seeded with woodland field layer species in 1991. In addition to the similarity of the conditions of the new site with those that were seeded in 1987 (see Site details), the composition of the seed mixture was comparable with those first used in the 1987 experiment. Whilst any seed mixture is governed by species' current availability, the present composition of Milton Keynes seed mixtures has developed from knowledge gained in the earlier experiments, and the 1991 species list reflects those species sown in 1987, with a balance of marginal and shade-tolerant woodland field layer species. It was considered that the monitoring of this site in 1991 and 1992 would give some useful and much needed information on the initial germination and subsequent establishment of the woodland field layer species.

2.2 Site details.

2.2.1 The large-scale introduction of woodland herbaceous species into young plantations in 1987.

The sites in Milton Keynes chosen for the extended studies were:

Site 1: Cotton Valley adjoining the sewage works. SP 886404

Site 2: Canal side adjoining grid road H7. SP 871385

Site 3: Milton Keynes Bowl. SP 875368

Site 4: Along the north side of grid road H3, between V8 and V10. SP 853411

Site 5: Along the north side of grid road H6, between V8 and V10. SP 870394

Site 6: Along the water main works on grid road V8, between H8 and H9. SP 876363

All of these sites were formed during the building of the town and result from the creation of roads or housing estates. The sites consist mainly of Oxford and boulder clay mounds covered with top soil, and are known as grid road plantations. Plate 2 shows examples of these plantations, which lie between housing areas and road systems. The sites were planted between 1976 and 1982 with varying species mixtures of trees and shrubs. After planting, a bare earth policy, was practised for a few years. This was achieved by repeated sprayings of herbicides, (which included glyphosate), which were applied to reduce competing weed growth and so enhance tree establishment. It was a serious problem of pernicious weed growth, particularly in areas covered with top soil, that lead to the development of the bare earth policy (Salter & Darke 1988). Plate 3 shows a young plantation with bare earth prior to field layer introductions in 1987.

The sites that were monitored fully during the course of this research are now described in more detail.

Site 2. Situated beside the Grand Union Canal, part of this site slopes down from the canal banks, before becoming more level. Drainage is therefore variable and the site is quite wet in some of the flat areas. The site was planted with a mixture of tree and shrub species in 1982-1983, and is now characterised by groups of *Populus tremula* (Aspen), *Pinus sylvestris* (Scots Pine), *Robinia pseudoacacia* (False-acacia), *Alnus cordata* (Italian Alder) and *Salix alba* (White Willow), as well as smaller numbers of *Acer campestre* (Field Maple), *Corylus avellana* (Hazel) and *Quercus robur*



Plate.2 *Aerial photograph of Milton Keynes, showing plantations between housing areas and road systems.*



Plate.3 *Milton Keynes plantation (Site 4) with bare earth, prior to field layer introductions in 1987.*

(Pedunculate Oak). Although the site is very heterogeneous in terms of canopy cover, with very open areas and patches of deep shade (Plates 4 and 5), it has a good structural composition, with a developing shrub layer. In this respect, it is similar to young natural woodland.

Site 4. This site on the north side of grid road H3, is situated on top of an earth mound that separates the road from the houses behind it. Much of the site is sloping and drainage is good. Young trees were planted at the site between 1977 and 1981, and they have established successfully. The site is shady throughout and the canopy is dominated by *Prunus avium* (Wild Cherry) (Plate 6), *Acer platanoides* (Norway Maple) and *A. campestre*. There is little understorey at this site, with only a few *Viburnum opulus* (Guelder Rose) and *Malus spp.* (Apple species) to form any structure beneath the tree canopy.

Site 5. This site was first planted with trees in 1975 and 1976, but was replanted in 1977 as most of the original trees failed to establish. The eastern edge of the site consists of a stand of *Aesculus hippocastanum* (Horse-chestnut), which is growing on a steep slope coming down from a grid road. The remainder is planted with *Alnus glutinosa* (Alder) and various non-native species, including more *A. hippocastanum*, and *Poplus* and *Salix* hybrids (Plate 7), and is bordered by a meadow at its western edge. Part of this mixed block has at some stage been completely thinned and is covered in a layer of deep wood chippings. The site is waterlogged in parts.

Site 6. This site lies in two sections along the east side of grid road V8. It was planted with trees between 1977 and 1980, and the canopy species include *A. hippocastanum*, *Fraxinus excelsior* (Ash), *A. campestre*, *Crataegus monogyna* (Hawthorn), and *Poplus* and *Salix* hybrids. A feature in part of the site is the presence of many *Prunus spinosa* (Blackthorn) bushes. These are dense and impenetrable, and allow only the minimum of light through to the ground beneath. Drainage conditions at the site are fairly good.

These four sites are all managed as mixed high forest and are thinned on a five year cycle.



Plate.4 *Open area of Milton Keynes plantation, Site 2, with* Betula pendula *and* Alnus cordata, *1990.*



Plate.5 *Shady area of Milton Keynes plantation, Site 6, with a group of* Acer campestre, *1990.*



Plate.6 *Milton Keynes plantation, Site 4, dominated by* Prunus *species, 1990.*



Plate.7 *Milton Keynes plantation, Site 5, dominated by* Aesculus hippocastanum *and* Populus *spp, 1990.*

2.2.2 An investigation of the initial establishment and survival of woodland field layer species introduced as seed into a young plantation in 1991.

The site is a grid road plantation on the west side of grid road V8, between H6 and H7. Planted with a mixture of trees and shrubs in 1980 and 1981, it is now predominated by *A. hippocastanum* and *C. monogyna*, which are growing on a slope up from the grid road. Prior to being seeded with woodland field layer species, the site had just come out of bare earth treatment, which aided tree establishment. Sowing conditions were comparable with the bare earth situation in the main experimental sites.

Many sites in the city were seeded with woodland herbaceous species during spring 1991, as part of the Development Corporation's continued plans to enhance young woodland plantations (Street & Mond 1992). This site was selected as being representative of the more suitable of these, as the growth of trees was very good and quite uniform over the entire site, producing more even shade levels than in the other sites.

2.3 Materials and methods.

2.3.1 The large-scale introduction of woodland herbaceous species into young plantations in 1987.

The design of the experiment is shown in Fig. 1. On each of the chosen sites, 40 experimental plots were positioned within an area of 28m x 160m. Each plot, of 28m x 4m, was further split into three sections:

i) the first 3m for the introduction of field layer plants,

ii) the next 1m for a restricted seed mixture of field layer species,

iii) the final 24m for the main seed mixture of field layer species.

Each plot to be sown with the main field layer mixture was therefore 24m x 4m. The planting areas of 3m x 4m were joined horizontally across the top of four of the sown plots, resulting in individual planting blocks of 16m x 3m.

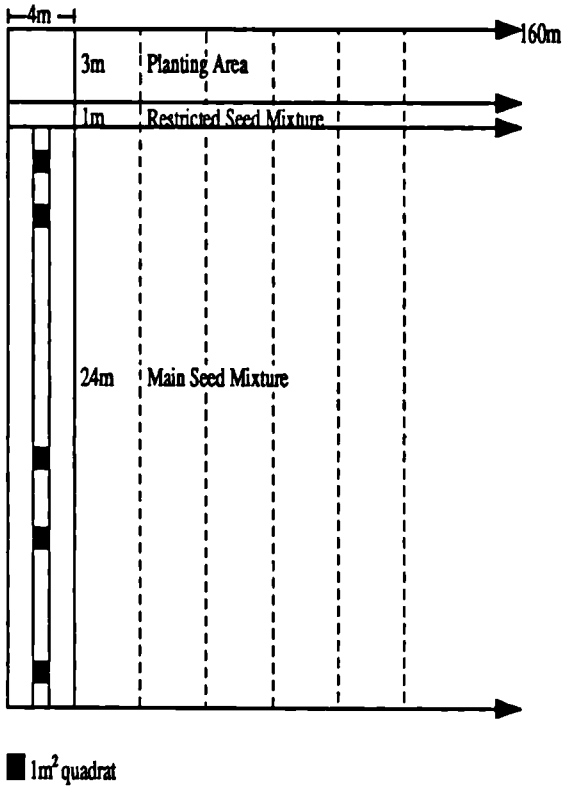


Fig.1 *Layout of experimental plots, indicating quadrat positions.*

2.3.1.1 **The main seed mixture plots.**

Two seed mixtures were each sown at two densities.

Main Mixture A		Density (m^{-2})
Alliaria petiolata	Garlic Mustard	180
Campanula trachelium	Nettle-leaved Bellflower	160
Digitalis purpurea	Foxglove	1160
Galium mollugo	Hedge Bedstraw	115
Geum urbanum	Wood Avens	270
Hyacinthoides non-scripta	Bluebell	195
Stachys officinalis	Betony	60
Teucrium scorodonia	Wood Sage	60
Torilis japonica	Upright Hedge-parsley	100

Main Mixture B		Density (m^{-2})
Campanula latifolia	Giant Bellflower	600
Conopodium majus	Pignut	180
Galium odoratum	Woodruff	55
Hypericum hirsutum	Hairy St John's-wort	310
Primula elatior	Oxlip	65
Silene dioica	Red Campion	215
Sison amomum	Stone Parsley	40
Stachys sylvatica	Hedge Woundwort	155
Viola odorata	Sweet Violet	80

Five treatments were selected for the sown plots:

i) High Density Seed Mixture A.

ii) Low Density Seed Mixture A.

iii) High Density Seed Mixture B.

iv) Low Density Seed Mixture B.

v) Control with no seed sown.

For Mixture A, the average sowing density per species was approximately 240 seeds m^{-2} at high density and 24 seeds m^{-2} at low density. For Mixture B, it was 190 seeds m^{-2} at high density and 19 seeds m^{-2} at low density. Hence, the sowing ratio within each seed mixture was 1:10. At high density, the total sowing density was 2300 seeds m^{-2} for Mixture A and 1700 seeds m^{-2} for Mixture B.

The mixtures, densities and controls were randomised among the 40 plots in each site. Sowing took place in March 1987 with the seeds being broadcast by hand throughout each 24m x 4m plot.

The September 1987 monitoring.

The top 10m of the sown section was examined for each plot at every site and seedling establishment was recorded by ITE staff.

The June-August 1988 monitoring.

Each plot at every site (except Site 3) was observed and individuals of each of the sown species were counted by ITE staff.

The 1989 monitoring.

No monitoring was carried out.

By Spring 1990, Sites 1 and 3 had become overgrown and neglected, and were therefore excluded from any further monitoring.

The May-June 1990 monitoring.

At each site, four plots were chosen at random from each of the five sowing treatments. The central 1m strip of each plot was then divided into 24 units of $1m^2$ (Fig. 1). From these, five $1m^2$ units were chosen at random and were subsequently monitored as quadrats. All species growing within the quadrats, including sown species, colonists from outside the plots, plants from the seed bank and regenerating tree seedlings, were listed. Individuals of each species present (even very small seedlings) were counted to give a record of species density m^{-2}. In addition, the area covered by each species within the quadrat was estimated by eye in order to obtain a percentage cover value.

The characteristics and distinguishing features of each of these quadrats were noted to aid relocation for further monitoring. Within the chosen plots, all plant species present throughout the whole of the 4m x 24m plot were also listed.

The May-June 1991 monitoring.

At each of Sites 2, 5 and 6, 48 of the random quadrats from 1990 were monitored to give current densities m^{-2} and percentage cover values for each of the sown species. This represents 12 quadrats from both seed mixtures at both sowing densities, and gives a total of 144 quadrats. Data were also obtained for the main components of competing vegetation, *i.e.* grasses, regenerating tree seedlings, perennial and annual weeds. The majority of Site 4 was thinned in winter 1990, and since growing conditions had changed, was omitted from further monitoring.

2.3.1.2 **The restricted seed mixture plots.**

A restricted seed mixture, the density of which was approximately 200 seeds m^{-2} at high density, and 20 seeds m^{-2} at low density, was made up of those species for which seed was in short supply. This seed mixture, which consisted of *Allium ursinum* (Ramsons), *Arum maculatum* (Lords-and-Ladies), *Geum rivale* (Water Avens), *P. vulgaris* and *Stellaria holostea* (Greater Stitchwort), was also sown in March 1987. The high and low density restricted seed mixtures were sown adjacent to Main Sowing mixture plots of the same density.

The 1990 monitoring.

The restricted seed mixture plots were observed for the presence or absence of the sown field layer species. Characteristics such as flowering, seed set and spread were also noted.

2.3.1.3 **The planted plots.**

In addition to the direct sowing at Milton Keynes, seed was sown in trays at the Institute of Terrestrial Ecology, Monks Wood to raise material for planting the following winter. This included another seven species for which seed was in very short supply. The six experimental sites were divided into two sub-groups, Sites 2 and 6 and Sites 4 and 5. Tables 9 and 10 give species lists and planting numbers.

The original sowing plan, consisting of 40 plots per site, allowed ten 3m x 16m plots to be positioned horizontally. This gave five plots planted at high density and five at low density at each site. The high density was seven times the low density, with 7, 14 or 21 plants of each species per plot at high density and 1, 2 or 3 plants at low density. The two treatments were randomised and planting was completed in February 1988.

The June-August 1988 monitoring.

The presence of all species at each plot in Sites 2, 4, 5 and 6 was recorded and site characteristics noted by ITE staff.

The 1989 monitoring.

No monitoring was carried out.

The 1990 and 1991 monitoring.

Between May and July of both years, the presence of all original plants and new seedlings was recorded at all sites. Characteristics such as cover, flower and seed production were noted.

2.3.2 An investigation of the initial establishment and survival of woodland field layer species introduced as seed into a young plantation in 1991.

In February 1991, a woodland field layer seed mixture was broadcast by hand onto the site at a rate of 2.83kg ha^{-1}. The seed mixture consisted of

Allium ursinum (Ramsons)
Aquilegia vulgaris (Columbine)
Campanula trachelium (Nettle-leaved Bellflower)
Conopodium majus (Pignut)
Digitalis purpurea (Foxglove)
Fragaria vesca (Wild Strawberry)
Galium mollugo (Hedge Bedstraw)
Geum urbanum (Wood Avens)
Hyacinthoides non-scripta (Bluebell)
Hypericum hirsutum (Hairy St John's-wort)
Hypericum perforatum (Perforate St John's-wort)
Lychnis flos-cuculi (Ragged-Robin)
Primula vulgaris (Primrose)
Prunella vulgaris (Selfheal)
Silene dioica (Red Campion)
Stachys officinalis (Betony)
Teucrium scorodonia (Wood Sage)
Vicia cracca (Tufted Vetch)

Details of the seed mixture were supplied by Milton Keynes Parks Trust, and from these the exact sowing density m^{-2} was calculated for each of the sown species. The average sowing density was 600 seeds m^{-2}. (For sowing densities of individual species see Table

11.) At sowing time, some less shaded areas of the site already had established grass swards within them. The introduced seed was targetted away from such areas, into bare earth and suitable shade.

Monitoring of the newly sown site.

Two sub blocks of $100m^2$ were selected within the sown areas to be representative of the site and 30 random $1m^2$ quadrats were sampled within each area. The monitored quadrats were therefore restricted random throughout the sown area.

The September 1991 monitoring.

All of the plants within the 60 quadrats, including the species introduced as seed, as well as annual and perennial weed species, grasses and regenerating tree seedlings, were identified and counted to give a record of species density m^{-2}.

The May 1992 monitoring.

The 60 quadrats were monitored to record any further establishment by either introduced species and any others that had colonised into the site.

The August 1992 monitoring.

The area covered by each species within the quadrat was estimated in order to obtain a percentage cover value. Indicators of performance, such as flowering and spread, were noted for the introduced woodland field layer species.

2.3.3 Tests on the germination success of woodland field layer species, 1991 and 1992.

In January 1991, seed was obtained for the 18 woodland field layer species that were introduced as seed into young plantations in Milton Keynes in 1987 (see Section 2.3.1.1). The majority of the seed was supplied by Milton Keynes Development Corporation, who had purchased large quantities of seed for sowing into young plantations that winter. (Seed was assumed to be from the 1990 harvest, but this was not guaranteed.)

Seed trays were prepared with J.Arthur Bowyer's Multi-Purpose compost which was watered once in the tray and allowed to drain prior to sowing. Seeds were sown onto the moist compost and then covered with a small amount of silver sand. For each species, 200 seeds were sown into each of three trays, making a total of 600 seeds. Trays were then placed outside and covered with netting to protect seeds from the activities of birds and small mammals. The sowing was repeated in late March with a further 600 seeds of each species. These trays were kept within a cold frame for about 6 weeks until the threat of frost had passed. (This ensured, as simply as possible, that one set of replicates was thoroughly chilled between January and April, whilst the other was not, being protected from the cold.) Once the second set of trays was removed from the cold frame, all trays were positioned together, and were treated similarly, receiving sufficient water to promote germination and keep seedlings alive.

The April 1991-April 1992 monitoring.

As seeds germinated, the seedlings were counted every few days, removed from the trays, and their numbers were recorded.

2.3.4 The data analysis.

2.3.4.1 The large-scale introduction of woodland herbaceous species into young plantations in 1987.

The 1990 monitoring.

From the field data, mean densities m^{-2} and mean percentage cover values, both with corresponding standard errors, were calculated for each of the sown species at each site. For each of the sown species in each sowing density, n = 20. For each species, the mean densities resulting from high and low sowing density were compared for significant differences using modified t-tests (Bailey 1969), to take into account unequal variances.

The 1991 monitoring.

From the field data obtained after another growing season, mean densities m^{-2} and mean percentage cover values, both with corresponding standard errors, were calculated for each of the sown species at each site. For each of the sown species in each sowing

density, n = 12. Modified t-tests were used for the comparison between densities resulting from high and low sowing densities. In order to directly compare the species mean densities between 1990 and 1991, mean densities for 1990 were recalculated using only the data from the quadrats that were remonitored in 1991 (*i.e.* n = 12). Mean densities from 1990 and 1991 were then compared using modified t-tests.

2.3.4.2 An investigation of the initial establishment and survival of woodland field layer species introduced as seed into a young plantation in 1991.

For each of the introduced species at the newly sown site, mean densities m^{-2}, with corresponding standard errors, were calculated from the 1991 and 1992 field data. The mean sowing densities for each species were also calculated from information obtained about the proportions of seeds sown and knowledge of individual seed weights. This enabled percentage establishment rates for each species to be calculated for the establishment recorded in 1991 and 1992. Mean percentage cover values, with corresponding standard errors, were calculated for the 1992 data.

2.3.4.3 Tests on the germination success of woodland field layer species, 1991 and 1992.

From the three replicates, each containing 200 seeds, mean percentage germination was calculated for each species in both sowing treatments. The percentage data were transformed, using the arc-sin transformation, and then were compared using Student's t-tests to indicate significant differences between the sowing treatments.

2.4 Results.

2.4.1 The large-scale introduction of woodland herbaceous species into young plantations in 1987.

2.4.1.1 The sown plots.

The 1987-1988 monitoring.

The monitoring in 1987 indicated that nine species out of the 18 had germinated in the first season, with *A. petiolata*, *G. urbanum* and *S. dioica* recorded at the highest densities (Boorman 1989). Many other seedlings were present which were too small to be accurately identified. Average plant density was 1.5 m^{-2} for Mixture A and 2.1 m^{-2} for Mixture B at high sowing density. The high sowing density plots had approximately ten times as many seedlings as the low sowing density plots. By 1988, seedlings of 14 sown species were recorded, with *G. mollugo*, *H. hirsutum*, and *T. japonica* being particularly abundant, together with the three species found to be abundant in 1987.

The 1990 monitoring.

The mean densities m^{-2} and mean percentage cover values, with corresponding standard errors, for each of the sown species at each site are presented in Tables 1-4. The average plant density was 12.69 m^{-2} for Mixture A and 19.05 m^{-2} for Mixture B, at high sowing density. This represents an 8.5-fold and 9-fold respective increase in the figures from 1987. The average total density for all species in each seed mixture was 79.26 plants m^{-2} for Mixture A and 106.35 plants m^{-2} for Mixture B, at high sowing density. Only one species, *C. latifolia*, was not recorded at any of the four sites.

The sites will now be considered separately in respect of the 1990 monitoring.

Site 2.

The total average plant density m^{-2} of sown species was:

	Low Sowing Density	High Sowing Density
Mixture A	93.6	88.75
Mixture B	26.1	148.65

Table 1. *Mean density m^{-2} and mean % cover in 1990 of sown species at Site 2.*

	Low sowing density				High sowing density			
SPECIES MIXTURE A	**Density**	**SE**	**%Cover**	**SE**	**Density**	**SE**	**%Cover**	**SE**
Alliaria petiolata	0.5	0.2	0.7	0.4	8.0	3.4	5.0	3.0
Campanula trachelium	0		0		0		0	
Digitalis purpurea	+		+		0.6	0.5	0.4	0.3
Galium mollugo	3.2	1.5	16.0	5.2	4.3	2.1	22.3	6.4
Geum urbanum	70.6	23.4	22.8	5.3	46.2	12.0	32.5	5.9
Hyacinthoides non-scripta	2.2	1.3	0.4	0.2	15.5	5.5	1.0	0.2
Stachys officinalis	+		+		0		0	
Teucrium scorodonia	+		+		+		+	
Torilis japonica	16.8	7.5	12.5	4.6	14.3	4.8	7.8	2.1
SPECIES MIXTURE B								
Campanula latifolia	0		0		0		0	
Conopodium majus	0		0		+		+	
Galium odoratum	0		0		+		+	
Hypericum hirsutum	1.0	0.4	2.1	1.1	2.2	0.9	3.7	2.2
Primula elatior	+		+		1.7	0.5	1.7	0.8
Silene dioica	24.7	12.9	11.5	3.6	144.3	51.4	39.0	7.3
Sison amomum	0		0		+		+	
Stachys sylvatica	0.4	0.3	0.5	0.5	+		+	
Viola odorata	0		0		+		+	

+ : Present at very low density

Table 2. *Mean density m^{-2} and mean % cover in 1990 of sown species at Site 4.*

	Low sowing density				High sowing density			
SPECIES MIXTURE A	**Density**	**SE**	**%Cover**	**SE**	**Density**	**SE**	**%Cover**	**SE**
Alliaria petiolata	6.2	2.9	1.8	0.8	16.0	4.9	10.2	4.5
Campanula trachelium	+		+		+		+	
Digitalis purpurea	+		+		+		+	
Galium mollugo	0.6	0.3	2.6	1.4	1.5	0.4	8.5	2.7
Geum urbanum	5.0	1.2	6.7	2.1	8.5	2.0	17.3	4.0
Hyacinthoides non-scripta	8.5	1.8	1.0	0.1	37.4	6.2	2.4	0.4
Stachys officinalis	+		+		+		+	
Teucrium scorodonia	+		+		+		+	
Torilis japonica	9.8	2.0	10.8	2.8	15.2	3.7	13.5	4.8
SPECIES MIXTURE B								
Campanula latifolia	0		0		0		0	
Conopodium majus	0.4	0.2	+		0.6	0.3	0.3	0.1
Galium odoratum	+		+		+		+	
Hypericum hirsutum	+		+		+		+	
Primula elatior	+		+		+		+	
Silene dioica	80.0	21.1	34.7	7.5	264.7	72.3	45.1	8.8
Sison amomum	+		+		+		+	
Stachys sylvatica	0.2	0.2	0.6	0.5	+		+	
Viola odorata	0		0		+		+	

+ : Present at very low density

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Table 3. *Mean density m^{-2} and mean % cover in 1990 of sown species at Site 5.*

	Low sowing density				High sowing density			
SPECIES MIXTURE A	**Density**	**SE**	**%Cover**	**SE**	**Density**	**SE**	**%Cover**	**SE**
Alliaria petiolata	+		+		2.3	0.9	+	
Campanula trachelium	0		0		0		0	
Digitalis purpurea	0		0		+		+	
Galium mollugo	1.1	0.3	1.1	0.3	+		2.7	1.4
Geum urbanum	+		+		24.6	11.2	11.2	3.2
Hyacinthoides non-scripta	0.5	0.5	+		32.6	8.1	2.8	0.7
Stachys officinalis	+		+		+		+	
Teucrium scorodonia	+		+		0		0	
Torilis japonica	+		+		7.1	2.8	3.5	1.5
SPECIES MIXTURE B								
Campanula latifolia	0		0		0		0	
Conopodium majus	0.5	0.2	0.3	0.1	1.5	0.6	0.5	0.1
Galium odoratum	+		+		+		+	
Hypericum hirsutum	+		+		0.7	0.4	1.8	1.3
Primula elatior	+		+		0.5	0.2	0.1	0.1
Silene dioica	+		+		1.6	1.1	0.5	0.2
Sison amomum	0		0		0		0	
Stachys sylvatica	+		+		+		+	
Viola odorata	+		+		+		+	

+ : Present at very low density

Table 4. *Mean density m^{-2} and mean % cover in 1990 of sown species at Site 6.*

	Low sowing density				High sowing density			
SPECIES MIXTURE A	**Density**	**SE**	**%Cover**	**SE**	**Density**	**SE**	**%Cover**	**SE**
Alliaria petiolata	9.2	7.5	3.8	3.0	43.0	25.1	9.5	4.1
Campanula trachelium	0		0		0		0	0
Digitalis purpurea	+		+		+		+	
Galium mollugo	+		+		+		+	
Geum urbanum	1.3	0.8	1.2	0.5	4.8	2.4	5.3	3.1
Hyacinthoides non-scripta	4.2	3.2	0.4	0.2	31.1	11.2	1.7	0.6
Stachys officinalis	0		0		0		0	
Teucrium scorodonia	0		0		0		0	
Torilis japonica	1.3	0.6	0.8	0.3	4.1	1.2	2.0	0.5
SPECIES MIXTURE B								
Campanula latifolia	0		0		0		0	
Conopodium majus	+		+		2.3	0.8	1.0	0.4
Galium odoratum	0		0		+		+	
Hypericum hirsutum	0.2	0.1	0.5	0.5	1.4	0.7	3.1	1.4
Primula elatior	0		0		+		+	
Silene dioica	+		+		0.5	0.4	0.8	0.5
Sison amomum	0		0		+		+	
Stachys sylvatica	0		0		+		+	
Viola odorata	+		+		+		+	

+ : Present at very low density

Both seed mixtures have been very successful and the figures demonstrate a large increase in both germination and colonisation subsequent to 1988. Unsown and sown areas of Site 2 are shown in Plates 8 and 9.

A study of the density and cover figures for individual species (Table 1), enables a more detailed interpretation of the results. In Seed Mixture A, *G. urbanum* is clearly the most successful species, followed by *T. japonica*, and *G. mollugo*. Another encouraging result is that of *H. non-scripta*, which has a good density value at high rates of sowing. Its corresponding cover value is low, since many of the plants are still small. For Mixture B, the total density of sown species is dominated by the result for *S. dioica*. The results indicate that *S. dioica* is extremely successful and is outstanding in its ability to germinate and colonise suitable new areas.

Site 4.

At this site, which is generally more shaded than the others, 17 species, out of the 18 that were originally sown, were recorded, (see Table 2). This is the best overall count for any site, and is possibly an indication of the semi-shade site conditions and shade-tolerant nature of the sown species.

In the shady conditions under a fairly dense canopy, *S. dioica* is able to reach an average of 264.7 plants m^{-2}, which is the highest recorded density for any species at any site. Another species favoured by the site conditions is *H. non-scripta*. Expressing the recorded density as a percentage of the sown density, the figures for *H. non-scripta* are 43.6% at low sowing density and 19.2% at high sowing density. This gives an indication of the success and survival of the species when it is introduced as seeds into a new woodland. The average density for *G. urbanum* at this site is rather low, but with a good associated cover value. This indicates the presence of fewer, larger and, therefore, older plants in shady conditions and suggests a light requirement for *G. urbanum* seedlings to grow and survive. The pie charts in Fig. 2 represent the recorded densities of species sown at high densities as proportions of the total recorded density.



Plate.8 *Unsown, grassy area of Milton Keynes plantation, Site 2, 1990.*



Plate.9 *Grassy area of Milton Keynes plantation, Site 2, with introduced field layer species, 1990.*

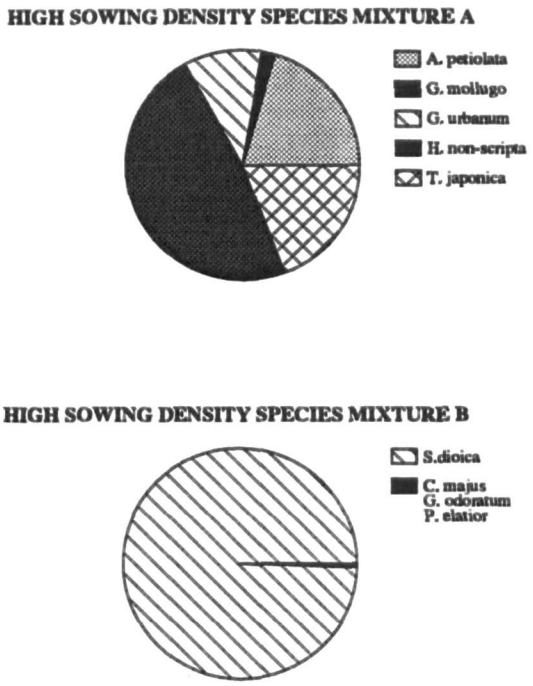


Fig.2 *Recorded proportional densities of sown species at Site 4, 1990.*

Site 5.

This site is extremely variable in nature and offers some peculiar conditions for colonising field layer species. The site slopes down from a grid road to undeveloped meadows in the north, and is characterised by drifts of tree species that are mostly non-native (see Section 2.2.1). It is often waterlogged in some areas and is covered by a layer of deep wood chippings in others. It has possibly the least potential of the four sites to become a *woodland* with a field layer.

Generally, the sowing results for this site are poor, especially for Seed Mixture B, (see Table 3). The most noteworthy success is that of *G. urbanum* and *H. non-scripta*, both at high densities. In the variable conditions, the *G. urbanum* result of 25 plants m^{-2} and 11% cover indicates that there has been enough light for seedling growth, whilst the *H. non-scripta* density figure of 32.6 plants m^{-2} is achieved in much shadier areas.

Site 6.

This is a very disturbed site due both to its proximity to houses and to the siting of a water main beneath the site. The closeness to houses, and hence to the inhabitants,

means that the site is heavily used. Some areas are traversed by regularly used paths, whilst others have become completely unsuitable for monitoring, resembling playgrounds and refuse tips more than developing woodland. Maintenance work on the water main has resulted in some of the planted shrubs and trees being uprooted and this has greatly disturbed the ground. With this disturbance and the areas of very dense shade cast by blackthorn bushes, many unfavourable conditions for field layer establishment exist at this site.

As a result, those species which have been typically successful at other sites were not so here. *G. urbanum* and *T. japonica* both had poor results, whilst *S. dioica* only achieved a score for presence (see Table 4). However, *A. petiolata* was more successful here than at any other site, with a very good result at high density. *H. non-scripta* was also successful, with a similar density to that in Site 5.

For each of the sown species at each site comparisons were made between the densities resulting from low and high sowing densities. Only three species throughout the four sites were recorded at significantly different densities, and these are shown in Table 5.

Table 5. *Significant differences between species mean densities in 1990, resulting from high and low sowing densities.*

SPECIES MIXTURE	SITE 2	SITE 4	SITE 5	SITE 6
MIXTURE A				
Alliaria petiolata	*	NS	NS	NS
Hyacinthoides non-scripta	*	*	*	*
MIXTURE B				
Silene dioica	*	*	NS	NS
Significance conventions: NS: $P > 0.05$; * : $0.01 < P < 0.05$.				

Control plots.

Four of the sown species, *A. petiolata*, *G. urbanum*, *S. dioica* and *T. japonica* were monitored within the control plots. These species were present only at low densities.

The 1991 monitoring.

Mean densities m^{-2} and mean percentage cover values for each of the sown species at each site are presented in Tables 6, 7 and 8. In 1991, the same number of sown species was found at each site, with only *C. latifolia* still not being found at any site. Only the recorded densities of *H. non-scripta* at Sites 2 and 5, and that of *G. urbanum* at Site 5, were significantly different between high and low sowing densities.

Generally, there is an overall increase in plant densities and cover values for all species at all sites between 1990 and 1991. For Sites 2, 5 and 6, the average plant density had increased to 143.35 plants m^{-2} for Mixture A, but decreased to 38.3 plants m^{-2} for Mixture B. This directly compares with 79.55 plants m^{-2} for Mixture A, and 52.63 plants m^{-2} for Mixture B in 1990 (since Site 4 was omitted from the 1991 calculations). However, with variation being high, the majority of these increases are not sufficiently large to make mean plant densities significantly different from those recorded in 1990.

Between 1990 and 1991, the average density of Mixture A species rose at all sites, due mainly to increases in the density of *A. petiolata*, *G. mollugo*, *G. urbanum* and *T. japonica*. This was due to the production of seedlings as the plants became more fully established in the young plantations. At Site 2, the main component of the total plant increase at high sowing density was *T. japonica*, the density of which rose from 11.7 plants m^{-2} in 1990, to 119.0 plants m^{-2} in 1991, mainly due to high numbers of seedlings. These mean densities, and those for *T. japonica* at low sowing density at the same site, are significantly different at the 5% level. At Sites 5 and 6, mean densities of some species, such as *A. petiolata*, *G. urbanum* and *T. japonica*, rose substantially in 1991. These increases are explained in the most part by large observed increases in seedling numbers. However, none of the rises in species mean densities at these sites were found to be significantly different.

The main exception to the observed increases in density was *S. dioica*, which actually decreased in density from 1990 to 1991. At Site 2, the total mean density of Mixture B species at high sowing density has decreased from 148.65 plants m^{-2} in 1990 to 84.5 plants m^{-2} in 1991, although the mean percentage cover value remains almost unchanged. This is due to a drop in seedling production by *S. dioica*, from 133.8 seedlings m^{-2} in

Table 6. *Mean density m^{-2} and mean % cover in 1991 of sown species at Site 2.*

	Low sowing density				High sowing density			
SPECIES MIXTURE A	**Density**	**SE**	**%Cover**	**SE**	**Density**	**SE**	**%Cover**	**SE**
Alliaria petiolata	11.3	10.8	2.3	2.1	45.8	24.5	4.8	2.6
Campanula trachelium	0		0		0		0	
Digitalis purpurea	0		0		+		+	
Galium mollugo	21.4	11.5	16.8	6.9	6.9	4.5	17.9	7.5
Geum urbanum	51.5	12.0	25.0	7.6	69.3	18.6	31.2	6.6
Hyacinthoides non-scripta	1.4	0.9	0.4	0.3	18.9	6.6	2.6	0.6
Stachys officinalis	+		+		+		+	
Teucrium scorodonia	0		0		+		+	
Torilis japonica	168.7	69.9	9.9	3.4	119.0	47.5	11.1	4.1
SPECIES MIXTURE B								
Campanula latifolia	0		0		0		0	
Conopodium majus	+		+		1.4	0.7	0.8	0.3
Galium odoratum	0		0		0		0	
Hypericum hirsutum	4.0	3.6	2.8	1.4	0.8	0.5	1.6	1.0
Primula elatior	+		+		4.0	1.8	1.7	0.7
Silene dioica	57.0	23.1	16.8	5.9	76.1	24.6	31.1	9.7
Sison amomum	0		0		0		0	
Stachys sylvatica	+		+		+		0	
Viola odorata	+		+		1.3	0.9	0.4	0.3

+ : Present at very low density

Table 7. *Mean density m^{-2} and mean % cover in 1991 of sown species at Site 5.*

	Low sowing density				High sowing density			
SPECIES MIXTURE A	**Density**	**SE**	**%Cover**	**SE**	**Density**	**SE**	**%Cover**	**SE**
Alliaria petiolata	0		0		6.5	2.9	1.1	0.4
Campanula trachelium	0		0		0		0	
Digitalis purpurea	0		0		+		+	
Galium mollugo	+		+		3.0	1.8	2.5	0.9
Geum urbanum	0.7	0.4	0.4		91.9	29.1	14.0	5.1
Hyacinthoides non-scripta	+		+	0.2	36.5	12.1	2.8	0.6
Stachys officinalis	0		0		+		+	
Teucrium scorodonia	0		0		0		0	
Torilis japonica	5.2	2.2	1.9	0.7	18.0	8.0	7.8	3.0
SPECIES MIXTURE B								
Campanula latifolia	0		0		0		0	
Conopodium majus	+		+		2.3	1.3	1.4	1.0
Galium odoratum	0		0		0		0	
Hypericum hirsutum	+		+		1.3	1.0	1.3	1.0
Primula elatior	0		0		+		+	
Silene dioica	+		+		1.1	1.0	0.2	0.1
Sison amomum	0		0		0		0	
Stachys sylvatica	0		0		0		0	
Viola odorata	0		0		+		+	

+ : Present at very low density

Table 8. *Mean density m^{-2} and mean % cover in 1991 of sown species at Site 6.*

	Low sowing density				High sowing density			
SPECIES MIXTURE A	**Density**	**SE**	**%Cover**	**SE**	**Density**	**SE**	**%Cover**	**SE**
Alliaria petiolata	19.6	10.4	7.6	4.0	26.1	9.5	13.7	5.9
Campanula trachelium	0		0		0		0	0
Digitalis purpurea	0		0		+		+	
Galium mollugo	+		+		+		+	
Geum urbanum	8.3	5.4	2.6	2.0	5.8	2.0	1.6	0.6
Hyacinthoides non-scripta	10.9	7.4	1.2	0.5	22.3	7.4	2.3	0.6
Stachys officinalis	0		0		0		0	
Teucrium scorodonia	0		0		0		0	
Torilis japonica	5.5	2.9	1.6	0.8	6.0	1.8	1.7	0.6
SPECIES MIXTURE B								
Campanula latifolia	0		0		0		0	
Conopodium majus	+		+		2.3	1.3	1.4	1.0
Galium odoratum	0		0		0		0	
Hypericum hirsutum	+		+		1.3	1.0	1.3	1.0
Primula elatior	0		0		+		+	
Silene dioica	+		+		1.1	1.0	0.2	0.1
Sison amomum	0		0		0		0	
Stachys sylvatica	0		0		0		0	
Viola odorata	0		0		+		+	

+ : Present at very low density

1990, to 61.3 seedlings m^{-2} in 1991, and to the low survival of seedlings which germinated in 1990. Whilst this, and the decrease in the density of *S. dioica* resulting from low sowing density, were substantial, neither were significantly different between 1990 and 1991. At high sowing density, the average densities of *C. majus*, *H. hirsutum*, *P. elatior* and *V. odorata* at Site 2, which were present in only very low numbers in 1990, increased between 1990 and 1991. However, these increases are not statistically significant due to large variances. At Site 5, there was a substantial increase, from 4.5 plants m^{-2} in 1990 to 25.7 plants m^{-2} in 1991, in the total density of Mixture B at high sowing density, but at Site 6 there was little change and the success of Mixture B species remained low, with total density of only 4.7 plants m^{-2} at high sowing density.

By 1991, all of the 17 species recorded in the quadrats had been observed to produce flowers. Most species had flowered by 1990, but *C. trachelium*, *C. majus*, *H. non-scripta* and *T. scorodonia* did not flower until 1991.

2.4.1.2 The restricted seed mixture.

The 1990 monitoring.

Four of the restricted seed mixture species were recorded, the exception being *G. rivale*. *A. ursinum*, *P. vulgaris* and *S. holostea* all flowered and set seed in 1990. *S. holostea* was noted to have spread well.

2.4.1.3 The planted plots.

The 1988-1991 monitoring.

Tables 9 and 10 show the recorded number of plants at all sites resulting from the introduction of species as young plants in 1988. Figure 3, which shows all of the planted species at Sites 4 and 5, indicates that whilst plant density declined immediately after planting, this has substantially increased since then. The species most responsible for this increase is *S. dioica*, which at high planting density, has increased from 140 original plants to 3191 in 1991. Other species which increased well at both planting densities are *G. urbanum* and *T. japonica*.

The individual bar charts for *H. non-scripta* and *P. vulgaris* show that these species have increased well at high planting densities by 1991, but much less at low planting densities. Results are similar for *A. vulgaris* and *S. officinalis*. At both planting densities, the number of *T. scorodonia* plants initially declined and then stabilised for two years before increasing in 1991. At Sites 2 and 6, *P. elatior* showed a similar pattern of establishment. For some species, very few of the original individuals were found by 1991. Many had simply not survived the transplantation, but others, despite declining in number, had established well. For example, at high planting density, *Ajuga reptans* (Bugle) had decreased from 140 original plants to 84 by 1991, but many of the remaining individuals had spread to over $1m^2$ during that time.

Table 9. *Survival and establishment of planted species between 1988 and 1991 at Sites 2 and 6.*

	LOW PLANTING DENSITY								HIGH PLANTING DENSITY							
	PL	1988		1990		1991		1991	PL	1998		1990		1991		1991
SPECIES	SITES:	2	6	2	6	2	6	TOTAL	SITES:	2	6	2	6	2	6	TOTAL
A. reptans	20	1	4	8	4	10	6	16	140	44	56	58	30	55	29	84
A. petiolata	10	2	0	33	23	191	104	295	70	11	0	17	38	50	0	50
C. pratensis	20	0	0	0	0	0	0	0	140	4	21	0	0	20	0	20
C. lutetiana	20	4	2	4	2	3	0	3	140	42	0	42	16	18	0	18
G. mollugo	20	3	0	2	1	1	1	2	140	13	0	16	8	24	1	25
H. hirsutum	20	5	0	5	3	5	0	5	140	31	11	33	16	31	6	37
L. galeobdolon	30	0	2	0	3	0	3	3	210	3	14	19	54	18	39	57
P. elatior	30	4	5	7	3	118	9	127	210	46	54	62	70	491	209	700
S. officinalis	20	2	2	6	2	6	2	8	140	43	35	36	29	119	161	280
S. sylvatica	20	2	1	3	4	3	0	3	140	21	14	43	29	29	12	41
ALL SPECIES	210	23	16	68	45	337	125	462	1470	258	205	326	290	855	457	1312

PL : Number planted Feb. 1988

Table 10. *Survival and establishment of planted species between 1988 and 1991 at Sites 4 and 5.*

	LOW PLANTING DENSITY								HIGH PLANTING DENSITY							
	PL	1988		1990		1991		1991	PL	1988		1990		1991		1991
SPECIES	SITES:	4	5	4	5	4	5	TOTAL	SITES:	4	5	4	5	4	5	TOTAL
A. vulgaris	20	5	2	3	0	5	2	7	140	44	13	51	68	126	361	487
C. latifolia	20	5	0	0	0	0	0	0	140	33	0	0	0	0	0	0
C. trachelium	20	0	0	0	2	2	2	4	140	0	1	35	13	30	13	43
D. purpurea	20	1	1	0	0	0	0	0	140	6	3	3	3	0	1	1
G. urbanum	20	0	0	53	52	360	212	572	140	59	23	1056	417	727	1728	2455
H. non-scripta	30	3	3	9	0	13	6	19	210	0	4	69	31	231	74	305
P. vulgaris	20	1	5	14	1	48	5	53	140	56	37	358	110	550	1047	1597
S. dioica	20	6	2	249	19	470	704	1174	140	4	29	421	260	1809	1352	3161
T. scorodonia	20	2	4	5	3	29	43	72	140	43	49	55	26	83	247	330
T. japonica	20	0	0	25	26	141	72	213	140	12	0	100	32	1260	86	1346
ALL SPECIES	210	23	17	358	103	1068	1046	2136	1470	257	159	2148	960	4816	4909	9725

PL : Number planted Feb. 1988

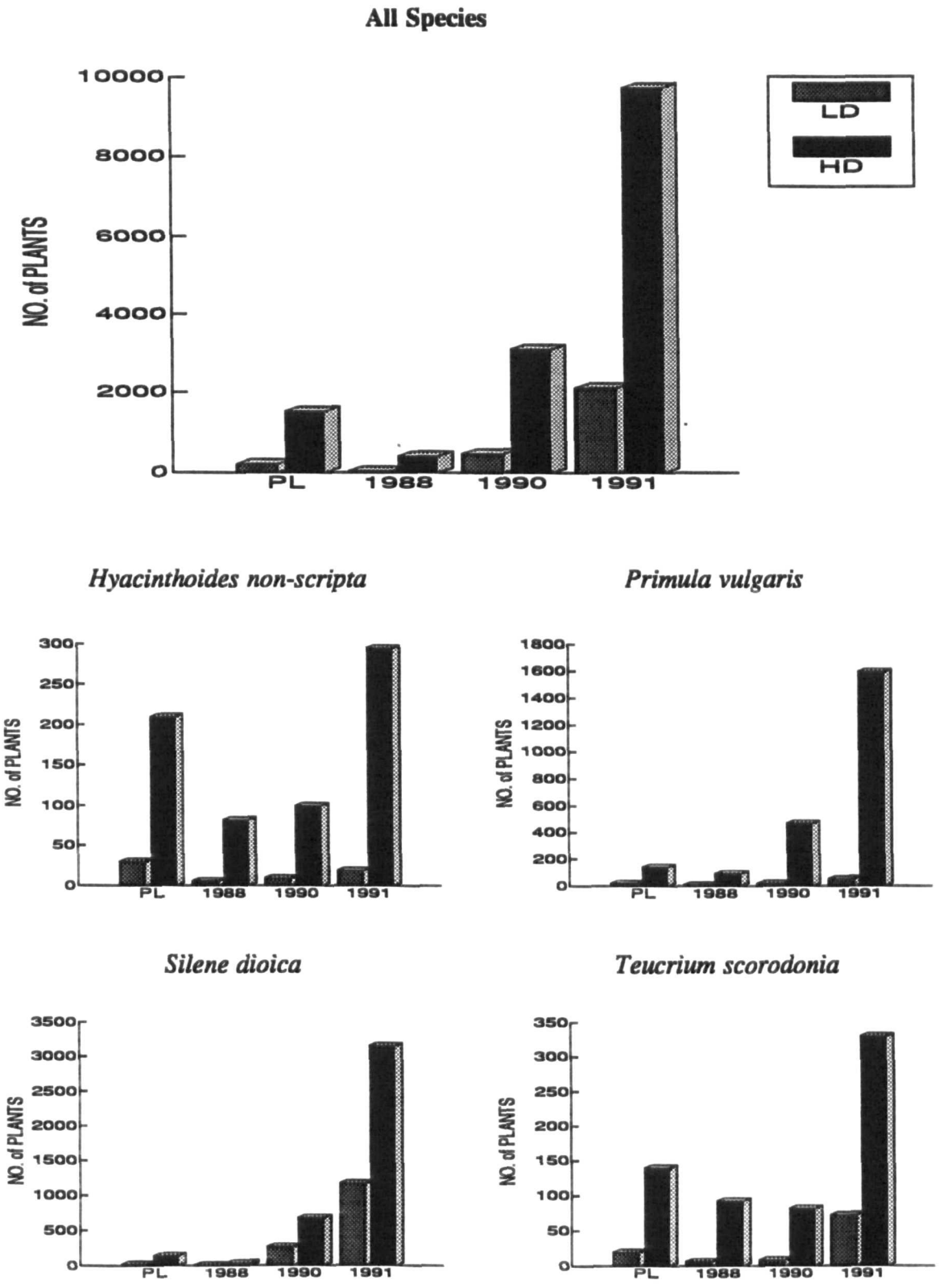


Fig. 3 Recorded density of species introduced as plants at Sites 4 and 5, Milton Keynes.

(LD: Low density planting; **HD:** High density planting; **PL:** Number planted Feb. 1988)

2.4.2 An investigation of the initial establishment and survival of woodland field layer species introduced as seed into a young plantation in 1991.

The 1991-1992 monitoring.

Table 11 shows the mean densities m^{-2} for each of the introduced species at the newly sown site. These were compared to the initial sowing rates to give values of established plants per seed sown for both years. Nine of the 17 sown species were recorded as small seedlings in the first season. The mean total percentage establishment was 0.6%, with species such as *G. mollugo*, *S. dioica* and *S. officinalis* having the highest mean densities. *V. cracca* was recorded at a density of 0.23 plants m^{-2}, which, though very low, represented a high percentage establishment of 46%, since it was sown at a rate of only 0.5 seeds m^{-2}. By the second year, two additional species, *A. ursinum* and *H. non-scripta*, were recorded. The mean percentage establishment had increased to 5.5% and the total mean density was 32.63 plants m^{-2}. *S. dioica* was the species recorded at the highest density, with 16.10 plants m^{-2}, representing an establishment rate of 23.7%. *H. non-scripta* had the highest establishment rate of 28.5%. Other species found in substantial numbers were *C. trachelium*, *G. mollugo*, *Hypericum* species, and *P. vulgaris*. By August 1992, the total percentage cover of the sown species was 15.88%. Species with high percentage cover values were *S. dioica* and *G. mollugo*.

By May 1992, the total mean density of competing species at the site was 40.4 plants m^{-2}, consisting of 2.6 saplings m^{-2}, 4.6 grasses m^{-2} and 33.2 perennial and annual forbs m^{-2}. In August, the mean percentage cover of the forbs was 16.0% and for the grasses was 6.5%.

2.4.3 Tests on the germination success of woodland field layer species, 1991 and 1992.

The 1991-1992 monitoring.

Table 12 shows the total number of seeds that germinated (out of 600) for each of the sown species, and gives the percentage of established plants per seed sown. The highest germination rate recorded was 59.8% for *C. trachelium* after chilling. Some species

Table 11. *Resulting densities in the first and second year at a newly sown site.*

	Feb 1991	August 1991			May 1992			August 1992	
	Sown	Density m^{-2}		%Estab.	Density m^{-2}		%Estab.	% Cover	
SPECIES	Density m^{-2}	Mean	SE		Mean	SE		Mean	SE
Allium ursinum	6.3	_	_	**0**	0.03	0.02	**0.5**	_	_
Aquilegia vulgaris	0.2	_	_	**0**	_	_	**0**	0.02	0.02
Campanula trachelium	43.0	0.38	0.17	**0.9**	2.15	0.50	**5.0**	0.65	0.16
Conopodium majus	0.2	_	_	**0**	_	_	**0**	_	_
Digitalis purpurea	58.0	0.03	0.02	**0.1**	0.30	0.10	**0.5**	0.15	0.07
Fragaria vesca	0.2	_	_	**0**	_	_	**0**	_	_
Galium mollugo	35.0	0.93	0.22	**2.7**	3.93	0.67	**11.2**	4.62	1.54
Geum urbanum	31.0	_	_	**0**	_	_	**0**	_	_
Hyacinthoides non-scripta	12.0	_	_	**0**	3.42	0.77	**28.5**	_	_
Hypericum spp.	281.0	0.23	0.12	**0.1**	4.55	1.16	**1.6**	0.47	0.13
Lychnis flos-cuculi	51.0	_	_	**0**	_	_	**0**	0.05	0.04
Primula vulgaris	12.0	0.05	0.03	**0.4**	1.63	0.28	**13.6**	0.37	0.10
Prunella vulgaris	0.6	0.02	0.02	**3.3**	0.02	0.02	**2.5**	0.02	0.02
Silene dioica	68.0	0.78	0.18	**1.2**	16.10	2.72	**23.7**	8.68	2.39
Stachys officinalis	9.0	1.07	0.28	**11.9**	1.37	0.31	**15.2**	0.72	0.21
Teucrium scorodonia	0.5	_	_	**0**	_	_	**0**	_	_
Vicia cracca	0.5	0.23	0.06	**46.0**	0.40	0.10	**80.3**	0.22	0.10
ALL SOWN SPECIES	**608.5**	**3.73**	**0.64**	**0.6**	**32.63**	**4.80**	**5.5**	**15.88**	**3.42**

Table 12. *The number of seedlings recorded of a range of woodland field layer species in different chilling treatments.*

SPECIES	C/N	- 1991 - March-June	October	1992 April	SD	Total % Germination
Alliaria petiolata	C	3	0	0	NS	0.5
	N	2	0	0		0.3
Campanula latifolia	C	64	0	0	*	10.7
	N	0	0	0		0
Campanula trachelium	C	359	0	0	*	59.8
	N	137	0	0		22.8
Conopodium majus	C	0	0	64	NS	10.7
	N	0	0	47		7.8
Digitalis purpurea	C	125	0	0	NS	20.8
	N	166	0	0		27.7
Galium mollugo	C	288	0	0	NS	48.0
	N	285	0	0		47.5
Galium odoratum	C	0	0	0	-	0
	N	0	0	0		0
Geum urbanum	C	5	0	0	NS	0.8
	N	0	0	0		0
Hyacinthoides non-scripta	C	0	171	0	NS	28.5
	N	0	146	0		24.3
Hypericum hirsutum	C	320	0	0	*	53.3
	N	174	0	0		29.0
Primula elatior	C	3	0	0	NS	0.5
	N	0	0	0		0
Silene dioica	C	140	0	0	NS	23.3
	N	141	0	0		23.5
Sison amomum	C	0	0	0	-	0
	N	0	0	0		0
Stachys officinalis	C	95	0	0	*	15.8
	N	16	0	0		2.7
Stachys sylvatica	C	79	0	0	*	13.2
	N	0	0	0		0
Teucrium scorodonia	C	181	0	0	NS	30.2
	N	201	0	0		33.5
Torilis japonica	C	9	0	156	NS	26.0
	N	28	0	139		23.2
Viola odorata	C	0	0	0	-	0
	N	0	0	0		0

C : Chilled N : Unchilled

SD :Significant difference between treatment means. NS, $P > 0.05$; * $P < 0.05$.

Number of seeds sown in each treatment: 600 for each species.

germinated at similar rates whether they were chilled or not, *e.g. G. mollugo* had a rate of 48.0% after chilling and 47.5% without chilling, and *S. dioica* had a rate of 23.3% after chilling and 23.5% without being chilled. Other species had significantly higher germination rates after chilling, *e.g. C. trachelium* seeds germinated at a rate of 10.7% after chilling, but not at all without being chilled. Two species, *C. majus* and *T. japonica*, germinated mostly in the second season after sowing. The seeds of *H. non-scripta* germinated in the autumn of the first year, with very similar rates for both treatments. Six species failed to germinate.

2.5 Discussion

2.5.1 The large-scale introduction of woodland herbaceous species into young plantations in 1987.

2.5.1.1 General success of the introductions.

Four years after the sowing and planting, all but one of the species introduced as seeds and all of the species introduced as plants have been recorded in the young plantations. These figures clearly demonstrate the feasibility of introducing field layer species into new woodlands, by simple hand-sowing and planting methods.

2.5.1.2 Species introduced as seed.

By 1990, plants of species that were introduced as seed were present in substantial densities throughout the young plantations. However, *S. dioica* is the only species to be recorded at a density higher than its original sowing density, and then only at Site 4. A comparison of the resulting species densities in 1990 with the original sowing densities indicates a mean survival rate of 9.5% for the species at Site 4, 5.3% at Site 2, and only 2.1% at Site 5 and 2.7% at Site 6, all at high sowing densities. Field observations in 1990 showed that many of the sown species, *e.g. G. urbanum* and *S. dioica*, had already flowered and set seed prior to the monitoring in that year, and so these survival rates include second generation seedlings as well as plants which have grown directly from

the originally introduced seeds. The survival rates calculated here can not therefore be directly compared with germination rates, which would be even lower. Germination rates and the early survival of seedlings must have been very low. Factors which influence the seeds and developing seedlings from sowing time to the detailed monitoring in 1990 are unknown, but it is likely that some seeds fell "on stony ground", some were eaten, and others died after germination when the droughts of 1989 and 1990 were at their worst. By 1991, a general increase in densities was recorded throughout the sites. This rise was not significant due to high variability. The increase was due to the increased seedling production as many of the field layer species, such as *G. urbanum* and *T. japonica*, became established and reached maturity.

The seed mixtures were sown at low and high densities in a ratio 1:10, yet by 1990 none of the resulting species densities at any of the four sites are in this ratio. At Site 4, the recorded density ratios for *H. non-scripta* and *S. dioica* are 1:4 and 1:3 respectively, and, for these two species only, the number of plants at high and low densities are significantly different (see Table 5). At Site 6, the recorded densities that result from low and high sowing densities are in the ratio 1:7 for *H. non-scripta* and 1:3 for *T. japonica*. Only the densities for *H. non-scripta* are significantly different. By 1991, only the recorded densities of *H. non-scripta* at Site 5 were significantly different in high and low sowing density plots. The recorded species densities are highly variable, as the standard errors indicate. This variation is partly responsible for the lack of significant differences between the species means at high and low densities. However, for the species that do have significantly different mean densities in 1990, the resulting ratios are much less than 1:10 and the differences are not as great as at sowing time. The gap between the sowing ratios has closed during the time from sowing to monitoring in 1990. Without germination and initial seedling survival data, it is not possible to give precise explanations for this change. Considering the original total sowing densities, at high sowing density, were 2300 seeds m^{-2} for Species Mixture A, and 1700 seeds m^{-2} for Species Mixture B, it is possible that density dependent effects occurred amongst young field layer seedlings sown at high density, causing increased competition for resources and hence lower percentage survival rates. Further, of those individuals that did germinate, whether sown at high or low density, the subsequent seedling production rates for species such as *G. urbanum* and *S. dioica* were probably

very similar. Thus, the ratio between high and low densities may have been reduced.

The mean established densities and their corresponding standard errors that have been presented indicate that the rate of establishment varies between the herbaceous species that were introduced. Some of the sown species were quick to establish and soon flowered and set seed, *e.g. A. petiolata, G. urbanum, S. dioica* and *T. japonica.* Many of these species even colonised into the control plots, where no sowing occurred. Others, such as *C. majus, G. odoratum, H. non-scripta* and *V. odorata,* have been much slower in their development from seed and are still very much in their establishment phase. Indeed, *C. majus* and *H. non-scripta* were amongst those species that only flowered for the first time in 1991. Variation of success within individual species is also apparent, both at the same and at different sites. The young plantations themselves are extremely variable, as described in Sections 2.2.1 and 2.4.1.1, and this must affect species establishment. The variation in performance is also probably related to environmental factors, such as light, soil type, canopy species and amount and type of existing vegetation. Such influences are investigated in Chapter 3. Additionally, the very urban nature of these sites may explain some of the variability, since factors such as trampling, vandalism, dumping of refuse and chippings, and routing maintenance work to drains and pipelines all cause disturbance and thereby affect species' performance.

2.5.1.3 Species introduced as plants.

The species that were introduced as young plants into the new woodlands, have generally shown a large increase in plant densities over the 4 years, but success is variable, as with the sown species. Similar categories of establishment are clear, with some of the species soon flowering and producing second and third generations from discrete individuals, *e.g. G. urbanum, S. dioica* and *T. japonica.* Other planted species exhibit less flower production and seed set, but have spread well and have established vegetatively. These include *A. reptans, C. lutetiana* (Enchanter's-nightshade), and *L. galeobdolon.* These results confirm observations made by Salisbury (1976) who writes that *C. lutetiana* and *L. galeobdolon* are characterised by rapid vegetative spread which compensates for their low rates of flowering and seed set. He notes that, with *A. reptans,* such vegetative modes of propagation may provide the means to ensure species survival and increase even in low light intensities.

Planting densities were in the ratio 1:7, and some species are still present in similar ratios, *e.g. H. hirsutum* and *P. elatior.* Others, *e.g. H. non-scripta* and *P. vulgaris* have been recorded at much higher ratios of 1:15 and 1:30 respectively. This is a particularly interesting result for *P. vulgaris*, a species that is rather slow to mature from seed. Where it has been introduced as plants, the results at high planting density show that it has already been very successful in the production of large numbers of seedlings. It is considered that the introduction of this species as young plants clearly enhances its establishment ability.

2.5.1.4 Establishment strategies.

Whether field layer species were introduced as seeds or plants, two distinct groups are recognisable:

1) those that are characterised by quickly establishing and reaching maturity,
and 2) those that are still in the establishment phase and have yet to mature.

When grouped together, this variation in establishment success between the species can be described in terms of different growth strategies. Peterken (1974) suggested the classification of woodland plants into three categories, namely canopy species, shade-tolerant field layer species, and woodland edge species. In this field trial, the group that are quick to mature are all light-demanding woodland edge, or marginal, species, whereas those with much slower establishment are the shade-tolerant, true woodland species. The woodland edge species, *e.g. G. urbanum*, *S. dioica* and *T. japonica*, can all be introduced as seed and require only moderate sowing densities. The shade-tolerant species are much slower to establish and reach maturity. Some, such as *G. odoratum*, *H. non-scripta* and *V. odorata*, can be introduced as seed from which they will slowly, but successfully, develop. Others, *e.g. A. reptans* and *L. galeobdolon*, are more successfully introduced as planted units from which they vegetatively establish and spread. These groups of species that can be introduced as either seeds or plants, can also be termed 'low and high risk' species respectively (Buckley 1987), denoting the ease with which introductions are made.

Whilst two growth strategies are apparent for woodland herbaceous species in general, for the purposes of field layer introduction three groups of species can be identified.

These are:

1) The woodland edge species that can be introduced as seed and that are quick to mature and establish, *e.g. G. urbanum* and *S. dioica.*

2) The shade-tolerant species that can be introduced as seed from which they slowly establish, *e.g. G. odoratum* and *H. non-scripta.*

3) The shade-tolerant species that are most successfully introduced as plants from which they establish by predominantly vegetative growth, *e.g. C. lutetiana* and *L. galeobdolon.*

2.5.2 Investigation of germination rates and seedling survival.

2.5.2.1 Monitoring of the newly sown site.

This was a very useful piece of work that followed as closely as possible the establishment and initial seedling survival of woodland field layer species introduced into a young urban plantation. The purpose was to gather information that was missing from the large-scale field trial. Despite the site having conditions that appeared to be highly suitable for the introduction of field layer species, mean establishment rates were found to be low, in both the first and second seasons. The seemingly poor mean establishment rates encompassed some species which were quite successful, *e.g. S. dioica* and *H. non-scripta*, and others that failed completely, such as *G. urbanum*. The percentage cover values recorded in the second growing season show that some species, such as *S. dioica* and *G. mollugo*, are quick to establish from seed. Field observations of flower production by the second season also indicate that some species mature very rapidly and soon have the ability to produce second generations of plants. Many individuals plants of *S. dioica* and *G. mollugo* flowered in the second year and set seed. *C. trachelium* and *P. vulgaris* were also observed to flower in the second season, but this was only for a very few individuals in areas of the site with very few competitive weed species.

The results give an indication of the generally low establishment rates for these woodland field layer species and of the high wastage of seed. The records made of other plant species at the site indicate that annual and perennial weeds, grasses and saplings soon colonise into areas of bare ground. By 1992, the total mean density of competing species was recorded as 40.4 plants m^{-2}, with a corresponding mean percentage cover value of

24.3%. Some will have been present in the seed bank at the site, whilst others will have been brought in by wind or animals. Many of these plant species are opportunists, present in the early stages of succession, and whilst they may not persist once the ecosystem stabilises, they are strong competitors making establishment of the woodland field layer seedlings difficult.

2.5.2.2 Interpretation of the germination tests.

All of the field layer species that were sown in the large-scale field trial, were used in the germination tests, to give an indication of the germination rates that can be expected in optimum conditions, particularly without any competition. The need for a species to be chilled prior to successful germination was also tested.

Whilst it is clear from the results that some species do require chilling to break seed dormancy, few of the recorded levels of germination are high, with only two species, *C. trachelium* and *H. hirsutum*, achieving values above 50%. Many of the germination percentages recorded for species that did not altogether fail, fall in a band between 10% to 50%, with much seed simply not germinating even in the second season after sowing. That the recorded percentage germination levels seem to be rather low in these tests is interesting, but not easy to interpret, but both Grime *et al.* (1981) and Buckley & Knight (1989) mention that many perennial woodland species do have low germination success. For many of the individual species there is very little information available on germination levels, though the tests of Grime *et al.* (1981) do include some of the species tested here. For some species, such as *H. hirsutum* and *D. purpurea*, Grime *et al.* (1981) report substantially higher levels of germination than were found here, whereas for other species, such as *C. latifolia*, results were similarly low.

Considering *D. purpurea*, germination levels between 21% and 27% were recorded here, which were not significantly affected by the two treatments. In contrast, this species germinated readily throughout Grime's investigations, with rates of above 90% in the majority of tests, only decreasing to 56% germination in the dark. These results and numerous field observations by Grime and other authors, indicate that *D. purpurea* is a 'light-promoted' seed (Wareing 1966), which is not affected by stratification. It is possible that high light levels are necessary for this species to germinate and that the

layer of sand covering the seeds therefore lowered the percentage germination in these tests. Due to the very low germination levels recorded, it is also considered likely that the seed was old and hence had reduced viability.

Some species, including both *Campanula* species and *S. sylvatica*, had significantly different levels of germination in the two treatments, and these species clearly have a requirement for chilling prior to germination. Slade & Causton (1979) found *S. sylvatica* gave the best germination with stratification alone, and Grime *et al.* (1981) also demonstrated the need for chilling in this species and *C. latifolia*. Other species, *e.g. C. majus*, may need longer periods of cold and so germinate most successfully after a whole winter season, rather than just a short chilling period. Grime *et al.* (1981) reported 90% germination in this species during a 9 month period at 5°C.

H. non-scripta was the only species which germinated in the autumn of the first season. This result can be explained by the work of Thompson & Cox (1978) who have studied the germination of this species in detail, and have demonstrated its requirement for a high temperature conditioning phase, followed by a low temperature germination phase. Bluebell seed falls from the plants in summer, is then exposed to high or moderate soil temperatures until early autumn, when it germinates as soil temperatures fall to about 11%. The initial chilling treatment in the germination tests was therefore insufficient to break the dormancy of *H. non-scripta* which germinated in the autumn, once it had been conditioned by high summer temperatures which are necessary for its successful germination.

A third of the field layer species tested completely failed to germinate in the seed trays. These species probably fall into two categories: those that have poor germination rates, and those that usually have reasonable or good germination rates, but whose seed in this instance was not viable. Shade tolerant species, such as *G. odoratum* and *V. odorata*, are examples of many common species that produce small quantities of seeds, which naturally exhibit low germination success (Buckley & Knight 1989). In natural woodland conditions, these species rely almost entirely upon vegetative growth for reproduction. Species such as *A. petiolata* and *G. urbanum* may have failed for quite different reasons. In woodlands and even young plantations, large numbers of seedlings are observed for

both of these species and so germination of seeds is naturally very good. The seed used for the germination tests is therefore presumed not to have been viable when sown. Both of these species were included in the extensive germination tests implemented by Grime *et al.* (1981). Throughout their tests, *A. petiolata* showed no germination whether fresh or stored, at high and low temperatures. The results obtained for *G. urbanum* were generally good, although germination was significantly decreased, from 82% in light or shade conditions, to a mere 4% in a dark treatment. Some 79% of fresh seed germinated, and though this figure fell to 66% after a 12 month storage period, this decrease was not significant. Earlier work by Slade & Causton (1979) demonstrated that light had a promotive effect on the germination of *G. urbanum* and that this produced a positive interaction with stratification. They also found that the highest germination rate for *G. urbanum* seeds of 87% was obtained after a pre-treatment with 0.1M Potassium nitrate alone. It is difficult to explain the lack of germination of *A. petiolata* seeds in both these tests and those carried out by Grime *et al.* (1981), when field observations made during the current research, and by Grime *et al.* (1984) indicate that germination rates are usually high. However, it is possible that seed of both species may have been stored for a long period of time (*i.e.* much more than 12 months), and was actually old seed. It is unlikely that the covering of sand on the seed trays in these tests was sufficient to cut out enough light to inhibit germination.

P. elatior and *S. amomum* also failed to germinate in these tests. Whilst some seedlings of both species have been observed in the field, no information is available to explain their failure to germinate in seed trays. It is considered possible that the seed supplied was very old and hence not viable. These species are not recognised as forming part of seed banks, and hence are not particularly known for their longevity. *P. elatior* is quite rare and *S. amomum* is unlikely to be in high demand from the suppliers, perhaps increasing the likelihood of a long storage period prior to supply.

2.5.2.3 Germination and initial seedling survival of woodland field layer species.

The results from the germination tests and the monitoring of the newly sown site in 1991 and 1992 provide very useful information about the germination and establishment of woodland field layer species. The results of the germination tests explain some of the results from the monitoring of the newly sown site. For example, the failure of *G.*

urbanum to germinate in the seed trays and its presumed non-viability immediately clarifies its lack of germination in the newly sown site, since the source of seed was the same in both cases. The observation that seeds of *H. non-scripta* germinated in the autumn in the seed trays explains why seedlings were not recorded in the newly sown site until the second season. For many species the germination levels in both the seed trays and in a site offering quite good conditions were often lower than the rates reported by other researchers from laboratory tests. It is difficult to extrapolate the information from physiological studies to field conditions (Wareing 1966), where the interactions between seed and environment are highly complex and germination depends upon many conditions being favourable at one time. In his study on the germination of *S. dioica*, Thompson (1975) notes that experiments with this species seldom result in complete germination and a residue of ungerminated seeds is normal, amounting sometimes to 20% of those sown. These residual dormant individuals are mostly viable, and naturally become available as part of the seed reservoir, which makes up a large proportion of the population of many wild species. In the present tests, some 70% of *S. dioica* seeds failed to germinate. Seeds may, again, have been stored for very long periods, thus reducing their germination potential. It is also possible that in field conditions higher numbers of seed are residually dormant. If the environmental conditions experienced by the seed at sowing time are not optimal, these dormant individuals can persist in the soil and germinate once conditions improve. Other species in these tests may have exhibited low germination for similar reasons.

The data and observations from both experiments can, in turn, elucidate some of the figures recorded in the large scale field trial. For example, it was suggested that insufficient light was available for the germination of *D. purpurea* in the seed tray tests. At the newly sown site, a mere 0.5% germination was recorded for this species by the second year. Cohn & Packham (1991) have recorded significantly reduced germination rates when sowing *D. purpurea* into plots treated with leaf litter. It is considered possible that since *D. purpurea* seeds are very small, weighing only 0.07mg each, they can easily become buried beneath leaf litter within the young plantations. In this way, light is greatly reduced, and hence they are unable to germinate. The results for *D. purpurea* were similarly low in the main field trial. Here the sites are extremely heterogeneous and whilst much seed may have fallen beneath dense canopies and into

patches of thick leaf litter, some should also have fallen in light areas where no tree canopy is present. Seeds should have germinated in such areas, but may have been very quickly eliminated by competition from other vegetation that rapidly colonises in light conditions. Whilst *D. purpurea* appears to have failed in these trials, it is known to be a long-lived seed bank component, and it is possible that many seeds have been incorporated into the seed bank. If so, these may germinate in the future when disturbance occurs and environmental conditions are more favourable. Other species, such as *C. trachelium*, had good germination rates in seed trays, but poor rates in the young plantation sites. These too may therefore be able to germinate readily in the field, but fail to establish due to high levels of competition.

2.5.3 Conclusions.

The majority of the field layer species that were introduced into young plantations at Milton Keynes were present four years after their introduction, whether they were sown or planted into the new sites. The monitoring of the large-scale field trial has demonstrated the success of simple and practical introduction techniques for field layer enhancement. A detailed study of species growth has identified three groups of herbaceous species for the purposes of introduction. The woodland edge species can be introduced as seed, from which they quickly mature and establish, whereas most of the shade-tolerant species are best introduced as plants. A third group, consisting of shade-tolerant species which can be introduced as seed from which they slowly establish, has also been distinguished.

The monitoring of a newly sown site has given an indication of establishment rates in the field for a wide range of species. This has shown that overall establishment is low and seed wastage is very high. Such information is useful for the development of adequate sowing rates. From experience in the larger trials, it is considered that the small nucleus of seeds that do germinate is sufficient for establishment and persistence. The germination tests also gave an estimate of the germination rates for a range of field layer species. Some species were found to require chilling prior to germination, whilst others were unviable, or simply had very low germination rates.

Whilst the results do indicate the feasibility of making introductions of woodland field layer species into young plantations by seed, the success is clearly variable and also rather unpredictable. The extreme heterogeneity within the sites is probably primarily responsible for this.

3. An analysis of the performance and distribution of woodland field layer species, during their establishment within young plantations.

3.1 Introduction.

That plant growth is controlled by light is fundamental due to its role in the photosynthetic mechanism. In plant metabolism, it has both direct and indirect effects (Fitter & Hay 1983). Light affects metabolism directly through photosynthesis, and plant growth and development indirectly both as a consequence of the immediate metabolic responses and, more subtly, by its control of morphogenesis. Particularly in woodland situations under tree canopies, light is important as not only are its levels very low for much of the year, but its intensity, quality and periodicity are all modified to produce a very distinct environment for plant growth. Some plant species have adapted to deal with these situations, and photosynthetic and morphological adaptations have occurred. Particular adaptations to low light levels exhibited by woodland field layer species are described in Section 4.1.1.

However, such species do not necessarily require shade, but make use of shady conditions to avoid competition. Indeed, most plants can grow in most conditions if they are free from competition. An important point to consider is not whether a plant can grow in a certain set of conditions, but whether it can hold its own in competition with the other members of the local flora, both as a seedling and as an established plant. Crawley (1986) stresses that for the majority of plant species the 'ecological optimum' is not equivalent to the 'physiological optimum'. In this way, plant abundance under a given set of field conditions is determined both by its relative competitive ability with other plants, and by its relative susceptibility to plant herbivores and pathogens. Often, therefore, plant distributions in the field are refuges from competitors and enemies, rather than places which present the plant with ideal environmental conditions. It is for these reasons that many woodland species have adapted to tolerate the extreme conditions beneath tree canopies, where no other species can survive, *i.e.* they have found a refuge. Similarly, seasonal effects whereby the inferior competitor grows much

earlier in the season than the superior competitors also gives a refuge (Al-Mufti *et al.* 1977). So, many woodland field layer species grow best at much higher light levels than they actually experience. For example, *H. non-scripta* grows well in full light away from competition, but survives under a leaf canopy because of a shade adaptation in its photosynthesis (Blackman & Rutter 1946). The longevity of many woodland herbaceous perennials enables them to grow vegetatively beneath a shady canopy for many years, only to flower and set seed when light increases sufficiently. Most other species of plants do not have the ability to persist in such conditions.

Light itself governs competition levels. Those plants not adapted to shade, can only grow well and flourish in high or moderate light conditions. As a result of this, canopy gaps and areas with no trees within young plantations, will allow much growth of ruderal weed species, grasses and so forth. Similarly, in bare, uncolonised areas of ground where light is at an optimum for plant growth, the primary colonisers in secondary succession are ruderals, fast-colonising annuals and biennials which thrive on disturbance (Cohn & Packham 1991), and can out-perform other species in high light. It is not until the succession has developed considerably, through the arrival of competitive perennials, establishment of woody species, and their replacement by shade tolerant trees, that conditions are suitably modified on the woodland floor to reduce the vigour of the herb competitors and thus allow species which are much weaker competitors to colonise successfully. Indeed, it is only when shade begins to increase that the woodland species, being tolerant of shade and very poor competitors, can exploit a particular niche and hence flourish by avoiding competition. In natural circumstances, therefore, the development of a woodland ecosystem with its complex components is very slow, taking many hundreds of years. The field layer species particularly are the last to colonise due to their specific requirements and need for a refuge. As Cohn & Packham (1991) suggest, the late successional stage of a woodland, when competition is beginning to diminish, would seem to be an ideal time to introduce woodland herbaceous species into secondary woodlands, but for "cultural, aesthetic and conservation reasons", practitioners often wish to enhance new habitats much earlier and cannot wait for the long successional development to occur.

Harper (1987) considers three aspects of succession which habitat creation schemes

could aim to bypass:

1) The different rates at which dispersal units of the later successional species arrive in the habitat,

2) The exclusion of earlier colonists by later ones,

3) Changes to the habitat by earlier species which favour later ones.

In woodland creation schemes, the introduction of field layer species into young plantations for enhancement purposes has therefore been attempted at a much earlier stage in the succession than that when they would normally be able to colonise. For example, in the large-scale field trial in Milton Keynes, which is described in Chapter 2, woodland field layer species were introduced into young plantations almost as soon as trees were established. If these plantations offered uniform shade conditions and remained 'weed-free', then they would be ideal refuges for the establishment of the field layer species. However, whilst some areas of the sites do offer suitable conditions for establishment, most do not. The plantations are extremely heterogeneous, because of patchy tree death, differential thinning, and uneven establishment rates. The tree canopy is therefore discontinuous and gaps are present, as well as quite substantially sized 'glades', where no trees have grown. Hence, light conditions are very variable. As has been explained, were no other plant species present, this itself would not be a problem to the establishing field layer species which would thrive. Even if, as is commonly practised, species are introduced into a bare-earth situation, other colonists very soon invade the site, whether from the seed bank and vegetative propagules in the soil, or by dispersal into the site from surrounding areas. In this way, the field layer species are introduced into conditions of varying light intensities and competition levels. These conditions are very unstable and dynamic, and do not resemble the conditions within established secondary woodlands in which the species proliferate naturally.

The results presented in Chapter 2 have demonstrated that quite substantial numbers of woodland field layer species do survive and establish successfully when introduced into young plantations. However, whilst different species clearly exhibit different growth strategies, the variation of establishment success within species is also high. It is expected that the field layer species, when subject to variable and, for them, unnatural conditions, will possibly behave in different ways. If the time scale of the work described here had been longer, a study of species population dynamics within the

young plantations could have elucidated their growth patterns and performance. As many authors indicate (Harper 1977, Tamm 1972a & b, and Barkham 1980) periods of many years are necessary for any meaningful studies of the population dynamics of herbaceous woodland perennial species and should be carried out on species populations within well established plant communities.

Nevertheless, by recording the distribution and performance of the establishing field layer species within the young plantations, and by attempting to characterise the environmental factors that are influencing them, the variation of establishment success may be explained. It is generally recognised (Harper 1977, Hutchings 1986, and Crawley 1986) that there is a difficulty in distinguishing exact plant ages, especially for herbaceous perennial species. Gatsuk *et al.* (1980) therefore opted to describe age states of plants, considering the stage of development which the plants have reached (*e.g.* juvenile, immature, reproductive, senile) rather than their actual ages. Due to great variations in environmental conditions, different individuals may reach a certain age state at different dates, and it is suggested by the authors that both the developmental stages and calendar ages should be determined wherever possible. In the present field trial, the time of species introduction is well documented and so, by considering species development and knowing their growth strategies, it is possible both to describe age states and to be fairly certain of calendar ages. Using this method, the establishing populations of woodland field layer species have been described. By measuring environmental variables such as light, canopy cover, soil type and competition levels within the plantations and relating these to the species performance, the variation should be explained.

With the light recording equipment available for use, only a simple measurement of % daylight was possible, without taking into account spectral quality. It is recognised that the spectral quality of light within woodlands is also important to the field layer species, particularly at low levels of % daylight. Consequently, the photosynthetically utilisable light is probably even less than that recorded here. For a more detailed study of woodland light conditions, the measurement of light quality would be necessary. However, in the present research, the overall measurement of the gross amount of light reaching the floor in the young plantations was considered sufficient.

The study of the influences of light, soil and competition on the distribution and performance of the establishing woodland field layer species should lead to the identification of areas within the young plantations where establishment and colonisation have been successful. To some extent, this should enable the behaviour and expected performance of individual species to be predicted. This may have implications for the management of young plantations, in terms of both the methods of species introduction and the continued management of the sites (*e.g.* thinning regimes).

3.2 Site details.

The sites are the young plantations in Milton Keynes that were described in Chapter 2, *i.e.* Sites 2, 4, 5 and 6. The only change to the sites is that during the winter of 1990/1991, the trees over about 75% of Site 4 were thinned as part of the management regime.

3.3 Materials and methods.

The large-scale field trial initiated by the I.T.E. in 1987 to study the introduction of woodland field layer species into young plantations was used for this investigation. Full details of the implementation of this field trial are given in Chapter 2.

3.3.1 The monitoring of the field layer species.

The 1991 monitoring. At each of three sites (Sites 2, 5 and 6), twenty four $1m^2$ quadrats in each of two sowing mixtures were randomly selected from those that were monitored in 1990. At Site 4, six quadrats in each of the two sowing mixtures were randomly selected from those monitored in 1990 within the section of the site that was unaffected

by thinning. Altogether 48 quadrats at each of three sites and 12 at Site 4 were monitored, giving a total of 156 quadrats, with 78 in each sowing mixture.

In order to characterise the individual field layer species, a description of different age states was attempted, and was related to sowing time and the species' growth strategies (see Table 13). Definitions of age states were kept simple to ease monitoring in the field and to enable non-destructive sampling methods to be used. It is important to note that these age states do not necessarily refer to the exact age of the plants in years, rather to the developmental stage to which they have established. Thus, the plants in age states 1 to 4 may broadly be described as juvenile, immature, young mature and established mature individuals respectively. It does not follow that a plant in age state 4 is 4 years old, rather that it is an established mature and, hence, flowering individual. The ages in the table are an approximate indication of age, but are included for information. For those species with shorter life cycles, *i.e.* biennials and annuals, only 3 age states have been described. Even if a plant was able to complete its life cycle within 1 year, seedlings were distinguished from immature, non-flowering plants, and from established mature flowering plants. Three age states are also described for *H. non-scripta.*

Within the selected quadrats, all of the field layer species that were introduced as seed in 1987 were identified, and their numbers and the area they occupied were recorded in each age state. From these data, plant density m^{-2} and percentage cover values were calculated for each species.

The 1992 monitoring. For two species found in low abundance in 1991, *G. odoratum* and *V. odorata*, twelve established populations were selected within the experimental sites. These populations were characterised by recording the number of individuals in each age state, shoot numbers and patch sizes (where appropriate), and by noting indicators of performance such as flowering and seed set.

At Site 2, the 48 quadrats monitored in 1991 were re-monitored for *G. urbanum* in Sowing Mixture A, and for *S. dioica* in Sowing Mixture B. Plant densities m^{-2} were obtained for each age state in both species.

Table 13. *A description of age states for woodland field layer species.*

SPECIES	Age state 1 Juvenile	Age state 2 Immature	Age state 3 Young Mature	Age state 4 Established Mature
Alliaria petiolata	Small seedlings, < 1yr old One pair of true leaves.	Young, non-flowering plants. % Cover ≃ 1. >1yr old.	Flowering plants. >1yr old.	
Galium mollugo	Small seedlings, < 1yr old. Only 1 main stem.	Young, non-flowering plants 1-2 yrs old. % Cover <1.	Small, flowering plants. 2-3yrs old. % Cover >1, < 4.	Large, flowering plants, 3yrs old+. % Cover >4.
Galium odoratum	Small seedlings, < 1yr old. Single stems.	Young, non-flowering plants 1-2 yrs old. % Cover <1.	Small, flowering plants, 2-3 yrs old. % Cover between 1 and 2.	Large, flowering plants, 3yrs old+. % Cover >4.
Geum urbanum	Small seedlings, < 1yr old. One pair of true leaves.	Young, non-flowering plants with the first properly divided leaves. 1-2 yrs old.	Small, flowering plants, 2-3 yrs old. % Cover >1	Large, flowering plants, 3yrs old+. % Cover ≃ 4.
Hypericum hirsutum	Small seedlings, < 1yr old. Only 1 main stem.	Young, non-flowering plants, consiting of a few shoots. 1-2 yrs old. % Cover <<1.	Small, flowering plants, 2-3 yrs old. % Cover ≃ 1.	Flowering plants, 3yrs old. % Cover >1.
Hyacinthoides non-scripta	Very small seedlings, < 1yr old. Only one leaf.	Small plants with 2-6 leaves. 1-3 yrs old. Height ≃10cm.	Flowering plants, 4yrs old.	
Primula elatior	Small seedlings, < 1yr old. 1 pair of true leaves.	Young, non-flowering plants, 1-2 yrs old. 2/3 leaf pairs.	Small, flowering plants, 2-3 yrs old. % Cover <1.	Flowering plants, 3yrs old +. % Cover >1.
Silene dioica	Small seedlings, < 1yr old.	Young, non-flowering plants, 1-2 yrs old. Height <10cm. % Cover <1.	Small, flowering plants, 2-3 yrs old. % Cover between 1 and 2.	Large, flowering plants, 3yrs old +. % Cover >2.
Torilis japonica	Small seedlings.	Young, non-flowering plants, % Cover <1.	Flowering plants, % Cover >1.	
Viola odorata	Small seedlings, < 1yr old. 1 pair of true leaves.	Young, non-flowering plants, 1-2 yrs old. % Cover <<1.	Small, flowering plants with runners, 2-3 yrs old. % Cover ≃ 1.	Flowering plants, 3yrs old +. % Cover >1.

3.3.2 The monitoring of the competing vegetation.

In each of the quadrats monitored in Section 3.3.1 in 1991, the area occupied was estimated for annual and perennial forbs, grass species and saplings. Percentage cover values were then calculated for each of these four groups of species to characterise the competition within the quadrats.

3.3.3 The measurement of percentage daylight.

On overcast days during the summer of 1991, light was measured using a two-cell EEL electrophotometer, with one cell placed in full daylight outside the woodland and the other placed above the field layer vegetation in the quadrats. At each of the 156 quadrats, five light readings were taken, one in the centre and the other four within the corners of the quadrat. From the readings obtained, the mean percentage daylight at each quadrat was calculated.

3.3.4 The estimation of percentage canopy cover.

Simultaneous with the light measurements, the percentage canopy cover was recorded above each of the 156 quadrats. This was a subjective measurement made by standing in the middle of the quadrat, looking upwards, and estimating the percentage cover afforded by the tree canopy. These estimates were placed into the groups 0-24%, 25-49%, 50-74% and 75-100% canopy cover.

3.3.5 The characterisation and analysis of soils.

At each of the four experimental sites, 10 of the quadrats monitored in 1991, were selected at random. A few days after heavy rainfall in May 1992, five replicate soil cores, which were 10cm in length and 3cm in diameter, were taken beside each of these 40 quadrats. Each set of cores was placed into polythene bags, labelled and weighed. A

proportion of each sample was dried at 30°C for 2 days and then sieved through a 2mm sieve to remove stones, roots and leaves. Each of the 10 soil samples from the four field sites was then analysed as follows:

The determination of soil moisture.

Between 10-20g of fresh soil was weighed into a dry dish. This was placed into an oven at 105°C and dried to a constant weight. It was then cooled in a desiccator and reweighed. The percentage fresh moisture of the soil was calculated from the recorded loss in weight.

The determination of percentage organic matter.

About 1g of dry, sieved soil was placed into a dry crucible. This was placed in a muffle furnace, the temperature of which rose to 550°C and remained there for at least two hours. When cool enough to handle, the samples were transferred to a desiccator, cooled and reweighed. The percentage loss on ignition was calculated from the weight lost during the combustion process.

The determination of soil pH.

An Electronic Instruments pH/Temperature meter was set up according to the manufacturers' instructions. The meter was calibrated against two buffer solutions of pH4 and pH7. A 50ml beaker was half filled with fresh soil, and then filled with distilled water. The soil and water mixture was stirred, and then shaken for about 30 minutes. An electrode was then immersed into the mixture, swirled gently and the resulting pH was recorded. The electrodes were rinsed between readings.

The mechanical analysis of soil.

200ml of distilled water and 15ml of saturated sodium oxalate solution were added to a weighed amount (about 50g) of dry, sieved soil in an 800ml beaker. This was allowed to stand overnight and was then dispersed for 30 minutes with an electrical stirrer and baffle. The soil suspension was then transferred to a 1000ml measuring cylinder, diluted to 1000ml with distilled water, and shaken thoroughly. After about 4 minutes, a Boyoucos soil hydrometer was carefully lowered into the suspension in order to obtain a reading at exactly 5 minutes of silt + clay as g l^{-1}. The suspension was then reshaken,

and after 5 hours the procedure was repeated to obtain the amount of clay g l^{-1} alone. The amount of sand in the soil was then calculated by difference. At the time of both readings, the temperature was recorded. As a temperature correction, 0.3g l^{-1} were added to the hydrometer readings for each degree above 19.4°C, or subtracted for temperatures below 19.4°C.

The determination of extractable phosphate.

0.25g of dry, sieved soil were accurately weighed into a glass bottle to which 50ml of Truog's reagent (Allen 1974) were added. The mixture was shaken for 30 minutes on a rotary shaker, and then filtered through Whatman no.44 paper. 25ml of the filtrate of each sample was taken for analysis. At the same time, 0-15ml of working standard (1M Potassium phosphate solution) were pipetted into 50ml volumetric flasks. The volumes were made up to 50ml to give a standard range from 0-0.3mg Phosphate. Both the samples and the standards were then treated in the same way. The samples were passed through a Technicon Auto Analyser, Model AA1. Within this process, a 0.1% aqueous solution of ascorbic acid and a 0.2% solution of ammonium molybdate dissolved in 4% sulphuric acid were automatically added to the sample in the correct proportions. The solution was then mixed thoroughly in two mixing coils and was passed through a heating bath at 90°C. The absorbance of the solution was then measured at 660nm using a colorimeter (Allen 1974).

3.3.6 **The data analysis.**

Throughout the monitoring period in 1991, and from the 1990 results (Chapter 2), it became clear that conditions in the sites were very variable. Analysis of variance (ANOVA) was carried out on the data obtained for each of 8 sown species over all four experimental sites. The ANOVAs indicated that within site variation was high for each species. Indeed, such was the extent of the variation, that it was considered that quadrats even at the same site were subject to quite different environmental conditions. It was therefore decided to pool all of the data within each of the original Sowing Mixtures A and B that had been gathered from the four experimental sites. This produced two main data sets for the purposes of further analysis, and all of the results that are presented

have been obtained from one of these data sets.

F values from the analysis of the between site variation indicated that this was just significant for 6 of the 8 sown species at the 5% level. The removal of Site 6, where species generally grew very poorly, from the data set considerably reduced the between site variation. Without Site 6, F values were not significant at the 5% level. The subsequent analyses may therefore have been more appropriately carried out on data from Sites 2, 4 and 5 only. However, analyses were carried out on existing species populations, *i.e.* only involving quadrats where species were present. Hence, the majority of Site 6 quadrats were not included in the calculations, as they did not contain introduced field layer species.

Mean densities m^{-2} were calculated for each of the introduced field layer species and are presented with either the corresponding standard errors or 95% Confidence Intervals where appropriate. Where mean percentage cover values are presented, whether for the introduced or naturally colonising species, these have been transformed using the arc-sin transformation prior to any statistical analysis. Student's t-tests were carried out to compare age state means for each species. Modified t-tests (Bailey 1969) were used, where necessary, to take into account unequal variances.

In order to investigate the distribution and performance of the introduced species further, it was decided to attempt a characterisation of the competing vegetation by Detrended Correspondence Analysis (DCA). This was effected with the program DECORANA (Hill 1979b). The intention was to reveal any distinct patterns which might be present within this naturally colonising vegetation to enable it to be characterised and grouped according to distinct assemblages of species. By overlaying such patterns with data from the introduced species, analysis of the distribution and the performance of the latter should then be possible.

3.4 Results.

3.4.1 The results of the 1991 vegetation monitoring and environmental measurements.

3.4.1.1 The age-state structures of populations of woodland field layer species.

Figure 4 shows the age structures of populations of *S. dioica*, *G. urbanum*, *T. japonica* and *A. petiolata*. The mean densities m^{-2} and standard errors have been plotted against age states (refer to Table 13).

For *S. dioica*, the density of seedlings was significantly higher than the number of individuals in the other three age states. There was no signficant difference between the number of plants in age states 2, 3 or 4.

The results were very similar for *G. urbanum*, the seedling density of which was significantly higher than the mean density of individuals in all other age states. These were not significantly different from each other.

The age structure of the *T. japonica* population indicates that the density of seedlings was significantly higher than the number of individuals in other age states.

The results for *A. petiolata* indicate that seedling density in age state 1 was significantly higher than the number of plants in age state 2, but not of those in age state 3. The density of mature plants was also significantly higher than the density of one year old plants. It is of interest that the number of plants in age state 3 was higher than that in age state 2 for this species.

Figure 5 indicates the age structures of populations of *G. mollugo*, *P. elatior*, *H. hirsutum* and *H. non-scripta* within the young plantations. The results for *G. mollugo* were very similar to those for *S. dioica* and *G. urbanum*, with a high mean density of seedlings, and low mean densities in all other age states. However, the mean seedling density was variable, and was only significantly higher than the mean densities in age

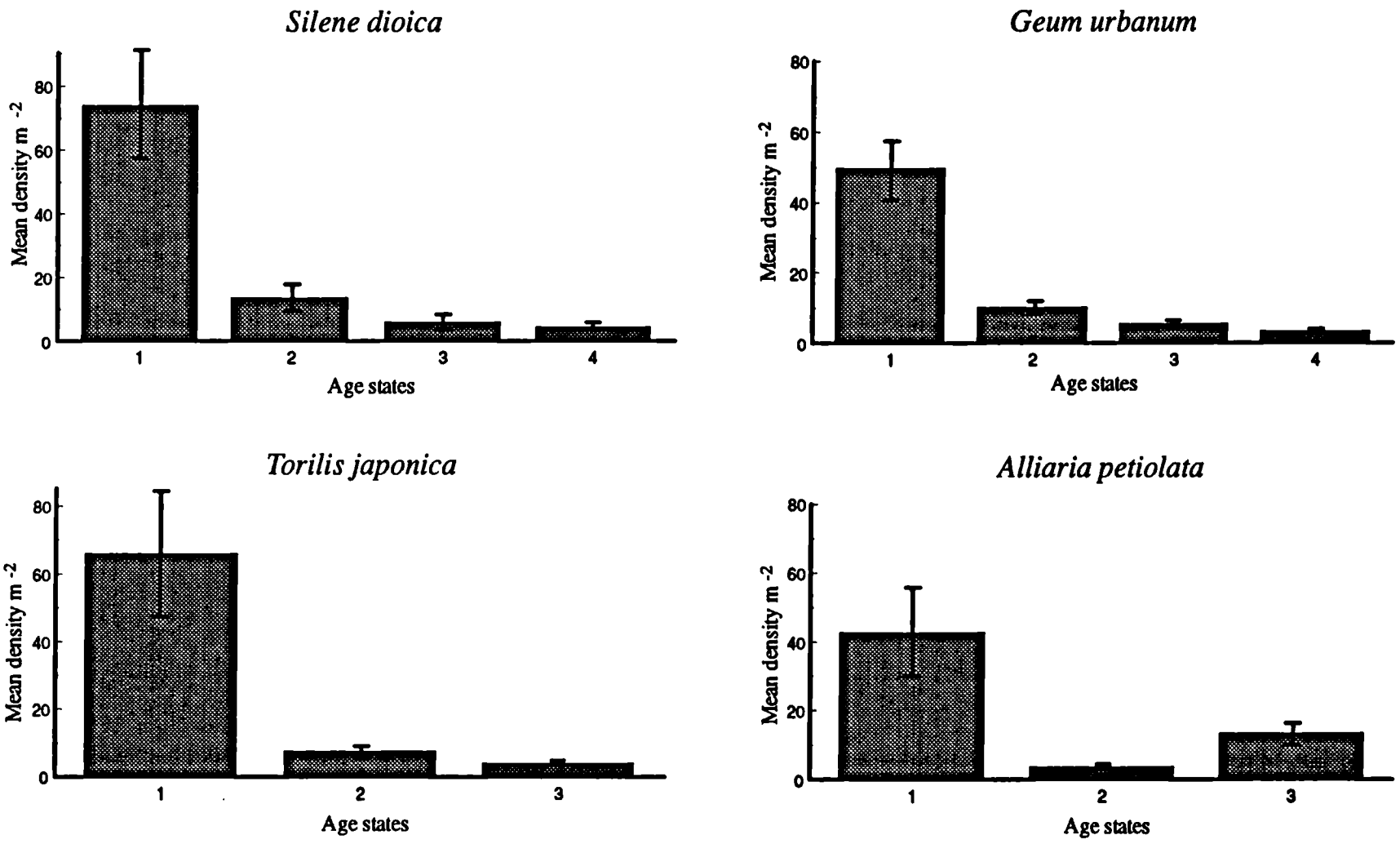


Fig. 4 *The age structures of populations of woodland field layer species in Milton Keynes.* I
Bars indicate Standard Errors.

states 3 and 4.

The mean seedling densities for both *P. elatior* and *H. hirsutum* were also variable, and there was no significant difference between any of the mean densities for these two field layer species.

The results for *H. non-scripta* indicate a different age structure to those exhibited by other species. For this species, only individuals in age state 2 were recorded in the quadrats. No individuals were recorded in age states 1 or 3 for this species. Individuals in age state 1, small seedlings, and in age state 3, young flowering plants, were observed at very low densities in the field.

3.4.1.2 The components of competing vegetation within experimental plots.

Figure 6 shows the relationship between the mean total % cover values for both the introduced field layer species and the components of competing vegetation. The four groups of competing vegetation are saplings, grasses, and perennial and annual forbs. The mean percentage cover of saplings within both Sowing Mixture A and B plots were similar, and were both significantly less than the mean percentage cover values for the other three groups of vegetation. In both A and B plots, the mean percentage cover values for grasses, perennial and annual forbs were not significantly different either within or between plots.

In Sowing Mixture A plots, *H. non-scripta* had the lowest mean total % cover value. The other four sown species all had % cover values higher than that for saplings, though this was only significantly higher for *G. urbanum*. The % cover value for *G. urbanum* was not significantly different from that of the grasses or that of the perennial forbs.

In Sowing Mixture B plots, only *S. dioica* had a mean total % cover value higher than that for saplings. The % cover values for the other components of competing vegetation were not significantly different from that of *S. dioica*.

3.4.1.3 The relationship between mean % daylight and % canopy cover.

Figure 7 indicates the relationship between mean percentage daylight and percentage

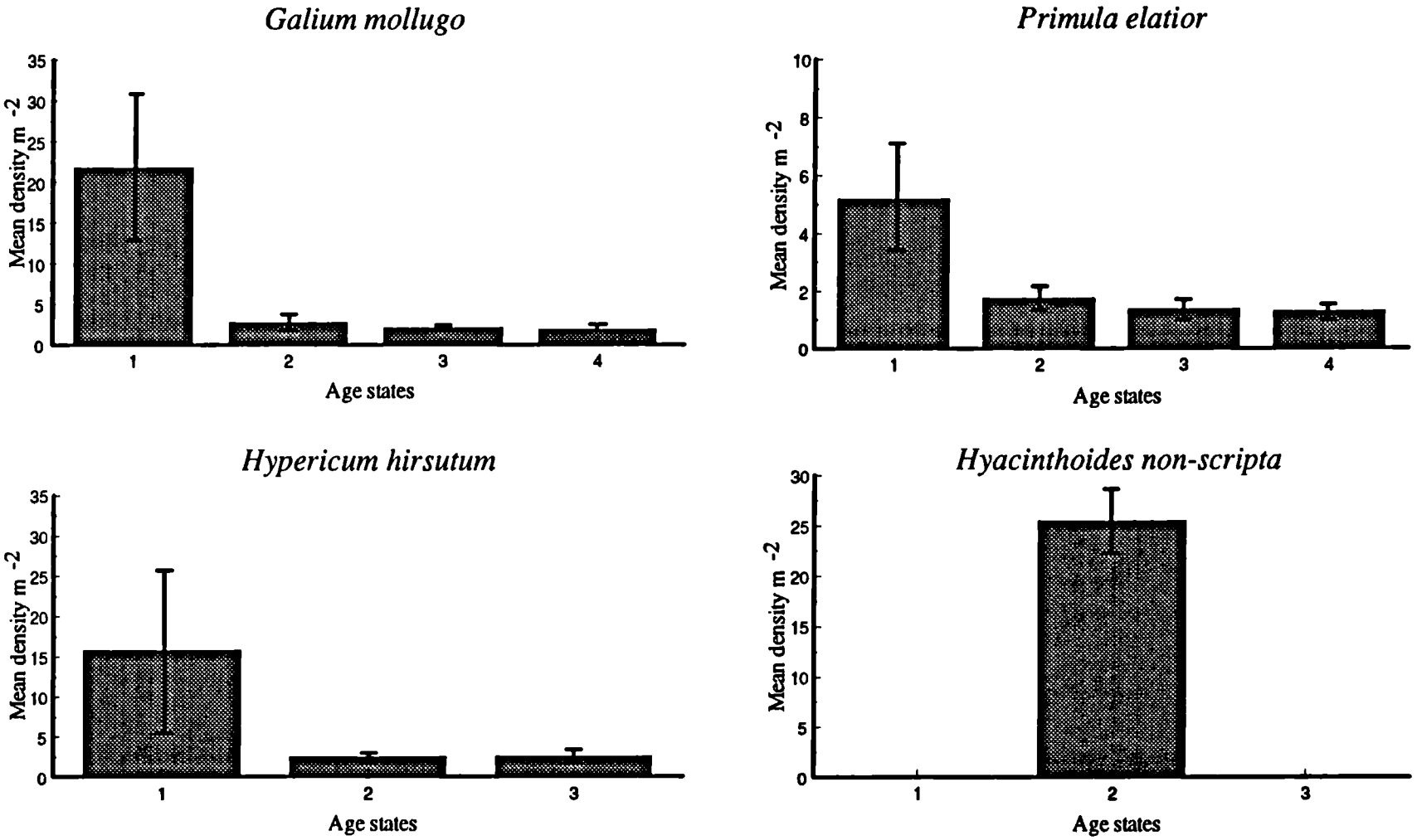


Fig. 5 *The age stucture of populations of woodland field layer species in Milton Keynes.* II
Bars indicate Standard Errors.

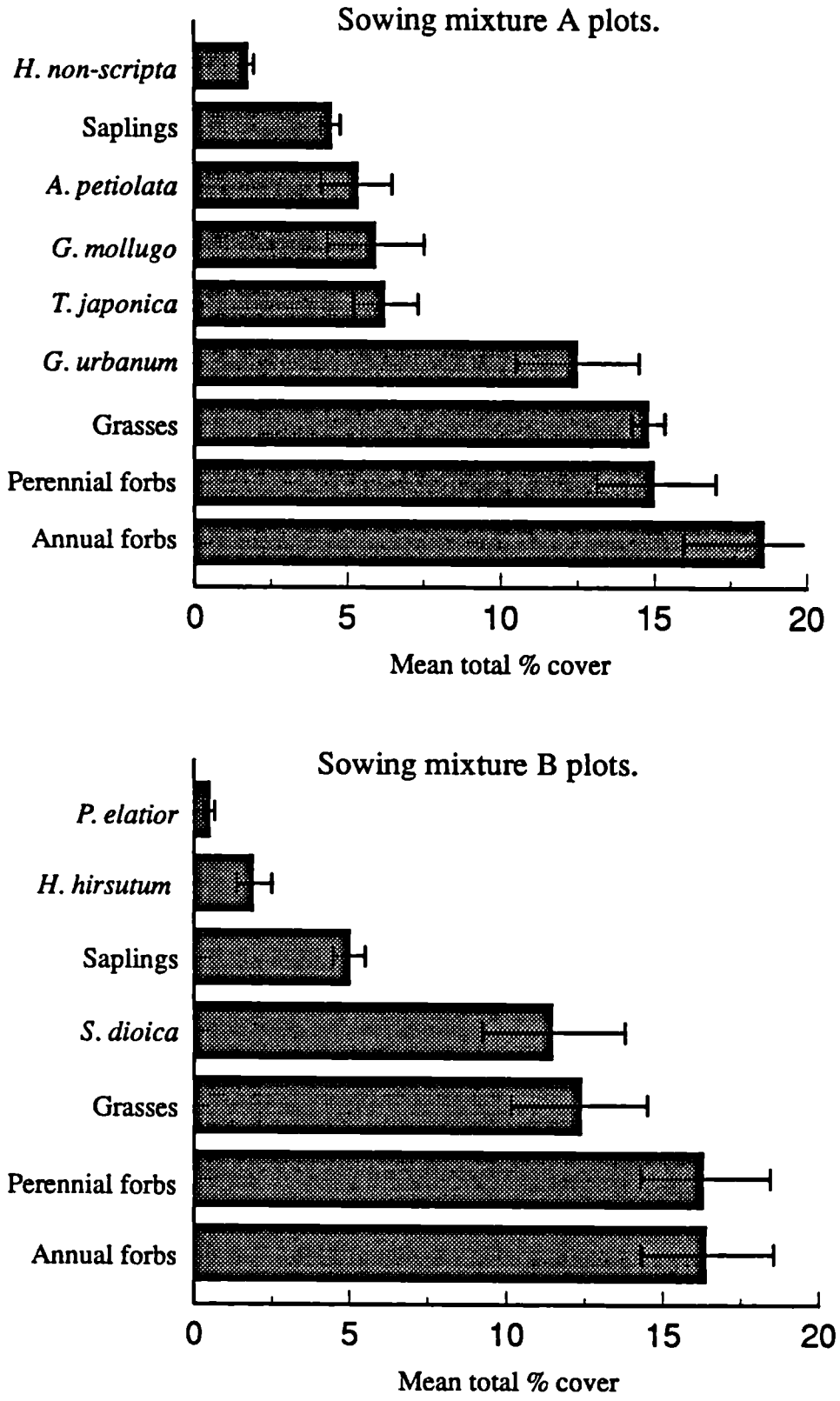


Fig. 6 *The relationship between the mean total % cover values for species in sowing mixture plots A and B.*
Bars indicate Standard Errors.

canopy cover in the young plantations. Mean percentage daylight values and the associated standard errors are plotted against percentage canopy classes 1 to 4. Each of the mean % daylight values was significantly different from the others. Low canopy cover of 0-24% was where highest daylight of 48.8% was recorded. In the areas with high canopy cover of 75-100%, the associated mean daylight was only 3.5%.

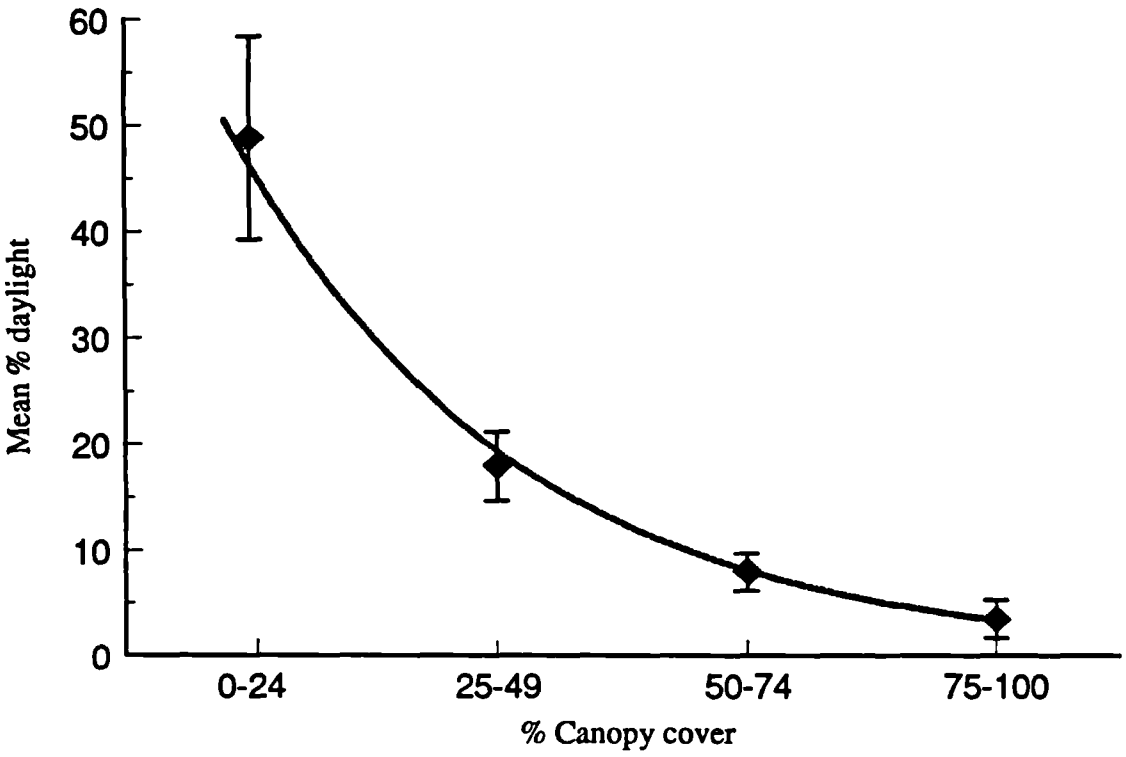


Fig. 7 *The relationship between mean daylight and canopy cover, 1991.*
Bars indicate Standard Errors.

3.4.1.4 The relationship between individual components of competing vegetation and % canopy cover.

Figure 8 indicates the relationship between the individual components of competing vegetation and % canopy cover. Mean % cover values, which were sampled per m^2, and 95% Confidence Intervals are plotted against the four classes of % canopy cover.

For saplings, the mean % cover values were low under all canopies, and ranged only from 2.0% to 4.8%. None of the values were significantly different.

For the grass species, the mean % cover values were significantly higher in the plots

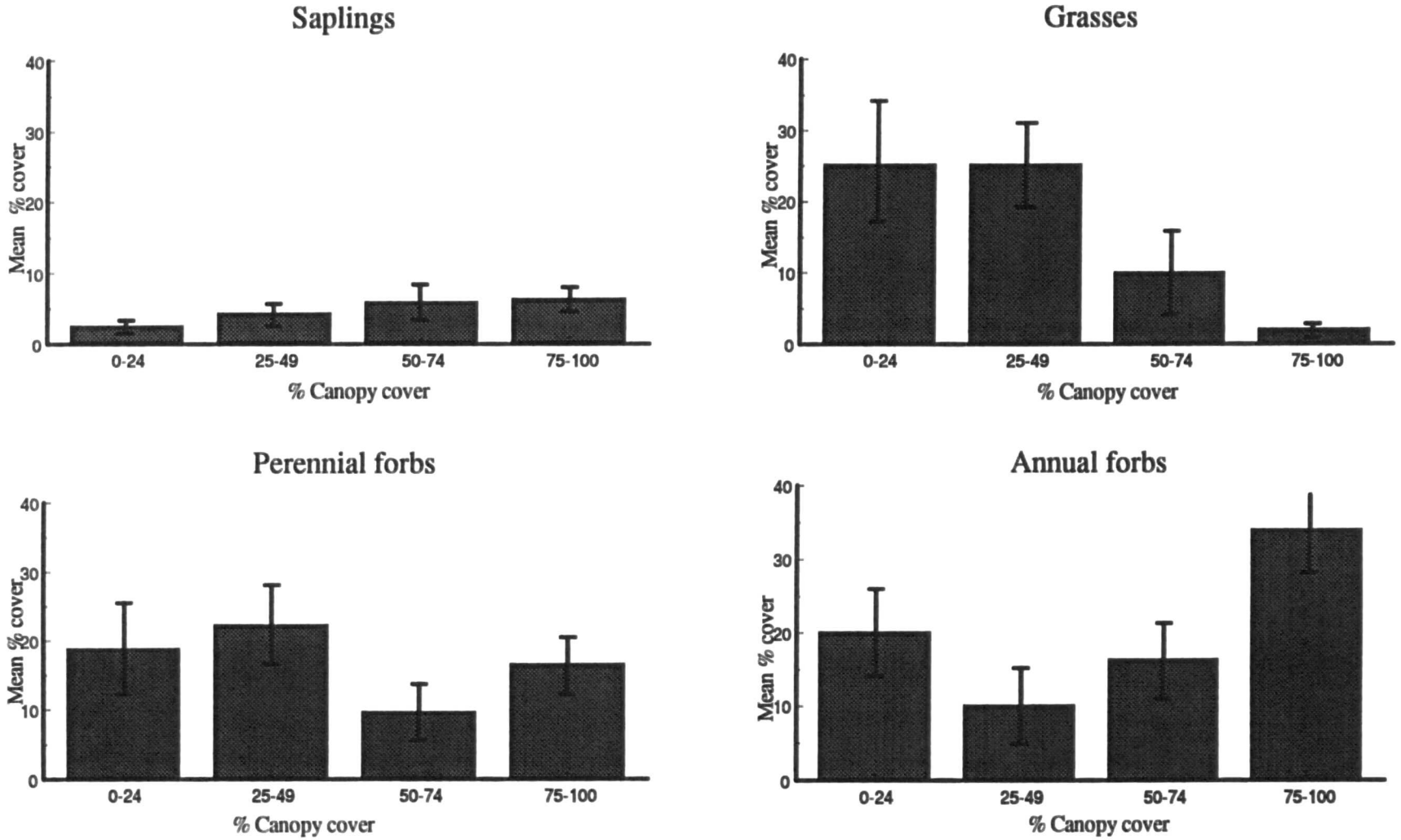


Fig. 8 *The relationship between individual components of competing vegetation and % canopy cover, 1991.*
Bars indicate 95% Confidence Intervals.

with low % canopy cover than in the shadier plots. As % canopy cover rose above 50%, grass species became only a small component of the competing vegetation, having a small % cover value.

The mean % cover values for perennial forbs ranged between 5.2% when canopy cover was 50-74%, to 16.9% when canopy cover was 25-49%. The graph indicates that the perennial forbs had significantly higher % cover values in lighter areas of the plantations, and were less prevalent in shadier places. The rise in mean % cover beneath the most developed canopy was due mostly to *Anthriscus sylvestris* (Cow Parsley).

The mean % cover values for annual forbs were lower in the quadrats with between 25-74% canopy cover and were not significantly different. However, in both the lightest and the shadiest places, the mean % cover values were significantly higher. In the open quadrats with low canopy cover, ruderals such as *Picris echioides* (Bristly Oxtongue), *Vicia hirsuta* (Hairy Tare), and *Lapsana communis* (*L. communis* ssp. *communis*, Nipplewort), were the predominant annual forb species, whilst in the shadier quadrats, *G. aparine* was the dominant, if not the only, annual forb species.

3.4.1.5 The analysis of soils within the young plantations.

Table 14 indicates the results of all the soil analyses that were carried out on samples taken from each of the four experimental sites. Although the soil texture varied between clay loam and sandy clay loam, the percentage values for sand, clay and silt were not significantly different between the four sites.

Table 14. *The analysis of soil properties in young plantations, Milton Keynes.*

		Soil texture				P_2O_5mg	%Organic	
	pH	%Clay	%Sand	%Silt	Type	$100g^{-1}$	Matter	%Moisture
Site 2	5.7	24.9	47.7	27.5	Clay loam	5.1	8.6	22.8
Site 4	6.3	21.9	58.0	20.1	Sandy clay loam	3.8	9.1	23.8
Site 5	6.5	27.1	50.7	20.8	Clay loam	5.0	8.8	21.0
Site 6	6.1	24.0	51.2	24.9	Sandy clay loam	3.4	8.4	20.5

The soil pH values ranged between 5.7 at Site 2 to 6.5 at Site 5. The values were not

significantly different throughout the young plantations. Soil pH in the young plantations is neutral to slightly acidic. The organic matter content of the soil ranged between 8.4% at Site 6 to 9.1% at Site 4, and was not significantly different between the sites. The soil moisture content in May was very similar throughout the young plantations, ranging only from 20.5% at Site 6 to 23.8% at Site 4. The amount of extractable P_2O_5 was slightly more variable, ranging from 3.4mg $100g^{-1}$ at Site 6 to 5.1mg $100g^{-1}$ at Site 2. Values were not significantly different between the sites, however.

These data indicate that the soils were fairly similar throughout the experimental sites.

3.4.2 An analysis of the distribution of introduced field layer species in young plantations in relation to environmental variables.

3.4.2.1 The relationship between population structures of introduced field layer species and % canopy cover within young plantations.

Figures 9 and 10 indicate the relationship between the population structure of field layer species and % canopy cover. For eight of the field layer species, the percentage of the population recorded beneath each canopy cover has been plotted for each age state. By referring to Fig. 7, the proportion of each age state can be related to % daylight. For some field layer species, distinct trends are apparent, indicating preferences for light or shady conditions, whereas for others, growth is not confined to specific areas. The species are now described separately.

The graph for *S. dioica* indicates no very clear trend of age state with % canopy cover. However, in age states 1, 2 and 3, the majority of the population grew in the shadiest conditions, whilst in age state 4, few individuals occurred here.

The data for *G. urbanum* indicate that the majority of individuals in each age state occurred in the lightest conditions where % canopy cover was low. Plants of each age state were also well represented in much shadier places. Plate 10 is an example of an age state 4 plant which is surrounded by age states 1 and 2 plants.

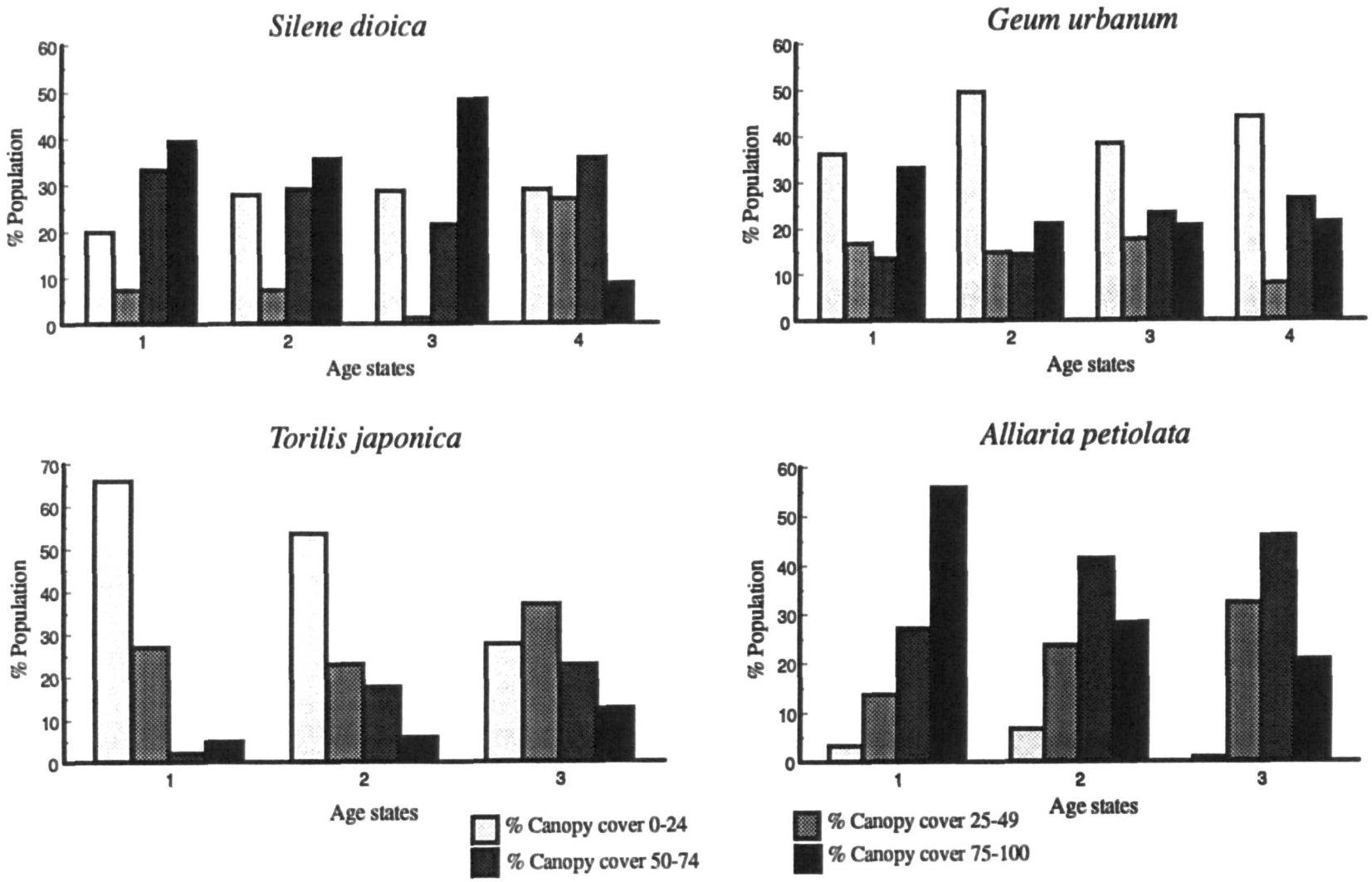


Fig. 9 *The relationship between the population structure of field layer species in young plantations and % canopy cover.* I



Plate 10. *A large* Geum urbanum *plant (age state 4), surrounded by age states 1 and 2 individuals.*

The graph for *T. japonica* indicates a clear trend for the population in each age state with % canopy cover. The majority of individuals, particularly of seedling and immature plants, were recorded in lighter areas with low % canopy cover (refer to Plate 11). Although the largest proportion of the population of mature plants was found in moderate canopy cover of 25-49%, these still showed a tendency to grow in lighter areas, with only a low proportion of the population recorded in the shadiest sites.

Another clear trend of population structure was apparent for *A. petiolata*. The graph indicates that this species was found mostly in shady plots. Only a very small proportion of *A. petiolata* in each age state was recorded in light areas with low % canopy cover.

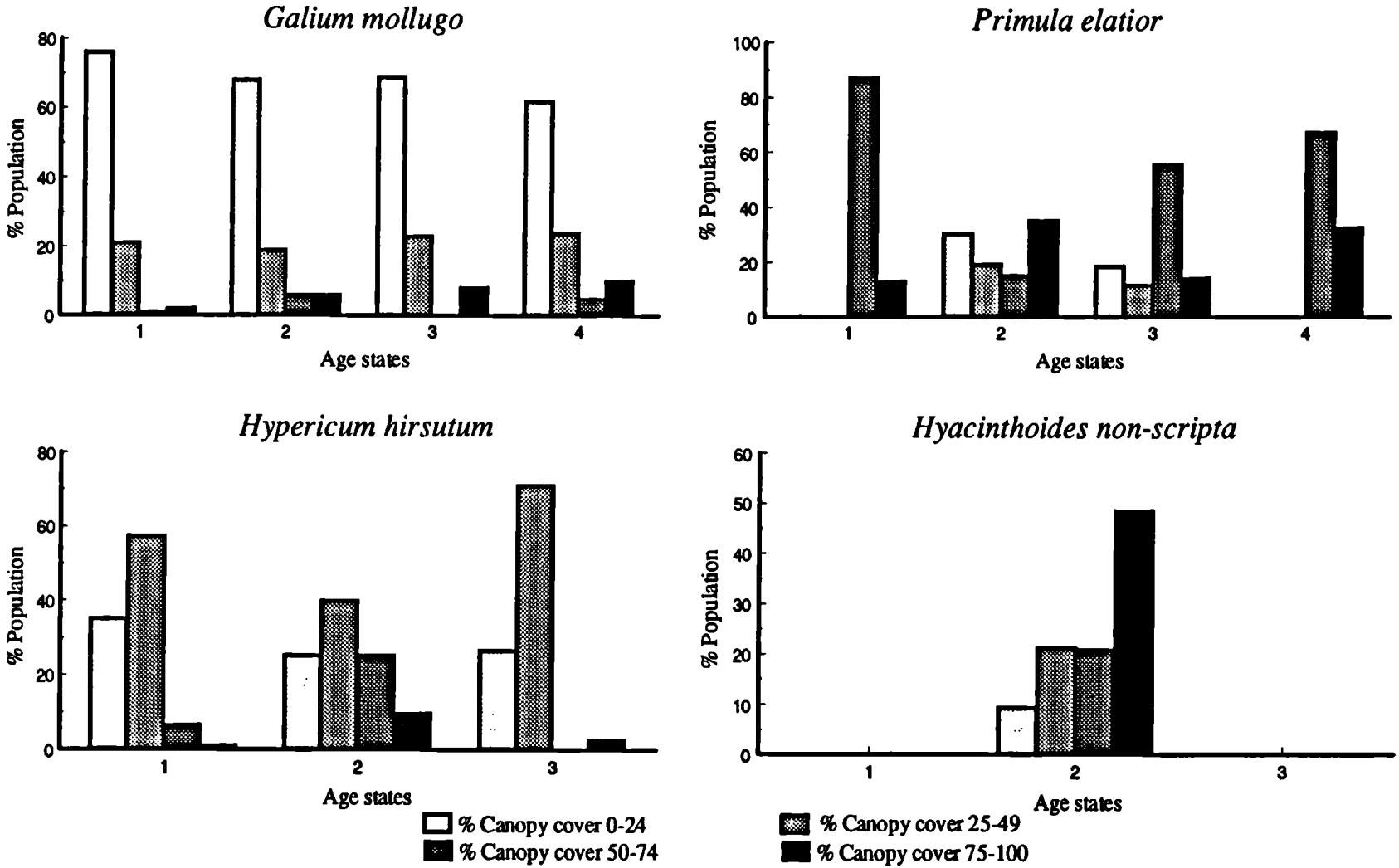


Fig. 10 *The relationship between the population structure of field layer species in young plantations and % canopy cover.* II

The majority of seedlings were found in the shadiest areas, whilst the majority of both immature and flowering individuals were recorded in quadrats with a canopy cover of 50-74%, where mean daylight was 18.8%.

Figure 10 shows the population structures of *G. mollugo*. *P. elatior*, *H. hirsutum* and *H. non-scripta* within the young plantations. *G. mollugo* shows a clear preference of this species for sites with low % canopy cover, and hence high light. A large majority of the population within each age state was recorded in 0-24% canopy cover areas. This decreased significantly to the proportion found in 25-49% canopy cover, and was only very small in shadier areas.

No trend is apparent for the population structure of *P. elatior* in the young plantations. The majority of seedlings and mature plants were recorded in semi-shade with 50-75% canopy cover, and none of the population of either of these groups were found in the lighter plots. Individuals of both one year old and young mature plants were recorded in lighter quadrats as well as in shadier places.

The graph for *H. hirsutum* indicates that the majority of individuals in each age state were recorded beneath 25-49% canopy cover. The populations tended to be in lighter areas, and only a few individuals of any age state were found in shadier sites.

The data presented for *H. non-scripta* show that the individuals found were all immature, non-flowering plants. In this age state, there was a tendency for plants to be growing in shady conditions. The majority of the population in age state 2 was recorded in 75-100% canopy cover. Few individuals were recorded in very light quadrats with low % canopy cover, except in areas where the competing vegetation was reduced by a layer of wood chippings (Plate 12).

3.4.2.2 The characterisation of populations of species present at low density.

For *G. odoratum* and *V. odorata*, which were only present throughout the experimental sites at very low densities, 12 populations were characterised within selected quadrats. Close examination of all the populations of both species revealed them to consist of just one main plant, which occasionally had one or two seedlings growing beside it. A

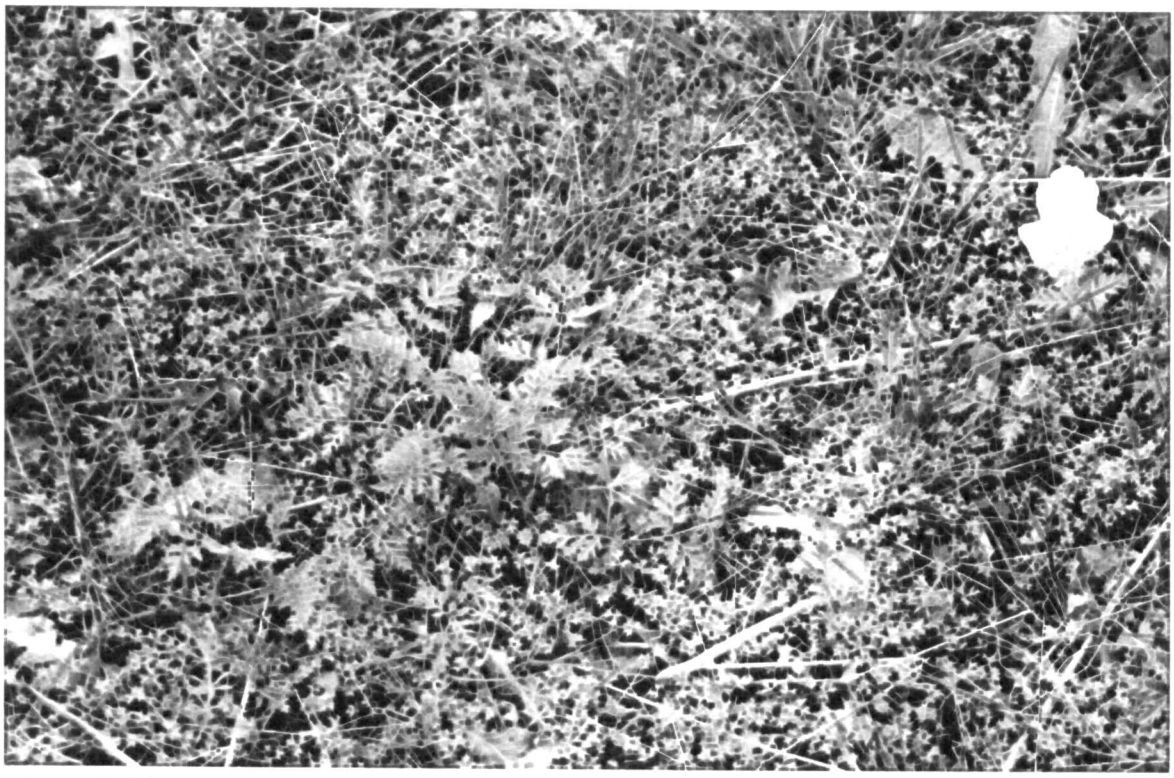


Plate.11 Torilis japonica *plants (age states 1 and 2), growing amongst grass in a light area.*



Plate.12 Hyacinthoides non-scripta plants *(age state 2) growing in wood chippings.*

diagrammatic example of a 'patch' of each species is given in Fig. 11. This indicates how both vegetative and flowering shoots are linked within the population. Plates 13 and 14 are examples of patches of *G. odoratum* and *V. odoratum* growing within the young plantations.

Table 15 shows the mean dimensions of the 'patches' of *G. odoratum* and *V. odorata* that were recorded within the young plantations. Mean vegetative and flowering shoot numbers are also presented. The mean dimensions of *G. odoratum* patches were 1.2m x 0.8m, with an average of 147.2 vegetative and 19 flowering shoots per patch. Two seedlings were found in association with the twelve selected patches. The majority of the *G. odoratum* populations were found beneath 75-100% canopy cover.

Table 15. *Analysis of the characteristics of selected 'patches' of* G. odoratum *and* V. odorata *within the young plantations.*

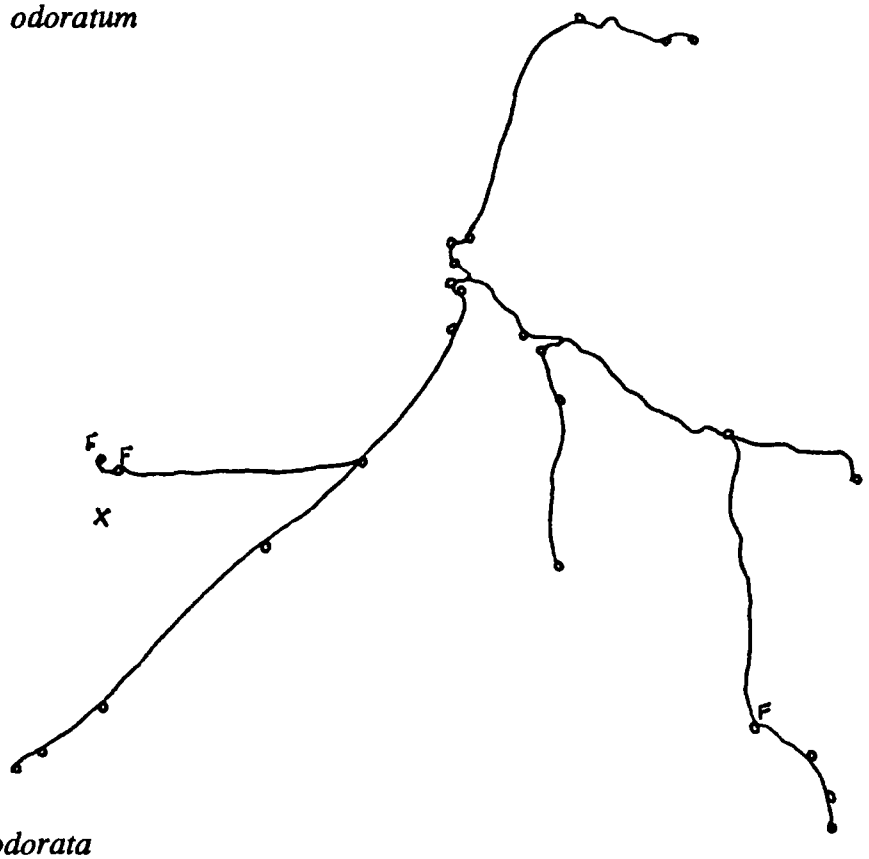
Species	Mean patch dimensions (m)	Mean number of shoots	
		Vegetative	Flowering
Galium odoratum	**1.2** $\pm$0.3 x **0.8** $\pm$0.2	147.2 $\pm$54.1	19.0 $\pm$10.7
Viola odorata	**0.5** $\pm$0.1 x **0.2** $\pm$0.1	8.6 $\pm$4.8	3.2 $\pm$1.4
95% Confidence Intervals are presented, where t_{11} = 2.201.			

Patches of *V. odorata* were much smaller than those of *G. odoratum*, with mean dimensions of 0.5m x 0.2m. The mean number of vegetative shoots was 8.6 per patch, and there was an average of 3.2 flowering shoots. A total of 3 seedlings was found in association with the *V. odorata* patches. The selected plants were found beneath 50-74% and 75-100% canopy cover.

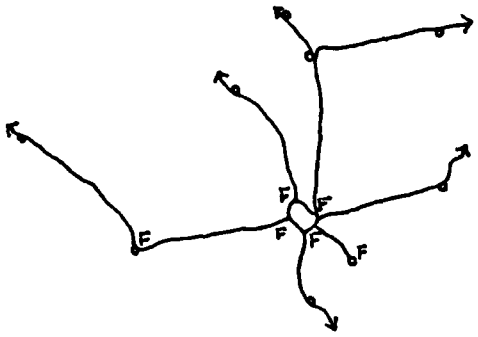
3.4.2.3 The analysis of *S. dioica* and *G. urbanum* populations monitored between 1990 and 1992.

Figure 12 shows the age structures of establishing populations of *S. dioica* and *G. urbanum* in the young plantations. In 1990, only small seedlings, *i.e.* less than one year old, and mature flowering plants were distinguished from the plants in the populations. The individuals in age states 2 and 3 were not distinguished from each other and these

Galium odoratum



Viola odorata



Key.
F: Flowering shoot
•: Shoot
X: Seedling
->: Runner

10cm

Fig.11 *A diagrammatic representation of 'patches' of two vegetatively spreading field layer species.*



Plate.13 *A large patch of a single* Galium odoratum *plant.*



Plate.14 *A patch of a single* Viola odorata *plant, growing amongst* Aesculus hippocastanum *leaf litter.*

have been plotted in equal numbers for the first year.

In 1990, 96% of the *S. dioica* population was seedling plants. This decreased to 83.0% in 1991, and further to 60.1% by 1992. During the three years, the percentage of the population in the other three age states increased. The population of mature flowering plants increased from 1.0% in the first year to 3.7% in 1992.

In 1990, 92.9% of the *G. urbanum* population was seedling plants, which decreased to 75.4% in 1991 and to 41.3% in 1992. As for *S. dioica*, the plants in other age states increased during the same time period. The line graphs in Fig. 12 indicate the survival of the first cohort, *i.e.* 1990 seedlings, from 1990 to 1992 for both species. Linear regression lines have been fitted through the natural log values of the population numbers to indicate the rate of seedling mortality in the populations. For *S. dioica* r^2 = 0.919 and for *G. urbanum* r^2 = 0.881. The gradient of the regression line for *S. dioica* is steeper than that for *G. urbanum*, which shows a higher rate of seedling mortality for *S. dioica*.

3.4.3 The analysis of the performance and distribution of the establishing field layer species within young plantations using Detrended Correspondence Analysis.

In order to obtain satisfactory DCA ordinations, the uncommon species amongst those that colonised naturally were omitted altogether from the analysis. Such species, *e.g. Dactylis glomerata* (Cock's-foot) and *Myosotis arvensis* (Field Forget-me-not), were defined as those present in less than 10% of the quadrats (stands) that were sampled. This lessened the noise generated by them in the ordination, and was found to be preferable to the downweighting option which did not remove their effects sufficiently.

The aim of the DCA was to analyse the distribution of the field layer species that had colonised naturally into the site. The species ordinations showed rather less obvious trends than had been expected. However, some ordinations did indicate that species associated with fertile soil, such as *G. aparine*, *U. dioica*, and *A. sylvestris*, and bird-sown shrubs, such as *Rosa canina* (Dog-rose) and *R. fruticosus* (*Rubus* sect.

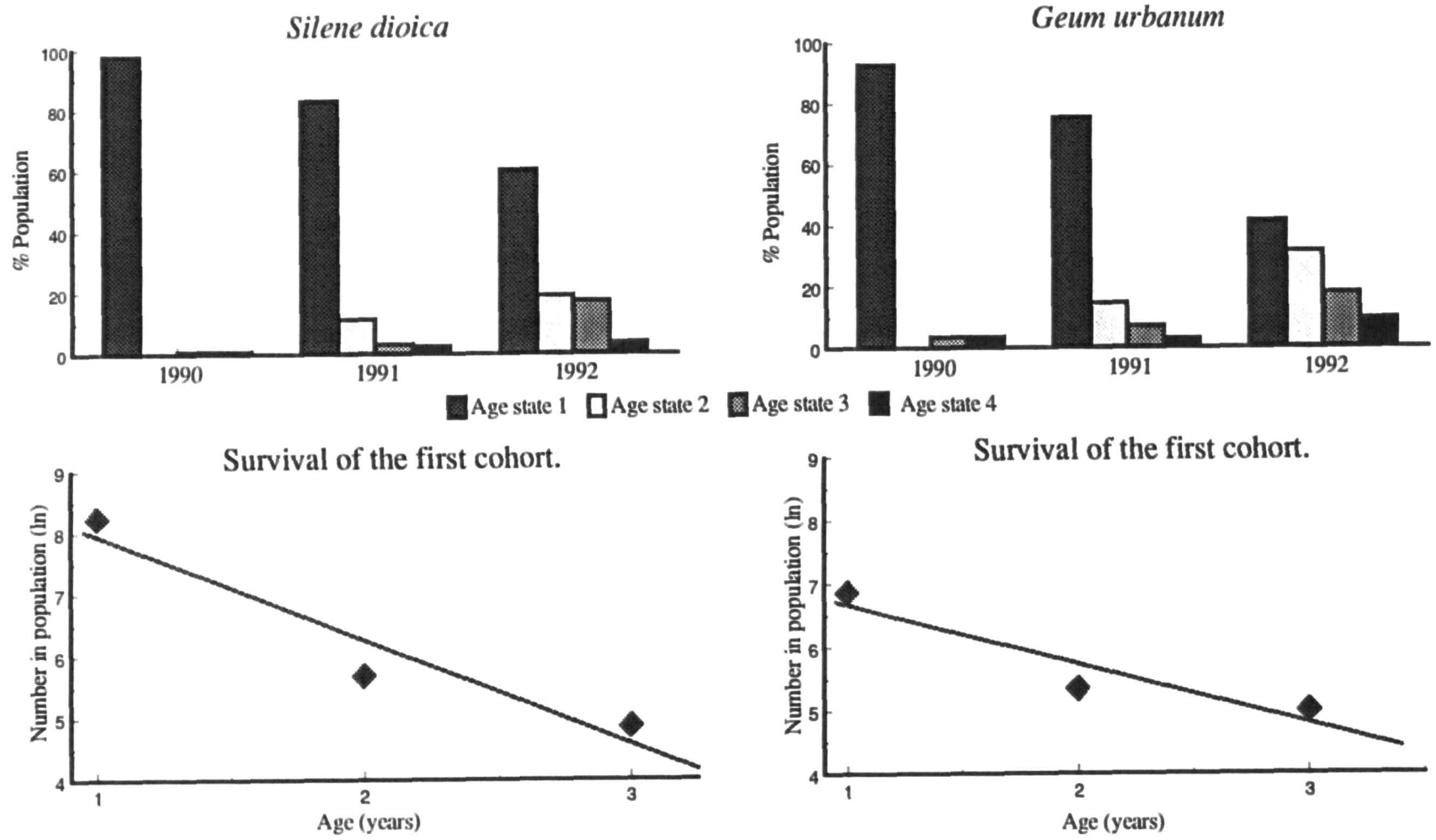


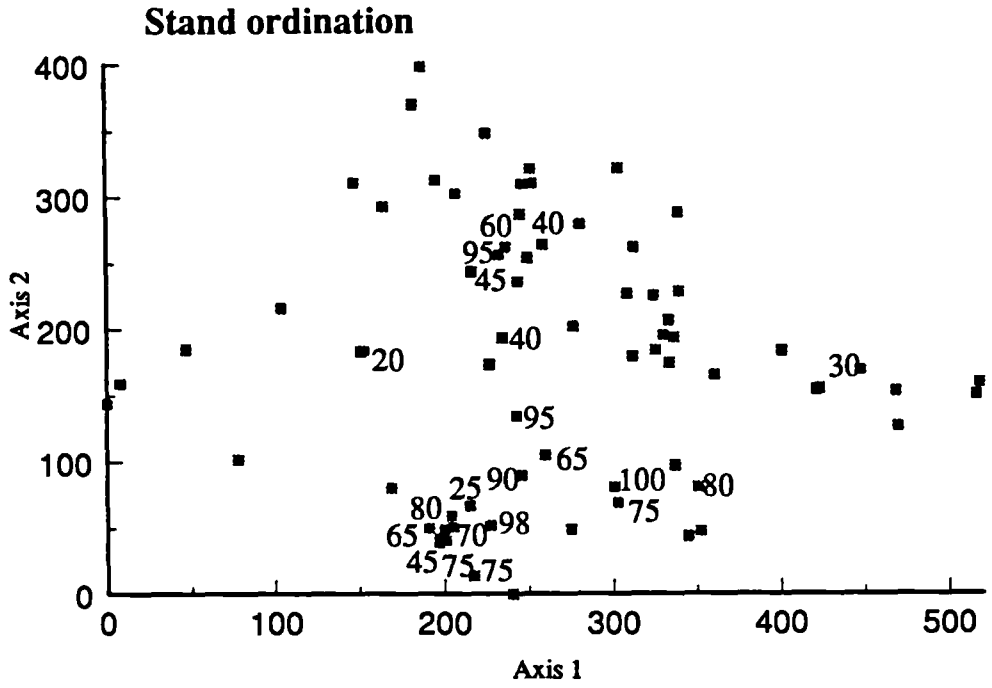
Fig. 12 Above: *Age structures within establishing populations of* Silene dioica *and* Geum urbanum *in young plantations from 1990-1992.*
Below: *Survival of first cohort from 1990-1992.*

Glandulosus, Bramble) tended to be grouped together. These were mostly shade-tolerant species. Further, grass species, such as *Lolium perenne* (Perennial Rye-grass) and *Alopecurus pratensis* (Meadow Foxtail), characteristic of high light areas, were generally separated from the shade-bearing species (see Fig. 13). These distinct groups of species were also observed in association with each other in the field.

By overlaying the stands ordination with data from the introduced species, an indication is given of whether the performance of the introduced species could be related to the composition of the competing vegetation. Since the interpretation of trends in the distribution of the natural colonists proved difficult, characterisation of the performance of the introduced species in this way was also likely to be difficult. However, information such as mean % cover values for some of the introduced field layer species was super-imposed upon the scatter plots of competing vegetation. Whilst strong trends were neither expected nor found, the distribution of the successfully establishing introduced species did produce some points of interest.

Figure 13 shows the ordinations of stands and species for the competing vegetation recorded in High Sowing Density Mixture B plots. In the ordination, the positions of some of the predominant natural colonists have been labelled. The % cover values for *S. dioica* have been super-imposed upon the stand ordination in the appropriate positions. Only % cover values above 20% were shown, in order to indicate areas where *S. dioica* was particularly successful. It was found that *S. dioica* tended to have high cover values near to the *G. aparine* location, but also in places where grasses were positioned. The performance of *G. urbanum* was found to have a very similar distribution.

Figure 14 shows the stands and species ordination of the competing vegetation in High Sowing Density Mixture A plots. In the ordination, the positions of some of the natural colonists have been labelled. Shade-bearing species, such as *G. aparine*, *U. dioica* and *R. fruticosus*, are positioned in the lower half of the ordination. The majority of grass and weed species, that are characteristic of high light, are positioned above the shade-tolerant species. The % cover values for *A. petiolata*, above 15%, have been super-imposed upon the stand ordination. The distribution of high % cover values for *A.*



Numbers indicate % cover of *S. dioica*, above 20%.

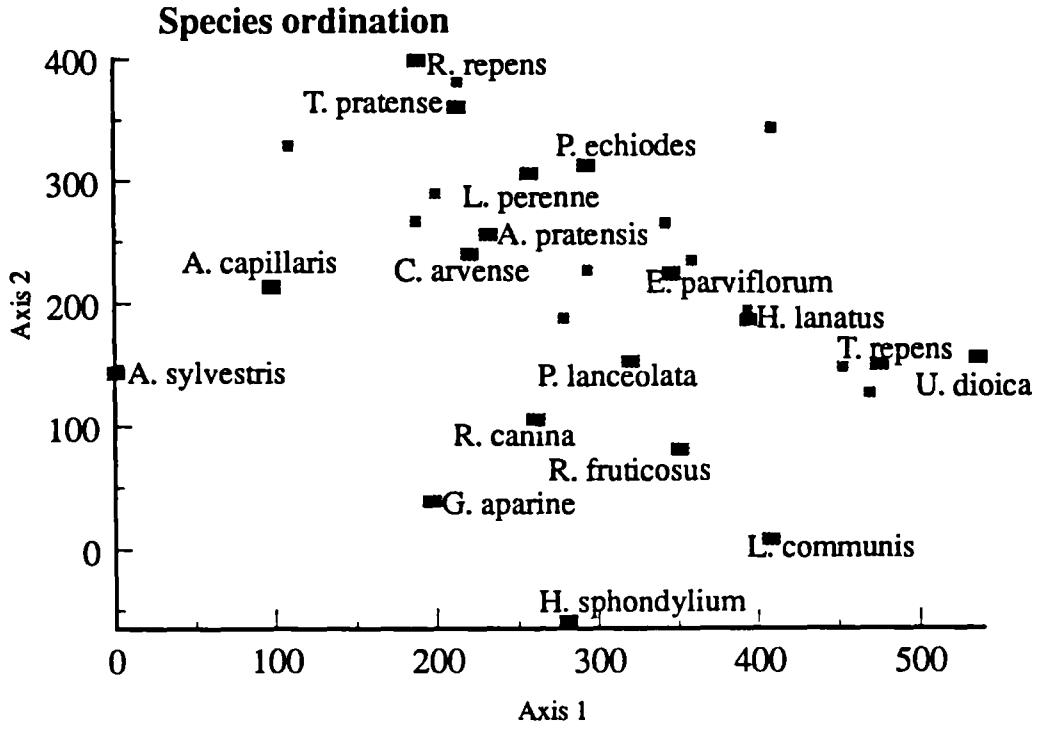
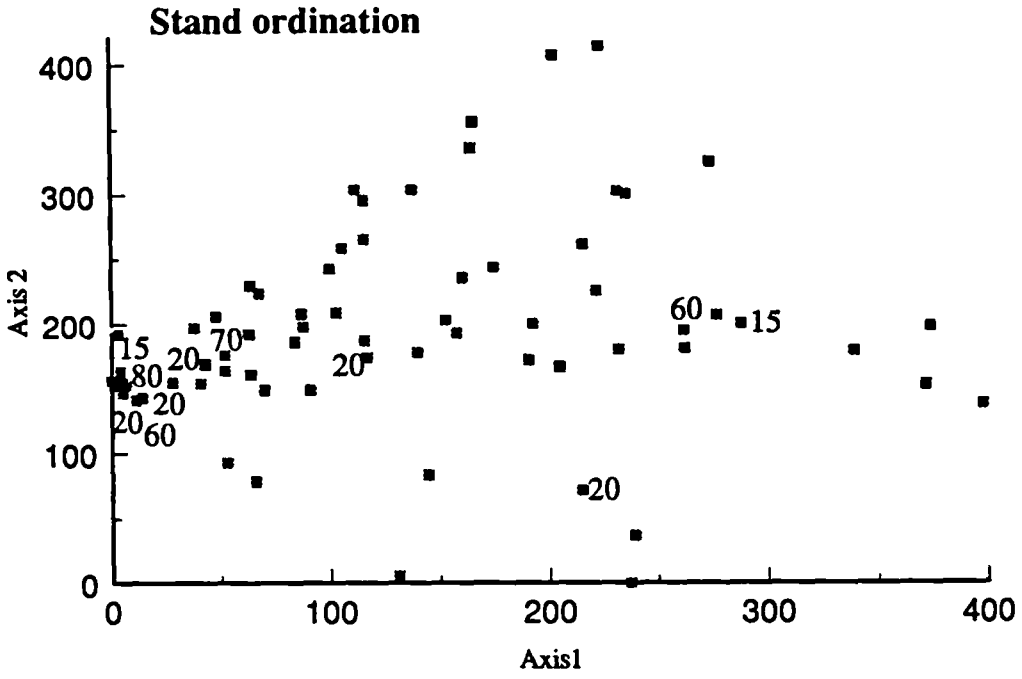


Fig. 13 *The relationship between the distribution of* S. dioica *and the DCA ordination of competing vegetation in High Sowing Density Mixture B plots.*



Numbers indicate % cover of A. petiolata, above 15%.

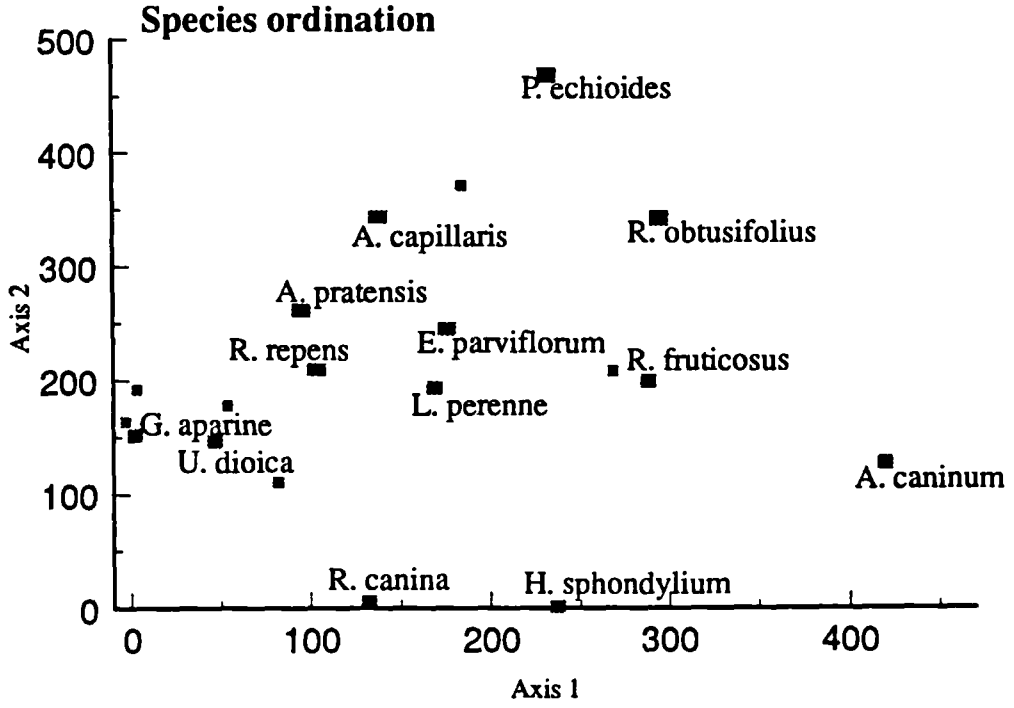


Fig. 14 *The relationship between the distribution of* A. petiolata *and the DCA ordination of competing vegetation in High Sowing Density Mixture A plots.*

petiolata indicates that this species was successful in areas where shade-tolerant species were situated, and particularly in places where species associated with good soil fertility, such as *G. aparine*, *U. dioica*, were located. *A. petiolata* was less successful in areas characterised by *A. capillaris* and *L. perenne*.

The distribution of high mean densities of *H. non-scripta* was found to be quite widespread over the scatter plots, but tended not to be in places where grass species were prevalent. A plot (not shown) of the mean densities of this species against percentage grass cover indicated that *H. non-scripta* was found mainly in quadrats with very low grass cover.

Although detailed analysis of the ordinations was carried out, and many scatter plots of species information were produced in an attempt to highlight trends in the performance and distribution of the introduced field layer species, no more trends were apparent, and only the few ordinations which show some kind of trend are presented.

3.5 Discussion.

3.5.1 The age structures of introduced field layer species populations.

The results presented in Figs. 4 and 5 show the different age structures that existed in 1991 within the populations of eight of the introduced field layer species. These are the populations present five years after the species were introduced into the plantations as seed. The species can be placed into three main groups, based upon the number of individuals present in age state 1, *i.e.* the seedling density. The groups are distinguished by whether seedling production has been high, moderate, or low or none. This criterion has been selected to group species, as it is the production of seedlings by the introduced species, *i.e.* their reproductive capacity, that gives an indication of species growth strategies and hence their capacity for establishment in an alien environment, as well as their ability to persist within this environment.

In the first group, *S. dioica*, *G. urbanum*, *T. japonica*, *A. petiolata*, and *G. mollugo* are all species which had a high number of individuals within age state 1, *i.e.* they had already produced high numbers of seedlings within the environment of the young plantations. (All of these species had produced an average of >20 seedlings m^{-2} by 1991.) All of these species, except *A. petiolata*, are iteroparous herbaceous perennials, (*i.e.* plants which reproduce more than once), for which the highest recorded age state represents individuals that were introduced as seed in 1987. These species generally flower in their second year, if conditions for germination and subsequent establishment are favourable. Only *S. dioica* is capable of flowering in the first season after germination (Grime *et al.* 1979) if conditions are suitable. With such knowledge of species' growth and establishment, flow diagrams can be compiled to describe the development of the 1991 populations. An example of this type of flow diagram is given given for *S. dioica* in Fig. 15.

The age structure for the *A. petiolata* population in 1991 was different from that of the other species, even though seedling density remained high. The density of individuals in age state 2 was lower than that in age state 3. *A. petiolata* is a biennial species, which generally exists as a seedling in its first year, and flowers in its second year, before dying (Cavers 1979). Age state 3 individuals are mature flowering plants. However, in the field, particularly in very shaded conditions, large rosettes of non-flowering individuals were recorded. These age state 2 plants were larger than young seedlings. Grime *et al.* (1979) describe *A. petiolata* as a winter-annual or a perennial, and clearly in some circumstances in the young plantations this species is exhibiting perennial behaviour. A flow diagram for *A. petiolata* is given in Fig. 16. This indicates that germination in this species may be staggered, as a long period of chilling is often required to break dormancy (Cavers 1979). It also illustrates the occurrence of non-flowering, vegetative plants, which may persist in shady areas.

All of the species which have their population structures dominated by seedling plants are woodland marginals. Reaching maturity quickly, they demonstrate a huge capacity for seedling production within the young plantations. These species were identified as a distinct group in Section 2.5.1.4.

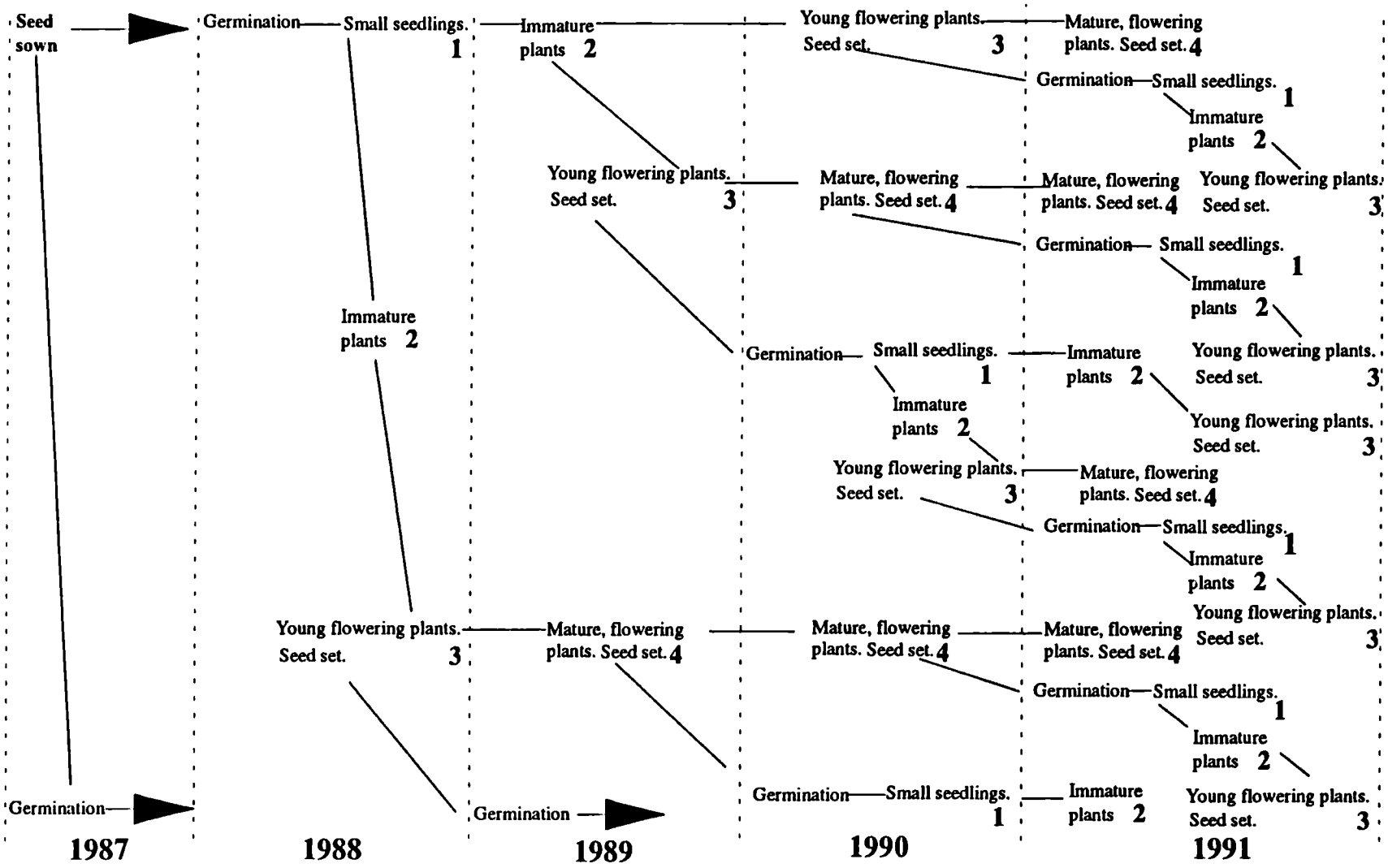


Fig. 15 *A flow digram for the growth and establishment of* Silene dioica. **(1, 2, 3, 4: *Correspond to age states.*)**

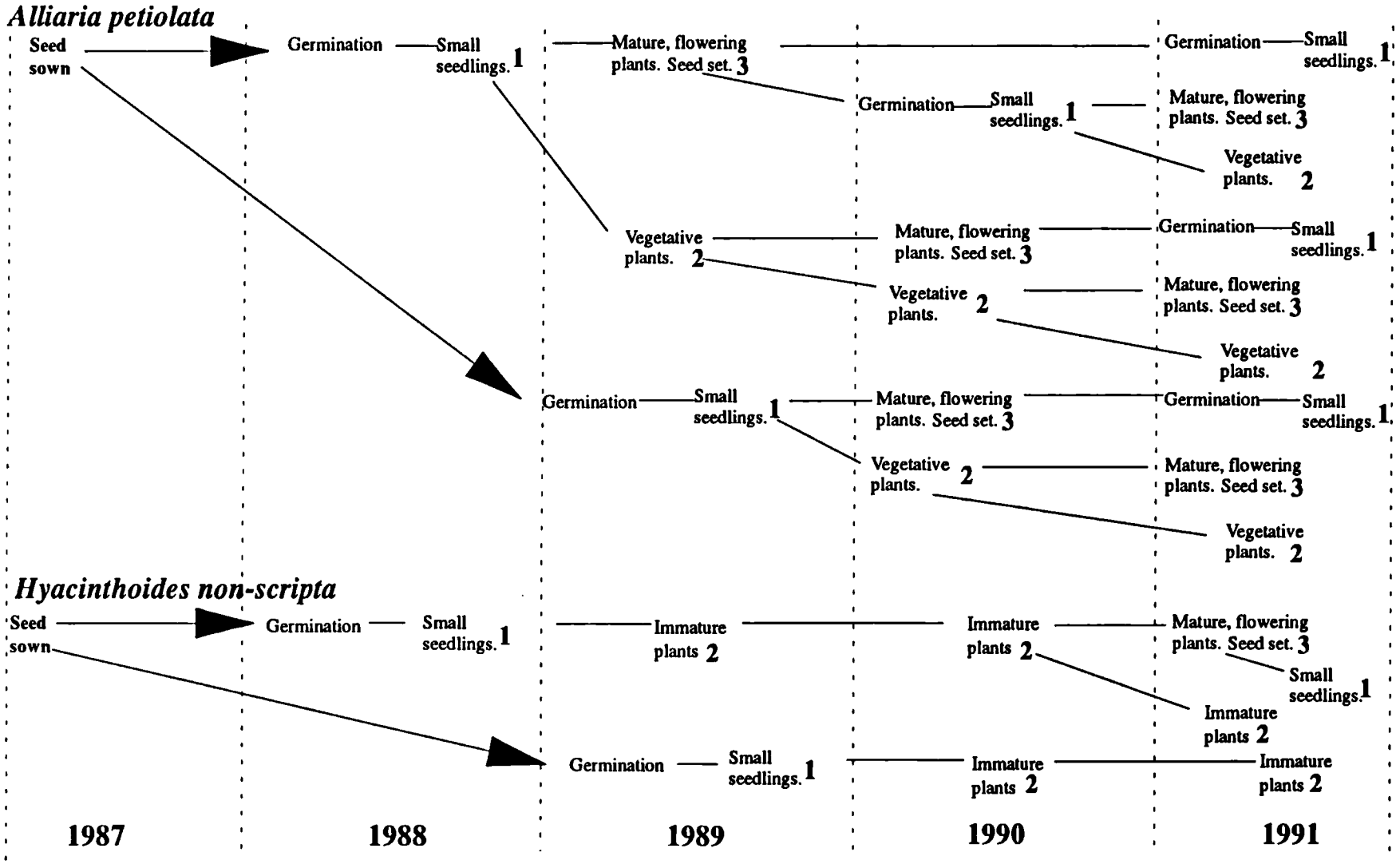


Fig. 16 *Flow diagrams for the growth and establishment of two woodland field layer species* **(1, 2, 3 : *Correspond to age states.*)**

In the second group of field layer species, with moderate seedling production, are *H. hirsutum* and *P. elatior*. Although seedling density was still higher than the number of individuals in other age classes for both of these species, seedlings were relatively less abundant than for those species with very high seedling production. Both *H. hirsutum* and *P. elatior* are also iteroparous herbaceous perennials, but are slower growing than the woodland marginal species. They are not as quick to reach reproductive age, and indeed do not usually do so until the third season. They also set fewer seeds and possibly have lower germination rates.

The final group of species consists of those with very few or no individuals in age class 1. This group includes *H. non-scripta*, for which an age structure is presented, as well as *G. odoratum* and *V. odorata*, two vegetatively spreading species which were described in terms of 'patches' (Fig. 11). These two species were found only in very low densities, but can be included in this group, as their growth until 1991 was predominantly vegetative, and little sexual reproduction occurred. Whilst *G. odoratum* and *V. odorata* both flowered in 1990, only a few of the *H. non-scripta* plants flowered in 1991. The age structure for *H. non-scripta* shows that all of the individuals recorded were immature, non-flowering plants in age state 2. A few young flowering individuals (age state 3) were observed in the field, which, by autumn 1991, had produced small numbers of seedlings (age state 1). This is shown in the flow diagram for the growth of *H. non-scripta* in Fig. 16.

The patches of the two vegetatively spreading species resulted from the original sowings, and increased in size each year with the addition of new shoots. These three species are shade-tolerant, long-lived woodland perennials. They were also identified as a separate group in Section 2.5.1.4. They are slow to establish, and reach flowering maturity only after a few years of vegetative growth.

The field layer species were therefore establishing within the plantations at different rates, which are particularly characterised by the differing amounts of seed production.

3.5.2 The influence of environmental factors upon the age structures of the woodland field layer species.

In an attempt to determine the influences upon the success of the introduced species, soil characteristics, light levels and components of competing vegetation were all carefully analysed throughout the young plantations.

3.5.2.1 The influence of soil characteristics on the growth of the field layer species.
The soil characteristics were found to be very similar throughout the young plantations. The small differences that were observed are considered insufficient to have a substantial impact upon the development of the populations of woodland field layer species. Although some woodland plants, *e.g. Mercurialis perennis* (Dog's Mercury), are known to have very specific requirements for soil nutrients and moisture (Martin 1968), it is suggested that the amount of soil variation found at Milton Keynes is unlikely to affect the introduced species.

The phosphate levels that were measured in the soil analysis were moderate, indicating average soil fertility. Also, vegetation growth was observed to be generally good in all areas of the young plantations, and in no areas did no plant growth occur. Soil nutrient levels within the plantations, though probably limiting, were considered to be sufficient to allow adequate growth of both the introduced field layer species and those that colonised naturally.

3.5.2.2 The influence of light on the growth of the field layer species.
An analysis of the relationship between the population age structures and % canopy cover (Figs. 9 and 10) was carried out to determine the effect of light levels in the plantations on species distribution. By ascertaining the location of the majority of individuals in each age state, trends were apparent. The field layer species can be grouped according to whether they were found predominantly in light conditions, shady conditions, or beneath a range of canopy covers.

The bar charts for *T. japonica*, *G. mollugo* and *H. hirsutum* show that these species were found mostly in lighter areas of the plantations, as the majority of individuals in

each age state are present in areas of low canopy cover. *T. japonica* and *G. mollugo* were found mainly in very open areas with only 0-24% canopy cover. Both species occur naturally in hedges, grassy areas and open woodland, and *T. japonica* is also found on roadsides (Clapham *et al.* 1962). In the plantations, swards of *T. japonica* seedlings were observed around mature plants in light areas where competition from other species was low. This annual species is clearly better suited to light areas of the plantations. Large spreading rosettes of *G. mollugo* were seen in similar conditions. Individuals of *H. hirsutum* were most prevalent beneath 25-49% canopy cover. This species is usually found in woods and damp grassland (Clapham *et al.* 1962), perhaps suggesting a slightly more shady natural habitat.

The majority of individuals of both *A. petiolata*, *H. non-scripta* and *P. elatior* were situated beneath 50-74% or 75-100% canopy cover, and hence were prevalent in the shadier areas of the young plantations. *A. petiolata* is described as "most frequent in lightly shaded habitats" where it grows avoiding "the vigour of more robust species" (Grime *et al.* 1979). It is suggested that when this species was first introduced into the plantations at a stage when competition was negligible, (due to the bare earth conditions), it may well have been successful in much lighter areas. As a biennial, or short-lived perennial, the majority of plants that resulted from the initial sowing would have flowered in their second year, set seed and died. By this time, competition from natural colonists had possibly increased sufficiently to reduce the success of the second generation seedlings. Thus the distribution of this species was then restricted to shady areas of the plantations.

H. non-scripta is a true woodland plant, which evades shady conditions with its vernal habit. It is a 'sun-plant' (Packham *et al.* 1992), which thrives in high light, but which grows within woodland to avoid disturbance and competition. Similar to *A. petiolata*, seedlings of *H. non-scripta* may have been present throughout the full range of light conditions when germination took place. However, this species is very slow growing, and establishes vegetatively for the first few years. Once again, as competition levels increased, particularly that of grass species, in the lighter areas of the plantations, the small seedlings of *H. non-scripta* will have been ousted by competition. Hence, its present distribution in the shadier areas of the plantations. A very small minority of

individuals did survive in areas of low % canopy cover and low competition. It is interesting to note that these plants were the first to produce flowers, and had clearly benefitted from the high light levels in such areas.

The distribution of *P. elatior* is less easy to explain, as this species showed some persistence in the higher light levels, but was mostly confined to shadier areas. The lack of seedlings in the lightest situations indicates that they may have been ousted by competition from the naturally colonising species. In age state 2, some young plants were present in such areas, but few persisted to become age state 3 individuals. By maturity, in age state 4, none were present again.

Both of the vegetatively spreading species, *G. odoratum* and *V. odorata*, were also found in shady areas with high % canopy cover. These are true woodland species, S-strategists (after Grime 1979), which avoid competition by tolerating deep shade. As with *H. non-scripta*, they could have germinated successfully in a range of light conditions, but would have soon been ousted by competition as they are very slow growing.

S. dioica and *G. urbanum* were both found growing beneath a range of % canopy cover. The bar charts show that whilst for *G. urbanum* the majority of individuals in each age state was in 0-24% canopy cover, and for *S. dioica* most individuals were found in shadier areas, growth of both species was well-represented in other conditions. *S. dioica* is naturally confined to lightly shaded situations, such as woodland, scrub and hedgerows, where the vigour of potential dominants is reduced by low light levels (Grime *et al.* 1979). However, whilst it can survive in a non-flowering condition in deep shade, it is most prominent during the open phase of the coppice cycle, and produces most flowers at woodland margins (Baker 1947). It therefore clearly benefits from increased light levels, when competition from other species is relatively low. Similarly, *G. urbanum* is naturally found in woodlands and hedgerows, where it tolerates shade again to avoid competition (Grime *et al.* 1979). However, "flowering and seed set are greatest in unshaded conditions" (Grime *et al.* 1979), and light is beneficial to this species if competition is low. Both of these species are winter-green perennials (Grime *et al.* 1979), which tolerate shade to avoid high competition levels, but that perform best when light levels are increased. In this way, they both exhibit a degree of morphological

plasticity. By increasing their leaf, stem and root production in areas of high light, they are able to ameliorate their foraging effort (Tilman 1988). In general, the size and height of these species appeared greater in light conditions. Also, both species are able to reach maturity more quickly and hence flower earlier in areas of high light. Plants that are morphologically plastic can increase their competitive abilities, provided there is no cost to such adjustments (Tilman 1988). These changes in growth and establishment rates, which are dependent on growing conditions, complicate the production of the flow diagrams that describe species growth. For example, the flow diagram for *S. dioica* shows that flowers can be produced in the same year as germination, or one or two years afterwards. This will depend to a large extent upon the amount of light that is available to the establishing plant, and the level of competition from other plant species.

It is suggested that at the start of the field trial, both species would have germinated throughout the site, and those plants in light situations would have been able to grow well in the absence of competition at that time. The recruitment of *S. dioica* is controlled primarily by germination and early growth, and depends heavily on the open or closed nature of the herb layer at a particular site (Matlack 1974). With the capacity to reach maturity quickly and to produce more seed, populations of both species would have developed rapidly in such conditions. Both species have demonstrated some similarites to 'r' strategists (Grime 1979), with their quick growth and high levels of seed production. Indeed, *S. dioica* has been described as possessing the 'weed' syndrome (Baker 1974). In contrast, their perennial nature has enabled persistence, and has given them an advantage in the early years over annuals and short-lived colonising species. The established strategy for *S. dioica* is C-S-R, whilst *G. urbanum* is described as intermediate between C-S-R and stress-tolerator (Grime *et al.* 1979). Both therefore have the ability to compete with other species, particularly if conditions are optimal for growth.

It is considered that the present distribution of both species is strongly dependent on their growth in the early years of the trial. Some plants have persisted in light areas of the plantations where they have benefitted from quick early growth, whereas others are found in semi-shade or deep shade, as they are able to tolerate these conditions.

The distributions of the established field layer species do appear to be influenced by the light levels within the plantations. There is already a tendency for these woodland species to predominate in shadier areas, where competition, particularly from grass species, is low. However, some, *e.g. T. japonica* and *G. mollugo*, still persist in light situations, as do others, *e.g. S. dioica* and *G. urbanum*, which have benefitted from high light levels early in their establishment.

3.5.2.3 The influence of competing vegetation on the growth of the field layer species.

An analysis of the composition of the components of competing vegetation which had naturally colonised the site, was carried out in an attempt to classify the growth and success of the introduced field layer species. It was thought that the composition of the competing species may have been such that the introduced species were associated with certain elements but not others. Alternatively, the introduced species may always have been found in association with the natural colonists, as plants in general grow in optimal conditions. Hence, whether introduced or naturally colonising, all may have grown in similar areas of the plantations. However, strong trends were not found, particularly within the growth of the competing species. These species did not fall into very distinctive groups when analysed with DCA, although with knowledge of species' distribution in the field, groups that grew in areas of shade or light could just be distinguished. No more definite groupings than this were found. Further, imposition of the introduced field layer species data on these weakly defined assemblages did not show any strong trends. This analysis did indicate, however, that species such as *S. dioica* and *G. urbanum* were associated with groups of both shade-tolerant and light-demanding species, whereas *A. petiolata* was successful in areas where shade-bearing colonists with high nutrient requirements grew.

In general, therefore, the analysis of the distribution of the introduced field layer species by studying that of the competing vegetation, was less successful than expected. It is possible that the chosen quadrat size was partly responsible for the lack of correlation between the growth of the introduced and naturally colonising species. There is an inherent link between quadrat size and spatial pattern within plant populations. Quadrat size affects both the detection and interpretation of patterns and associations between

plant species (Grieg-Smith 1983). In the present sampling, quadrat size may have been too small, so that species appear negatively correlated since two individuals cannot occupy the same space. Species such as *S. dioica* have formed quite extensive patches of plants (due to poor dispersal mechanisms). The $1m^2$ quadrats could easily have been filled entirely by such species, thus excluding others.

Other factors such as heterogeneity in the original sowing, the enormous variation in canopy species, the amounts and persistence of the leaf litter that they produce, site aspect and, importantly, disturbance must also have greatly influenced the development of the vegetation. However, it would have been both time consuming and difficult to measure such influences with any degree of accuracy, and hence this was not attempted.

The short time-scale of the present study is also a very possible reason for the lack of trends that were found in the species composition and areas of successful growth. Between 1943 and 1971, Tamm (1972a) carried out a very long-term study of some herbaceous plant species in Swedish meadows. Conclusions from his studies were that survival varies from species to species, survival within a species varies from site to site, and survival within a species at a particular site varies from time to time due to changing conditions. It is therefore unsurprising that the present study revealed few patterns to explain the growth and establishment of the field layer species.

Further explanations for the variability of the distribution and success of the field layer species will be discussed in Section 3.5.4.

3.5.3 The comparison of the growth and establishment of *S. dioica* and *G. urbanum.*

The similarities between the growth of these two woodland marginal species have already been mentioned in Section 3.5.2.2. They both require lightly-shaded conditions for growth away from competitive species, are able to reach maturity quickly, produce high numbers of seeds, relying little on vegetative reproduction, and are winter-green. The bar graphs in Fig. 12 show the establishment of the populations of these species over a three year period. For both species during 1991 and 1992, there was an

accumulation of individuals in age classes 2, 3 and 4, compared with a reduction in the number of individuals in age state 1. Thus, within a certain area, more plants became mature, whilst fewer seedlings were present. In spite of these similarities, differences in the establishment patterns of the two species are apparent. By 1992, a larger proportion of *G. urbanum* plants had reached maturity, whilst seedling density had been reduced. In contrast, whilst some *S. dioica* individuals had reached maturity, a high proportion of the population remained as seedling plants. Following the survival of the first cohort, *i.e.* those individuals that were seedlings in 1990, it is clear that there was a higher mortality rate for the *S. dioica* seedlings. Seedling numbers in the *S. dioica* population were higher than in the *G. urbanum* population, yet fewer individuals reached maturity. These high seedling densities have led to increased density dependent effects, with the survival rate for *S. dioica* lowered by intraspecific competition amongst seedlings. Further, it is suggested (Donelan & Thompson 1980) that *G. urbanum* is one of a group of shade-tolerant woodland herbs in which recruitment takes place mainly from a pool of slow-growing, shade-tolerant seedlings, as seeds are largely absent from the seed bank. Thus, the mortality rate of the *G. urbanum* seedlings would be expected to be lower than that for *S. dioica* seedlings.

3.5.4 The development of field layer vegetation within a young plantation.

The lack of strong trends that has emerged from studying both the populations of naturally colonising species and the introduced field layer species can probably be explained in much wider terms than merely incorrect quadrat size, site variation, or even the short time-scale of the study.

Primarily, the development of vegetation during the first five years must be considered. In 1987, the plantations consisted of young trees and 'bare-earth'. There was no field layer vegetation in existence as a result of previous management practices. Since this management regime has ceased, three groups of plant species have been able to colonise the sites. The first group consists of species that were present in the soil as seeds, buds, roots and other perennating organs, which have since been able to colonise the bare-earth. Secondly, other plants, whether aided by wind, animals and birds, or human

activities, have dispersed into the site from colonisation pools nearby. Finally, in addition to these naturally colonising species, the woodland field layer species that were deliberately introduced as seeds have germinated and established. Whilst the first two groups of naturally colonising species must have been extremely variable in terms of densities, time of arrival, persistence and establishment, the introduced species themselves, although seemingly 'controlled', will also have contributed to variation at the site. It is suggested that, even prior to the observed variation within the germination and establishment of these species, the initial sowing must have been extremely heterogeneous. The plots, which measured 4m x 24m, were sown by walking along the length of a plot a single time, and scattering seed by hand from a container. In some plots, it is quite noticeable that species have established predominantly within the middle two metres of the plot. This observation suggests that more seed fell around the sower in the centre of the plot, than reached the plot edges. Practical experience of large-scale sowings at other sites in Milton Keynes, has demonstrated that it is very difficult to distribute seed evenly. The existence of established trees and shrubs not only makes hand-sowing the only realistic method of seed introduction, but also greatly obstructs and hinders the progress of the sower. In this way, the sowing of the introduced species added to site heterogeneity.

As soil nutrients were not particularly limiting in the young plantations, all of these species, however they arrived at the site, have had the opportunity to grow and flourish. These early colonisers constitute the 'Initial Floristic Composition' (Egler 1954) of the site, and are important in the long-term development of the vegetation communities. Despite the large range of species present at the start of field layer vegetation development, there were still some bare patches present in the young plantations in 1991. These were sometimes due to shade, build up of leaf litter, or disturbance to the sites. It is evident that the field layer is at an early stage of development, and is still both dynamic and unstable. Indeed, it is considered that the developing vegetation within the young plantations is at a stage of early to mid secondary succession.

According to the theories of Tilman (1988), secondary succession is driven by transient dynamics, and by long term soil changes during which there is an accumulation of nitrogen in poor soils. The control of a successional sequence by transient dynamics

results in a period during vegetational development when many species compete within a habitat where nutrients are non-limiting. Transient dynamics, which often follow experimental manipulation or disturbance at a site, occur when different species within a population become dominant for short periods, only to be displaced by others. Such dynamics are influenced by maximal growth rates, allocation patterns and resource availability (Tilman 1988). The initial nutrient status of the soil is an important factor in succession, as it controls the relative importance of colonisation, transient dynamics, and further nutrient accumulation (Tilman 1988). Additionally, the more nutrient-rich a soil is at the start of secondary succession, the longer the transient dynamics dictate the successional development.

In this study, trees have been present from the beginning of the field layer development, which is clearly not usual in succession. However, it is considered that their influence upon the vegetational development has been limited mostly to their capacity to cast shade. This has allowed an increase in the diversity of the establishing vegetation, and has particularly encouraged the woodland field layer species to persist. With the knowledge that soil nutrients are not limiting, it is suggested that the crucial driving force of vegetational development within the young plantations is still that of transient dynamics, and, until shade increases further, this will continue. Also, it is thought that any disturbance or experimental manipulation that reduces plant densities, or otherwise increases the availability of resources within a site, usually leads to a successional sequence that is controlled by transient dynamics (Tilman 1988).

The source pool of species (including the introduced field layer species) that were potential colonisers of the plantations will have been a critical determinant of the successional dynamics of the sites. In particular, species can never become dominant if they cannot reach a site. Also, the dynamics of displacement between the competing species will have been strongly influenced by the maximal growth rates of the competing vegetative species. The initial dominants in the newly disturbed, low plant density habitat would have been species with rapid rates of growth. These early dominants would be displaced by species with lower maximal growth rates, which would be increasingly superior competitors for the conditions offered by the habitat. In some areas of the plantations it is envisaged that *A. petiolata* may have been dominant in the

early years, prior to its replacement by other species. In places, *S. dioica* and *G. urbanum* are now dominant, but it is possible that their numbers will yet be reduced in high light areas where grass swards have been able to flourish. Further, species such as *S. dioica*, whilst possessing considerable plasticity which enables the exploitation of a range of habitats, will not persist as tall herb species colonise and become established in open areas. As the trees provide more shade, the woodland perennials will be favoured, and the ruderal and competing vegetation components will be reduced. However, it will inevitably be some time before a stable, and more typical, woodland field layer community has developed.

3.5.5 Conclusions.

The study of the biotic and abiotic influences on the distribution and performance of the introduced field layer species within the young plantations may be considered rather inconclusive, as patterns were not forthcoming and trends were elusive, despite thorough analysis of the data. However, if other possible outcomes of the field layer introductions are considered, some very positive conclusions can be made. In the previous chapter, it was shown that the field layer species were present throughout the plantations at varying densities, as a result of their introduction by seed some years previously. It is possible that these plants may have survived for a while due to lack of competition, but then dwindled and perished. They may have shown few signs of establishment or persistence, especially once the huge influx of naturally colonising species became dominant. Despite the presence of trees, the species had, after all, been introduced into a habitat very early in its development. They would not normally have colonised until much later in the succession, once further canopy development had naturally reduced competition by increasing shade levels. Alternatively, a few plants may have survived in very shady areas with low competition, and demonstrated predominantly vegetative growth and no spread or establishment. In this respect, the results of this study are very encouraging, because, in spite of the lack of clear trends in the distribution of the vegetation, due to the probable governance of its development by transient dynamics and high small-scale heterogeneity, the field layer species are establishing and reproducing.

It has been shown that all 10 of the field layer species included in this part of the study have either produced seedlings or reproduced vegetatively during the last few years. Figure 6 shows that the field layer species were an important component of the vegetation community in 1991. Whilst *G. urbanum* and *S. dioica* were the most prevalent species, all of the other introduced species were present in a similar order of magnitude to those species which have colonised naturally. Some, *e.g. H. non-scripta*, *G. odoratum* and *V. odorata*, have exhibited slow, vegetative growth within niches which allow them to avoid competition from other species. Many *H. non-scripta* plants are now reaching maturity and, indeed, a few flowering plants set seed for the first time in 1991. The slow-growing vegetatively spreading species are also establishing well, and whilst they may have not produced many seeds or seedlings, they have spread to form sizeable patches. The woodland marginal species, *e.g. S. dioica* and *G. urbanum*, have matured rapidly, and have shown very high seed production. With fast maximal growth rates, they have grown as ruderals exploiting high light levels. By virtue of their morphological plasticity and perennial nature, they have demonstrated a competitive advantage over other species in places where they initially germinated in optimum conditions.

As the succession proceeds, and shade develops further, the development and establishment of the field layer species will continue. The inevitable reduction in competing vegetation, much of which will not be shade-tolerant, will enable the further establishment and proliferation of the field layer species. Many of these will have actually benefitted from the high light levels in the early years. It is considered that the woodland field layer species are not able to invade young plantations unaided, due to the barriers to colonisation and the competition from other species, as well as the isolation of such sites from old woodlands. This study has demonstrated that as a result of simple introduction techniques, species can establish successfully and persist within plantations.

4. The experimental introduction of ancient woodland field layer species into woodlands of different ages.

4.1. Introduction.

4.1.1. Factors controlling the growth of field layer species.

The field layer species in any woodland are influenced by many factors such as canopy species, soil type and site hydrology, but possibly the most important ecological factor that controls their growth is light. It is the maturity of the trees and the resulting density of the canopy that dictates the amount of light that reaches the woodland floor. Many researchers have considered woodland light conditions and some have measured the amount of photosynthetically active radiation (P.A.R.) that field layer species receive. The relationship between the amount of available light and the corresponding species composition of the field layer has also been investigated. Coombe (1966) found that mature broadleaved canopies can reduce light values at the ground to 10%, or less, of full daylight values in summer and noted that non-woodland flora were encouraged to develop in as little as 15-25% P.A.R. Hill (1979a), working in conifer plantations, suggested that the average minimum relative illumination for the growth of vascular plants was about 12-13%, although this fell as low as 6% underneath certain canopy species.

It is known that the truly shade-tolerant woodland plants, many of which are ancient woodland indicator species, can exist in light levels as low as 5% P.A.R (Crawford 1989). In many cases, these plants, which occur mainly inside woods, need some other feature of the woodland environment in addition to low light. Indeed, Rackham (1980) writes that "many plants do not require shade: they require freedom from grazing, ploughing and competition". It is for this reason that many are so closely associated with woodlands and have found niches where they can thrive in conditions that are undisturbed and relatively free from competition. For them, the woodland habitat is a refuge.

There are some woodland plants that grow better in shade than full light, *e.g. O. acetosella* (Packham 1978 and 1983), but the majority have developed strategies to enable them to survive in the very low light levels that exist in mature woodlands. Some are **shade-evaders**, or **vernal** species, which appear in early spring and grow and flower whilst the light is around 30-50% P.A.R. prior to canopy closure. In this way, species such as *A. nemorosa*, *Ranunculus ficaria* (Lesser Celandine) and *H. non-scripta* can utilise the absolute peak period for light beneath a temperate deciduous woodland canopy. Many vernal species are associated with the woodland coppice system and are particularly floriferous in the second spring after coppicing. Other species which are able to grow in deep shade are referred to as **shade-tolerators**. These can photosynthesise at very low light intensities when the canopy is in full leaf, *e.g. A. reptans*, *C. lutetiana*, and *R. fruticosus*. Some shade-tolerators are **winter-green**, or ever-green, including *Euphorbia amygdaloides* (Wood Spurge) and *V. odorata*, and have the opportunity to photosynthesise throughout the winter months as well as the summer. As a final adaptation to low light levels, some **shade-resistors**, *e.g. L. galeobdolon*, produce larger and thinner leaves in very shady conditions (Packham 1983), so that they may make optimum use of the limited light available. With these various strategies, ancient woodland field layer species are able to live in deep shade away from the disturbance and competition in which they would otherwise not survive. Some may grow vegetatively for long periods of time, but all receive enough light at some stage to flower and set seed.

4.1.2 Experimental objectives.

Because of the importance of the woodland light regime, the habitat creator who wishes to enhance a young woodland by introducing field layer species, is faced with a dilemma: whether to introduce species at any early stage and therefore manage sites accordingly, or whether to wait for many years in order for canopy closure to occur. The experiment described in this chapter is designed primarily to study the feasibility of introducing ancient woodland field layer species into habitats other than ancient woodlands. It encompasses a wide range of practical objectives to be tested in field situations. These are the timing of such introductions, the necessity of ground pre-

treatment, the method of species introduction and species choice. The results of such a study should aid habitat managers and farmers to enhance young woodland habitats with successful introductions of field layer species.

4.1.2.1 **The timing of introductions.**

The light conditions in woodlands are obviously critical to the growth and survival of the field layer species. It is because of this that the timing of any field layer introductions in relation to canopy closure is very important. To avoid competition from other plants, introductions could be made after the canopy is mature and light levels beneath have been reduced to less than about 12% P.A.R. In this way, the shade-tolerant species would survive and need little management. However, this option is unattractive to most urban habitat designers as the canopy often takes years to become mature and the waiting time is unacceptable. Most introductions are likely to be made at a considerably earlier stage, when light levels are still relatively high. It is possible that woodland species could thrive in such high light conditions, but *only with very intense management* which would be necessary to reduce the effect of competitors.

Another factor that will influence the growth of field layer species is the condition of the woodland soil. Ancient woodland field layer species grow in soils that are undisturbed and high in organic content. Many new woodlands, especially those on ex-agricultural land, will have soils that are highly disturbed and in some cases fertile, encouraging the growth of competitive ruderals. The timing of any introduction scheme will also be important from this consideration.

To test the timing of making introductions of field layer species, a range of woodlands of different ages were selected as experimental sites. They varied in age from a two year old urban woodland to an ancient copse which had been in existence for at least 400 years.

4.1.2.2 **Pre-treatment of sites.**

When a newly-planted woodland is establishing, it typically develops a very rough field layer, which is characterised by species such as brambles, nettles, cleavers and coarse grass species. If woodland field layer introductions are made prior to canopy closure,

it may be necessary to remove these robust and persistent weeds in order to reduce competition and allow the introduced species to survive. Foresters have long advocated the treatment of weeds around young trees with herbicides as a good practice which enables rapid tree establishment. This treatment is often only around the base of individual trees, but since there is an increasing requirement for managers to consider objectives other than just those of tree growth, different schemes for weed control have been developed. A bare earth policy, practised at Milton Keynes (described in Section 2.2.1), involves the regular application of herbicide throughout establishing plantations. Tree establishment is therefore encouraged and the pool of weed colonists at the site is substantially reduced. The site is prepared for the introduction of field layer species in this way and, since non-residual herbicides are used, the establishment of these should not be affected by the previous treatment.

Another method of weed supression is the use of mulch, in the form of wood chips, bark, mushroom compost or leaf litter. Baines & Smart (1984) suggested this to accompany the introduction of field layer species, although they did not test it experimentally. Some woodland field layer species, *e.g. H. non-scripta* and *L. galeobdolon*, have adapted to grow well in deep leaf litter and benefit from its presence (Salisbury 1916, Sydes & Grime 1981b). Cohn & Packham (1991) suggest that the differential ability of shoots of herbaceous species to penetrate dense leaf litter can be exploited to suppress competitors and to promote the growth of woodland herbs. In an experiment using different depths of oak leaf litter and seasoned woodchip, they found that by the second growing season the growth of *H. non-scripta*, *L. galeobdolon* and *O. acetosella* was better in litter and mulch plots than it was in control plots. They suggested that that the mulches partly reduced desiccation in the plots and encouraged stoloniferous herbs to 'forage' for suitable sites in which to root. In the same experiment, the growth of both *D. purpurea* and *S. dioica* was much reduced by the litter and mulch applications.

Whilst the use of mulch is more expensive and labour intensive than the application of herbicide, some local authorities may have large quantities of chipped tree thinnings at their disposal, or may be reluctant to repeatedly apply herbicide to control weeds. In situations where leaf litter has naturally built up beneath establishing trees, mulch is

unnecessary, as the litter itself will prevent weed seeds from germinating and will restrict the growth of potentially dominating grasses (Sydes & Grime 1981b). However, in very open situations with little leaf litter, mulch could be applied relatively easily and effectively suppress weed growth. This may be especially useful where there is a grass sward beneath young trees.

The existing vegetation in young plantations can also be reduced by cutting the competing herbaceous plants. This is a very simple treatment which produces a lower sward in which to sow or plant, and which reduces the potential vigour of the dominant plant species, at least in the short term.

It is anticipated that anyone wishing to introduce field layer species into woodlands, whether in an urban or farm situation, will treat the ground in some way to reduce competition from coarse and invasive weeds. This experiment described here was designed to consider the three options of herbicide, mulch and cutting, and to test the appropriateness of each for competition control. The field plots designated for the introduction trials were either treated with herbicide or were cut and merely hand-cleared of weeds prior to field layer species introduction. The application of herbicide was intended to represent policies which are commonly practised. The cutting of weeds, on control plots, tested the effect of minimal site pre-treatment. On sites where trees had been planted into grass, or where there was little build-up of leaf litter, mulch was also used as one of the pre-treatments. By measuring the survival and subsequent performance of the introduced species in the conditions that resulted from the various ground pre-treatments, the suitability of each was investigated.

4.1.2.3 Choice of introduction material: seeds *v* plants.

If a farmer or urban habitat manager decides to introduce field layer species into a woodland, the choice of whether to use seeds or plants as introduction material will have to be made. In the majority of large-scale schemes, *e.g.* the enhancement of newly planted woodlands in Milton Keynes, species are usually introduced as seeds, which are very easily distributed and relatively inexpensive. However, seeds can only be randomly or haphazardly positioned, high proportions may be wasted and the resulting plants of some species are slow to mature. Planting schemes, on the other hand, are extremely

costly and labour intensive, although they do allow exact positioning and more ready establishment of the field layer species.

The species that are more suited for being introduced as seeds are mostly light-demanding woodland edge species and those regularly found in the woodland seed bank. Many ancient woodland species, with which this project is particularly concerned, produce few seeds, have very poor, slow germination but are readily propagated vegetatively (Peterken 1974). It is therefore apt, and indeed possibly necessary, to introduce such species as plants if they are to survive. Futhermore, the time scale of this project was short and it was considered more beneficial to monitor the growth of plants, with their shorter establishment period, than that of species grown from seed. In other studies (Ellarson & Craven 1982, and Cohn & Packham 1991), woodland herbaceous perennials have been successfully established as plants into new areas.

4.1.2.4 Species choice.

With any introduction scheme, it can be argued that species choice should be limited to those regularly found in local woodlands, *i.e.* plants that are neither locally rare, nor from woodlands in other regions. Packham & Cohn (1990) stress that rarities should only be used in habitat creation schemes if there is to be no doubt in the future about their origin, as such species are important environmental indicators whose "indiscriminate planting could entail an important loss of information". For the experiment reported in this chapter, species were chosen from the English Nature South Region ancient woodland vascular plant list (refer to Appendix A), with reference to a local flora (Bowen 1968), although the choice was also governed by availability. Forbs with relatively attractive flowers were chosen for their public appeal, and some representative woodland grasses and sedges were also selected so that a wide range of woodland field layer components was involved.

4.1.3 The experimental work.

The main objective of the experiment detailed in this chapter, was to study the introduction of ancient woodland field layer species into woodlands of various ages. Six species chosen from the English Nature South Region ancient woodland vascular plant list were planted into five woodland sites, including a very recently planted copse, an establishing farm woodland and an ancient wood. At each site, four individual plots were fenced to eliminate grazing pressure, pre-treated, planted, and subsequently monitored.

The study was particularly concerned with the subsequent establishment and growth of the chosen species under the different conditions imposed upon them. The feasibility of making species introductions into woodland sites other than ancient woodland was tested. Information was gathered concerning the importance of the timing of any introduction scheme, and whether pre-treatment of a site is necessary. The effects of a variety of light and soil conditions upon the performance of the introduced species were of particular interest. The amount of associated field layer species, (*i.e.* those which occur naturally), at each site were monitored, and the effects of this 'competing vegetation' on the introduced species were assessed. It was also considered that by studying the behaviour and performance of ancient woodland species which had been planted outside their natural growing conditions, important ecological information could be gained.

4.2. Site details.

Details of the five experimental woodland sites are given below. These include the geology, size, tree species and age of the woodlands. The soil properties of the experimental sites are presented in Section 4.4.3.3.

4.2.1 New plantation, Domesday Copse, Bracknell, Berkshire. SU 862688

This is a truly urban plantation, situated between main roads, housing and industrial estates in the centre of Bracknell (Plate 15), which was initiated in 1989 to commemorate the thousand year anniversary of the Domesday Book. The intention of the Borough Council and Forest Ranger Service, was to attempt the creation of an "ancient woodland-type of urban copse with good public access" (Bracknell Forest Borough Council internal document 1989). The 0.5ha site, which is on Bagshot Beds, was previously an area of recreational grassland and has been mown regularly for many years. The western edge of the site is bordered by a remnant of a green lane. In November 1989, whips and standard trees were planted into the site at 2m spacings, with no pre-treatment given to the ground or grass sward.

The species and quantities planted were:

670 *Quercus robur* (Pedunculate Oak)
200 *Crataegus monogyna* (Hawthorn)
150 *Prunus spinosa* (Blackthorn)
100 *Fagus sylvatica* (Beech)
100 *Betula pendula* (Silver Birch)
50 *Fraxinus excelsior* (Ash)
50 *Sorbus aucuparia* (Rowan)
50 *Prunus avium* (Wild Cherry)
30 *Acer campestre* (Field Maple)
15 *Viburnum opulus* (Guelder Rose)
10 *Rosa canina* (Dog Rose)
10 *Ilex aquifolium* (Holly)
1 *Sorbus torminalis* (Wild Service-tree)

The site is very open and the planted trees have not established well. The existing field layer beneath the trees contains species representative of a neutral grassland. These include *L. perenne*, *Agrostis capillaris* (*A. tenuis*, Common Bent), *D. glomerata*, *Taraxacum* sect. *Ruderalia* (*T. officinale*, Dandelion), *Bellis perennis* (Daisy), *Ranunculus repens* (Creeping Buttercup), *Cerastium arvense* (Field Mouse-ear) and *Tripleurospermum inodorum* (Scentless Mayweed).



Plate.15 *Domesday Copse, Bracknell: the new urban plantation, 1990.*



Plate.16 *The young farm woodland belt at Woolley Firs, Burchett's Green, 1990.*

4.2.2 Young farm woodland, Woolley Firs, Burchetts Green, Berkshire. SU 855794

These narrow strips of woodland (Plate 16), between 10m and 15m in width, are situated on Upper Chalk. They were planted into arable fields in 1982, both to straighten up the field edges and to create shelter belts. Funded by the Woodland Grant Scheme, the tree species, planted at 2m spacings, include *Q. robur*, *F. excelsior*, *B. pendula*, *A. campestre* and *F. sylvatica*. Establishment has been good and the trees cast a significant amount of shade when they are in full leaf. The existing field layer is characterised by *A. sylvestris*, *H. sphondylium*, *U. dioica* and coarse grasses, particularly *Elytrigia repens* (*Elymus repens* ssp. *repens*, *Agropyron repens*, Common Couch).

4.2.3 Young forest at Holiday's Plain, Windsor Park, Berkshire. SU 923745

This 5.3ha forest block on London Clay was originally planted with *Picea sitchensis* (Sitka Spruce), and much smaller numbers of *Q. robur* and *F. sylvatica* in 1927. It was underplanted with *Q. robur* between 1959 and 1961. The *P. sitchensis* were subsequently felled in 1963. After some thinning, the young *Q. robur* are now at approximately 3m spacings, and in mid-summer, light levels beneath the trees are 5-7% of full daylight (Plate 17). The existing field layer is poor, and consists of *R. fruticosus*, *Lonicera periclymenum* (Honeysuckle), *Deschampsia flexuosa* (Wavy Hair-grass), *Dryopteris dilatata* (Broad Buckler-fern) and *Rhododendron ponticum* (Rhododendron). In September 1990, before the field layer introductions were made, trees within and around the plots were thinned to create light levels of 10-15%.

4.2.4 Mature Forest, High Standing Hill, Windsor Park, Berkshire. SU 924752

Previously old semi-natural woodland, this 2.0ha forest block on London Clay was planted in 1935 with *Q. robur*, *F. sylvatica*, *F. excelsior* and *Larix decidua* (European Larch) (Plate 18). The majority of the *L. decidua* were removed between 1958 and 1962, and only very few remain. The canopy is mature, with some gaps due to tree death, and light reaching the woodland floor in summer is about 8% of full daylight. The existing



Plate.17 *A young forest plot in Windsor Forest, 1990.*



Plate.18 *A mature forest plot in Windsor Forest, 1990.*

field layer is characterised by *R. fruticosus*, *Carex remota* (Remote Sedge), *L. periclymenum*, *Holcus mollis* (Creeping soft-grass), *R. canina* and seedlings from the regeneration of tree species such as *F. excelsior* and *P. avium*. In addition, there are small remnants of the previous woodland field layer, including *O. acetosella* and *E. amygdaloides*.

4.2.5 Ancient woodland, West's Copse, Winkfield, Berkshire. SU 893741

This is a small copse of just under 2ha, which is situated on London Clay. It consists of old *F. excelsior* and *C. avellana* coppice with *Q. robur* standards (Plate 19). Whilst the field layer is dominated by *M. perennis*, *H. non-scripta* and *R. fruticosus*, many species present are on the English Nature South Region ancient woodland vascular plant list and are indicative of the ancient nature of the woodland. These include *Orchis mascula* (Early-purple Orchid), *Ranunculus auricomus* (Goldilocks Buttercup), and *Moehringia trinervia* (Three-nerved Sandwort). Canopy and shrub species that indicate longevity are *Malus sylvestris* (Crab Apple), *A. campestre*, *V. opulus* and *S. torminalis*. These particular canopy and field layer species indicate that the copse is ancient and possibly about 400 years old, or more.

4.3 Materials and methods.

4.3.1 The propagation of the field layer species.

4.3.1.1 The main introduction experiment.

The plant species chosen for the main introduction experiment were:

Forbs:

Circaea lutetiana (Enchanter's-nightshade)

Lamiastrum galeobdolon (Yellow Archangel)

Primula vulgaris (Primrose)



Plate.19 *An ancient copse plot, West's Copse, Winkfield, 1990.*



Plate.20 *The young farm woodland herbicided plot, after planting in spring 1991.*

Grasses and sedge:

Bromopsis ramosa (Hairy-brome)

Festuca gigantea (Giant Fescue)

Carex sylvatica (Wood-sedge)

In March 1990, large clumps of *B. ramosa* and *F. gigantea* were collected from beside Chawridge Bourne, Winkfield, and *C. sylvatica* plants were removed from Cheriton Wood, Hampshire (SU 608295). All three species were split into small propagative units, consisting of 1 or 2 tillers. About 700 of each of these were potted into a multi-purpose compost. These were kept in a semi-shaded position during the summer months and flowering tillers were removed as they appeared.

About 700 plants of *L. galeobdolon* and *C. lutetiana* were vegetatively propagated from stock plants at ITE, Monks Wood in April 1990, and *P. vulgaris* was grown from seed in 1989. The plants of *P. vulgaris* and *C. lutetiana* were bedded in leaf mulch in a semi-shaded position at Silwood Park, Berkshire during the summer. All plants were fed with liquid fertiliser in August 1990.

4.3.1.2 **The screening experiment.**

Additional species, of which only small quantities could be obtained, were used for a small-scale screening exercise. These were *A. nemorosa*, *C. majus*, *E. amygdaloides*, *O. acetosella*, *Scrophularia nodosa* (Common Figwort), and *Veronica montana* (Wood Speedwell).

Clumps of *E. amygdaloides* and *O. acetosella* were collected from Cheriton Wood, Hampshire, and *C. majus* was collected from Charlwood Farm, Hampshire (SU 676319). Eighty plants of each of these, along with 60 plants of each of *A. nemorosa*, *S. nodosa* and *V. montana*, (which were bought bare-rooted from Old Hall Wildflowers, Warrington), were potted into multi-purpose compost and kept near the plants for the main experiment.

All plants, except for *A. nemorosa* and *C. majus* (which had died back), were fed with liquid fertiliser in August 1990.

4.3.2 The preparation of the field plots.

At each of the five field sites, experimental plots of 10m x 5m were positioned in areas that were considered to be representative of the site, though away from edges of wooded sites to avoid the effects of increased light. Four plots were appointed in each of the two forest sites and in the ancient copse, two plots in the farm woodland, and six plots in the urban copse, making a total of twenty plots. All of the plots in existing woodland were fenced to prevent grazing by rabbits and deer, whilst those at the new urban copse were left unfenced to attract less public attention. There was no evidence of grazing at the urban site. In summer 1990, two plots in each of four sites and one plot in the farm woodland were treated with ' Round-up', a glyphosate-based herbicide manufactured by Monsanto, at a rate of 1 part herbicide to 200 parts water. The other plots (control plots) were hand-cleared of weeds. A strimmer was used to reduce sward height in the new plantation and farm woodland, and the existing field layer was removed by hand at the other three sites. At the new urban plantation, an additional two plots were marked out and, after strimming, were covered with a layer of mulch to a depth of approximately 10 cm. This was supplied by Bracknell Forest Borough Council and was produced from tree thinnings.

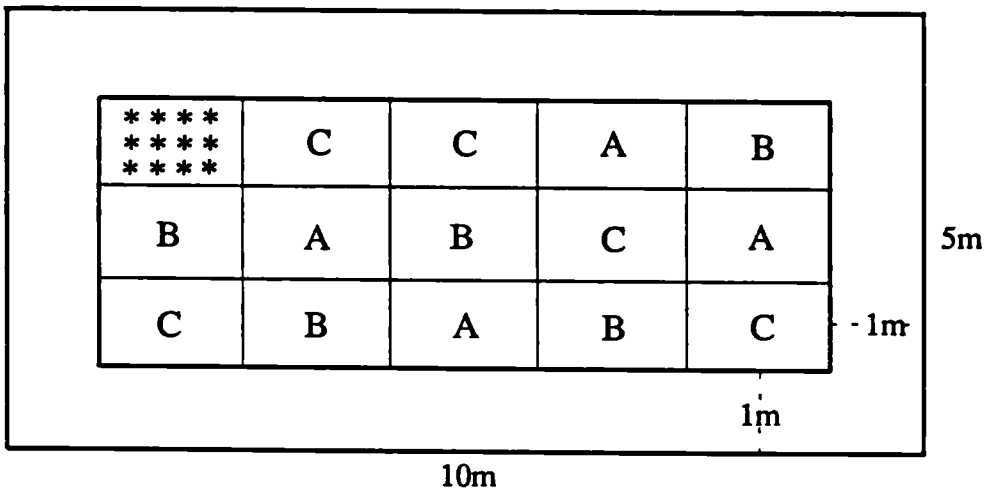
4.3.3 The design of the field plots.

Figure 17 is a diagram of a field plot with the planting grid. In each of the 10m x 5m plots, the first metre inside the fence was unplanted. This was to allow access to the planted area for monitoring purposes, and to be a deterrent to grazing deer. In each plot, 60 plants of each of three species were planted in a randomised block design. For each species, this allowed five blocks of 12 individual plants at 30cm spacings.

4.3.4 The planting of the field plots.

Most of the preparations for planting had been completed by May 1990, but the planting was postponed until Winter 1990/1991 to avoid the predicted summer drought, during

which it was considered that the newly introduced species would not survive. The 12 woodland field layer species were planted between mid February and mid March 1991, during a period of suitable weather conditions, with considerable rain. Plate 20 shows the farm woodland herbicide plot after planting in March 1991.



A, B, C, Planting blocks of different species.
* Individual planting positions. (Shown for one block only).

Fig. 17 *Representation of a field plot with planting grid.*

4.3.4.1 **The main introduction experiment.**

At each site except the farm woodland, half the plots were planted with the three forb species (*C. lutetiana*, *L. galeobdolon* and *P. vulgaris*), and the others were planted with the sedge and grass species (*B. ramosa*, *C. sylvatica* and *F. gigantea*). At the farm woodland site, only the forbs were planted, as space for plots was limited. Twenty plots were therefore planted in all, making a total of 3,600 introduced field layer plants in the main experiment.

4.3.4.2 **The screening experiment.**

Sixty of each of the six additional field layer species were planted within the metre just inside the plot boundaries at the new plantation and young forest sites. For each species, five groups of 12 individuals were planted, three groups into the herbicided, mulch and control plots at the new plantation, and two groups into the herbicided and control plots at the young forest site.

4.3.5 The monitoring of the field plots.

4.3.5.1 The monitoring of the field layer species in the main experiment.

The 1991 monitoring.

The initial monitoring of the introduced plants was designed to record their establishment success. In August 1991, the presence or absence of every individual plant was recorded to indicate the initial percentage survival of each species. Some features of plant growth, such as stolon length of *L. galeobdolon* and maximum height of *C. lutetiana*, were measured and recorded.

The 1992 monitoring. The presence or absence of each individual plant was again recorded to indicate the percentage survival after a second growing season. To quantify species establishment success, records were made of performance characteristics. These characteristics varied between the chosen field layer species so the monitoring of each species is described separately.

Bromopsis ramosa. By summer 1992, only three plants remained, so there was no further monitoring.

Carex sylvatica and ***Festuca gigantea.*** In July, maximum leaf length (from stem to leaf tip) was measured for 30 plants per plot, for both species. The number of vegetative shoots, and the number of flowering tillers on each individual plant were counted.

Circaea lutetiana. By June, it was difficult to distinguish the individual plants of *C. lutetiana*, and so the number of shoots was counted in each original block of 12 plants. The number of leaves per shoot was counted and the maximum leaf lengths (leaf blade plus petiole) were measured for 30 plants in each plot.

Lamiastrum galeobdolon. In June, the number of vegetative shoots (stolons) and the number of flowering shoots were counted and recorded for each surviving individual plant. Maximum stolon lengths and maximum leaf lengths (leaf blade plus petiole) were measured and recorded for 30 plants in each plot in late August.

Primula vulgaris. In March, the number of flowers and the number of leaves were counted and recorded on each individual plant. Maximum leaf lengths were measured for 30 plants per plot.

The monitoring described for each of the five surviving field layer species was carried out in every treatment plot at all five sites.

4.3.5.2 The monitoring of the field layer species in the screening experiment.

The 1991 monitoring.

In May, the presence or absence of each individual plant was recorded to indicate the survival for each species.

The 1992 monitoring.

In May, the presence or absence of each individual plant was again recorded for each of the six species, to indicate survival after another growing season. Features such as flower production, seed set and vegetative spread were noted for each species at each site.

4.3.5.3 The monitoring of competing vegetation.

In order to characterise the competing vegetation in terms of the percentage cover of grass and broadleaved species, 200 regularly spaced point quadrats were recorded in each of the 20 field plots in July 1992. The number of touches made by any grass species, broadleaved species and the introduced field layer species were recorded.

4.3.5.4 The measurement of daylight.

Once the tree canopies in the woodland sites were fully developed in mid to late summer, the average percentage daylight at each plot was measured on overcast days using a two-cell EEL photometer. At 30 random points within the plot, one cell was placed just above the field layer vegetaton and the other was placed outside the woodland in full daylight. From the readings obtained, the mean percentage daylight was calculated for each of the 20 field plots.

4.3.5.5 The characterisation and analysis of soils.

At each of the five field sites, four replicate soil cores, which were 10cm in length and 3cm in diameter, were taken at six randomly selected positions near the experimental plots, a few days after heavy rainfall in May. Each set of cores was placed into bags, labelled and weighed. A proportion of each sample was dried at 30°C for two days and then sieved through a 2mm sieve to remove stones, roots and leaves. Each of the six soil samples from the five field sites were then analysed as described below.

The determination of soil moisture.

Between 10-20g of fresh soil was weighed into a dry dish. This was placed into an oven at 105°C and dried to a constant weight. It was then cooled in a desiccator and reweighed. The percentage fresh moisture was calculated from the recorded loss in weight. This procedure was repeated for another set of soil samples which were collected in early September.

The determination of percentage organic matter.

About 1g of dry, sieved soil was placed into a dry crucible. This was placed in a muffle furnace, the temperature of which rose to 550°C and remained there for at least two hours. When cool enough to handle, the samples were transferred to a desiccator, cooled and reweighed. The percentage loss on ignition was calculated from the weight lost during the combustion process.

The determination of soil pH.

An Electronic Instruments pH/Temperature meter was set up according to the manufacturers' instructions. The meter was calibrated against two buffer solutions of pH 4 and pH 7. A 50ml beaker was half filled with fresh soil, and then filled with distilled water. The soil and water mixture was stirred, and then shaken for 30 minutes. An electrode was then immersed into the mixture, swirled gently and the resulting pH was recorded. Electrodes were rinsed between readings.

The mechanical analysis of soil.

200ml of distilled water and 15ml of saturated sodium oxalate solution were added to a weighed amount (about 50g) of dry, sieved soil in an 800ml beaker. This was allowed

to stand overnight and then dispersed for 30 minutes with an electrical stirrer and baffle. The soil suspension was then transferred to a 1000ml measuring cylinder, diluted to 1000ml with distilled water, and shaken thoroughly. After about 4 minutes, a Boyoucos soil hydrometer was carefully lowered into the suspension in order to obtain a reading at exactly 5 minutes of silt + clay as g l^{-1}. The suspension was then reshaken, and after 5 hours the procedure was repeated to obtain the amount of clay g l^{-1} alone. The amount of sand in the soil was then calculated by difference. At the time of both readings, the temperature was recorded. As a temperature correction, 0.3g l^{-1} were added to the hydrometer readings for each degree above 19.4°C, or subtracted for temperatures below 19.4°C.

The determination of extractable phosphate.

0.25g of dry, sieved soil were accurately weighed into a glass bottle to which 50ml of Truog's reagent (Allen 1974) were added. The mixture was shaken for 30 minutes on a rotary shaker, and then filtered through Whatman no.44 paper. 25ml of the filtrate of each sample was taken for analysis. At the same time, 0-15ml of working standard (1M Potassium phosphate solution) were pipetted into 50ml volumetric flasks. The volumes were made up to 50ml to give a standard range from 0-0.3mg Phosphate. Both the standards and samples were then treated in the same way. The samples were passed through a Technicon Auto Analyser, Model AA1. Within this process, a 0.1% aqueous solution of ascorbic acid and a 0.2% solution of ammonium molybdate dissolved in 4% sulphuric acid were automatically added to the sample in the correct proportions. The solution was then mixed thoroughly in two mixing coils, and was passed through a heating bath at 90°C. The absorbance of the solution was then measured at 660nm, using a colorimeter (Allen 1974).

4.3.6 **The data analysis.**

4.3.6.1 **The main introduction experiment.**

The survival of the introduced species.

From the 1991 and 1992 field data, the percentage survival was calculated for each species at each site. For the 1992 data, the number of individual plants that survived

within each plot was analysed using the survival data for each block of 12 plants, of which there are five replicates for each species in each plot (Fig. 17). Using the replicated block data, Student's t-tests were carried out on the mean block survival value in each plot (P <0.05). The half-lives of each species, *i.e.* the time taken for the population of each species to fall to 50% of the number that was originally planted, was calculated over the two year period of the experiment.

The performance of the introduced species.

For each set of data, (*e.g.* the number of flowers per plant for *P. vulgaris*), a two-way analysis of variance (ANOVA) was carried out using the mean values for each block of 12 plants. The two-way ANOVAs indicated whether the variance in the data set arose from site or treatment effects. F values for each data set are presented in Appendix B.

From the mean values for each block of 12 plants, of which there were five replicates in each plot, plot means and their corresponding 95% Confidence Intervals were calculated using the appropriate value of t at P= 0.05. Means were then compared both within treatments and within sites. An assumption was made that the data sets approximated to a normal distribution. This is considered to be appropriate because means and sample sizes were mostly high. The graphs presented for each species, Figs. C to G, indicate plot means and 95% Confidence Intervals. The bars are annotated with letters which indicate significant differences between the means.

4.3.6.2 **The competing vegetative species.**

From the 200 point quadrats taken in each plot, % cover values were calculated for grass and broadleaved species.

4.4 Results.

4.4.1 The survival of the introduced field layer species in 1991 and 1992.

4.4.1.1 Survival of species in the main introduction experiment.

Table 16 shows the total percentage survival of the field layer species in each of the five experimental sites. By August 1991, some 6 months after planting, the majority of plants of five of the introduced species had survived. The exception to this was *B. ramosa*, in which some 491 individuals out of the 540 that were planted had already died, leaving only 9.1% surviving. Within the first six months after planting, all individuals of this species died in the new plantation. Numbers declined further by July 1992, when only three individual plants were counted throughout the five sites. This is illustrated in Fig. 18. *B. ramosa* had therefore failed to survive, and is not considered in any further analysis.

A total of 94.4% of the *C. sylvatica* plants survived the first six months of introduction into the experimental sites. The lowest recorded percentage survival in August 1991 was 85% in the new plantation. By summer 1992, very similar percentage survival rates were recorded at the young and mature forest sites, whilst percentage survival decreased at at the new plantation and ancient copse, to 55.6% and 46.7% respectively. These survival figures are also substantially lower than those recorded at the same sites in the previous year.

The percentage survival of *F. gigantea* during 1991 and 1992 was similar to that of *C. sylvatica*. In 1991, survival rates were high at all sites except in the new plantation. By 1992, the percentage survival at both the young and mature forest sites was still high, whilst at the new plantation and ancient copse survival had decreased to 27.8% and 68.3% respectively. These figures are considerably lower than the percentage survival recorded at these sites in the previous year.

In 1991, high percentage survival values were recorded for *C. lutetiana* at all five sites. The lowest survival rate was 83.3% at the new plantation. In the ancient copse, all individuals planted in March had survived to August of the same year. By 1992, the

Table 16. *% Survival of ancient woodland field layer species introduced into different woodland sites.*

SPECIES	SITE	NUMBER PLANTED 1991	% SURVIVAL 1991	1992
Bromopsis ramosa	New plantation	180	0	0
	Farm woodland	0	-	-
	Young forest	120	20.0	1.7
	Mature forest	120	10.0	0.8
	Ancient copse	120	19.2	0
TOTAL		**540**	**9.1**	**0.6**
Carex sylvatica	New plantation	180	85.0	55.6
	Farm woodland	0	-	-
	Young forest	120	99.2	94.2
	Mature forest	120	100	96.6
	Ancient copse	120	98.3	46.7
TOTAL		**540**	**94.4**	**71.3**
Circaea lutetiana	New plantation	180	83.3	65.5
	Farm woodland	120	85.0	82.5
	Young forest	120	99.2	99.2
	Mature forest	120	98.3	98.3
	Ancient copse	120	100	100
TOTAL		**660**	**92.3**	**85.5**
Festuca gigantea	New plantation	180	62.8	27.8
	Farm woodland	0	-	-
	Young forest	120	99.2	95.8
	Mature forest	120	99.2	92.5
	Ancient copse	120	98.3	68.3
TOTAL		**540**	**86.9**	**66.3**
Lamiastrum galeobdolon	New plantation	180	78.3	77.2
	Farm woodland	120	98.3	97.5
	Young forest	120	96.6	95.8
	Mature forest	120	96.6	96.6
	Ancient copse	120	97.5	90.8
TOTAL		**660**	**92.1**	**90**
Primula vulgaris	New plantation	180	88.3	91.7
	Farm woodland	120	87.5	83.3
	Young forest	120	88.3	87.5
	Mature forest	120	96.6	96.6
	Ancient copse	120	97.5	90.8
TOTAL		**660**	**89.1**	**90.2**

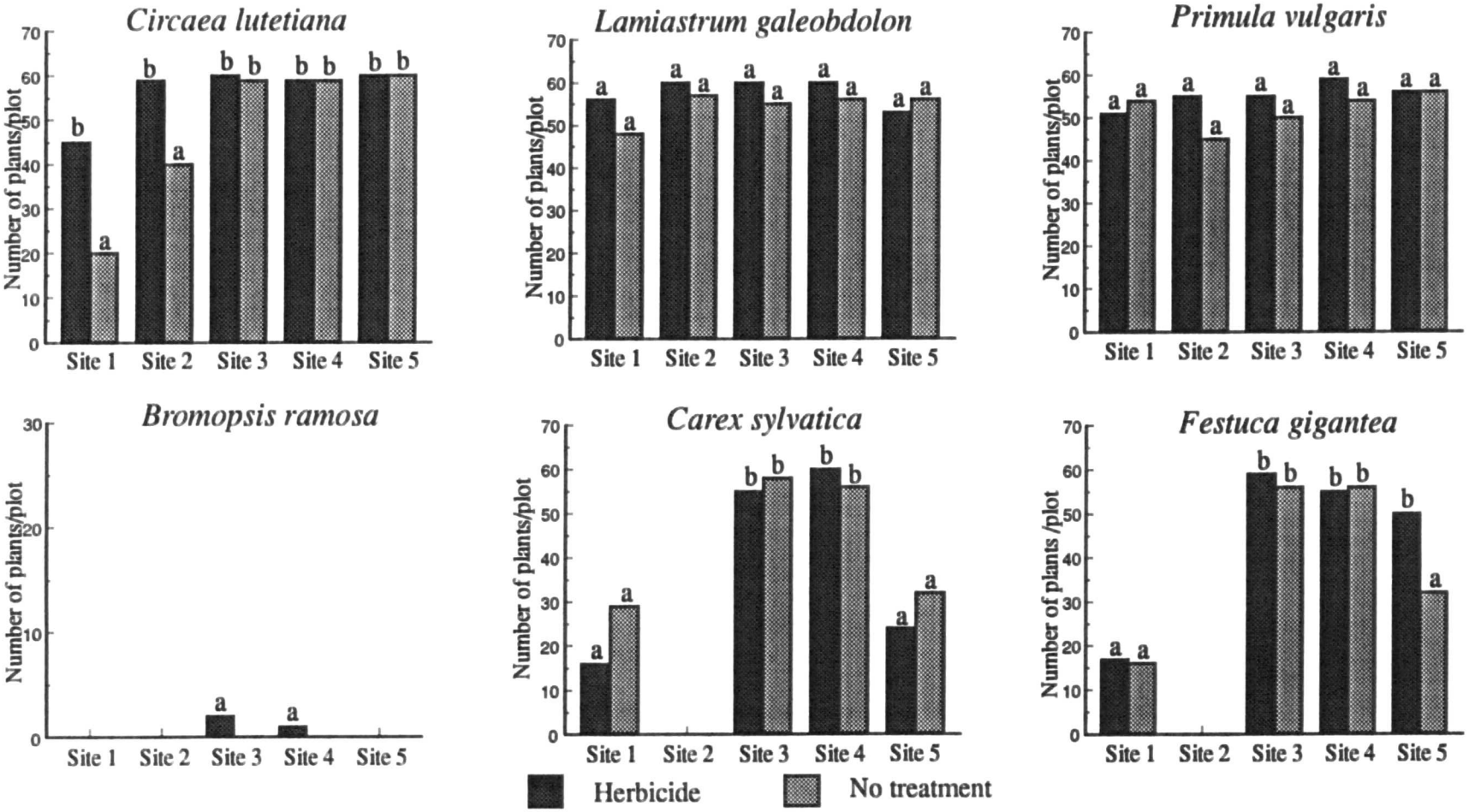
the number of individuals recorded was similar at all sites except in the new plantation. Here, the number of plants had decreased to 118, a survival of 65.5%. This is considerably lower than the percentage survival recorded at the site in the previous year.

For *L. galeobdolon*, the percentage survival rates at all sites in both years were generally high. The only exception to this is the percentage survival of *L. galeobdolon* in the new plantation. Here, 78.3% of individuals were recorded in 1991 and 77.2% in 1992. Whilst the slight decrease in survival from year to year is insignificant, the survival at the new plantation was considerably less than that for this species at all other sites.

The survival of *P. vulgaris* was also high in both years at all of the experimental sites. The total survival rate of 90.2% is the highest recorded for all the introduced species. The lowest survival rate for *P. vulgaris* was 83.3% in the farm woodland. At the new plantation, the survival rose from 88.3% in 1991 to 91.7% in 1992, representing six individual plants which were not found in 1991.

The bar graphs in Fig. 18 represent the survival in 1992 of the six field layer species that were introduced into woodlands of different ages in herbicided and non-herbicided plots. The non-herbicided plots will be referred to as control plots. The bar graphs show the total number of plants that survived in each plot, out of 60 that were originally planted. The bars are annotated with letters which indicate the results of t-tests carried out on the pairs of means. No plants of *B. ramosa*, *C. sylvatica*, or *F. gigantea* were introduced into the farm woodland site.

For *C. sylvatica*, the survival at the young and mature forest sites was high and was not significantly different between herbicided and control plots. Survival was reduced both in the new plantation and in the ancient copse. In the ancient copse, the survival was not significantly different between the two treatments, but was significantly lower than that at the young and mature forest sites for both treatments. In the new plantation the recorded number of individuals in the herbicided plot was only 16 out of 60 original plants. This was not significantly lower than the 29 plants surviving in the control plot, but was significantly lower than the survival in the mulched plot, where 55 individuals were recorded in 1992.



Site 1: New plantation. Site 2: Farm woodland. Site 3: Young forest. Site 4: Mature forest. Site 5: Ancient copse.

Fig. 18 *The survival in 1992 of ancient woodland field layer species introduced into woodlands of different ages.*

60 plants of each species were planted into each plot in spring 1991.

a,b indicate significant differences at $P<0.05$. (t-tests).

The number of individuals recorded for *F. gigantea* also showed high survival in the young and mature forest sites, and reduced survival in the new plantation and ancient copse. In the ancient copse the 50 plants which survived in the herbicided plot was not significantly different from that in the young and mature forest sites, or from that in the control plot at the same site. In the control plot, 32 plants survived which was significantly lower than the numbers recorded in the young and mature forest control plots. In the new plantation, the total survival of 17 plants in the herbicided plot and 16 plants in the control plot were not significantly different from each other, but were significantly lower than the numbers of plants in all other plots at all other sites. Seventeen plants also survived in the new plantation mulch plot, and so there was no significant difference in survival of *F. gigantea* between the three treatments at this site.

The survival of *C. lutetiana* was very similar in both the herbicided and control plots at the young and mature forest, and ancient copse sites. Survival was also high in the herbicided plot in the farm woodland, where 59 plants were recorded. In the control plot at this site, only 40 plants were present in 1992, which was significantly lower than the number that survived in the herbicided plot. In the new plantation, 45 plants survived in the herbicided plot, 20 in the control plot and 53 in the mulch plot. Whilst there was no significant difference between the survival in the herbicide or mulch plots, the survival in the control plot was significantly lower than that in the herbicided plot and in the mulch plot.

The survival of *L. galeobdolon* was not significantly different between treatments at the farm woodland, young and mature forest, and ancient woodland sites. In the new plantation, there was no significant difference between the survival in the herbicided or control plots, but the survival in the mulch plot was significantly lower than that in the herbicided plot.

The number of *P. vulgaris* individuals that survived was not significantly different within any of the experimental sites, whether in herbicided or control plots. The lowest recorded survival was 45 plants in the farm woodland, and the highest was 56 plants in the ancient copse. These survival rates were not significantly different. In the herbicided plots, 51 plants survived in the new plantation and 59 in the mature forest site, which

was a significantly different result.

4.4.1.2 The half-lives of the introduced field layer species.

Table 17 shows the half-lives for the six ancient woodland field layer species that were introduced into woodlands of different ages. The figures have been calculated over the two year period of the experiment, and represent the time taken for the population of each species to fall to 50% of the number that was originally planted. Half-lives are shown for the survival of each species in each of the three ground pre-treatments, and for the total survival of each species over all sites.

The half-lives of the woodland field layer species range from 1.0 years for *B. ramosa* in all treatments, to 27.3 years for *L. galeobdolon* in the herbicided plots. (The half-life for *P. vulgaris* in the mulch plot was infinity, since no individuals died). For *C. lutetiana*, *F. gigantea*, and *L. galeobdolon*, the longest half-lives were for plants in the herbicided plots, whilst for *C. sylvatica* and *P. vulgaris*, half-lives were longest in the mulch plots. In the control plots, *C. sylvatica* and *F. gigantea* had shorter half-lives than

Table 17. *The half-lives, in years, of ancient woodland species, calculated over 2 years, after introduction into woodlands of different ages, and with different ground pre-treatments.*

SPECIES	Treatments			TOTAL
	Herbicide	Mulch	None	
Bromopsis ramosa	1.0	1.0	1.0	1.0
Carex sylvatica	2.8	12.0	3.7	3.5
Circaea lutetiana	17.6	8.6	4.8	6.9
Festuca gigantea	4.1	1.4	3.0	3.0
Lamiastrum galeobdolon	27.3	2.4	10.7	10.0
Primula vulgaris	12.5	∞	7.3	10.2

those of the woodland forbs. This was the same for the overall half-lives that were calculated from total survival figures.

4.4.1.3 Survival of species in the screening experiment.

During the first growing season, the majority of species in the screening experiment

survived well. Only *S. nodosa* showed a significant decline in the first few months after planting.

Table 18 shows the survival of species in the screening experiment in 1992. Eighteen months after planting, some 181 individuals out of the 360 that were planted were recorded. Only *S. nodosa* survived very poorly in all treatments at all sites. The most successful species was *O. acetosella*, for which 48 plants out of the 60 planted were recorded.

Table 18. *The survival of species in the screening experiment in 1992.*

SPECIES	NEW PLANTATION			YOUNG FOREST	
	Herbicide	None	Mulch	Herbicide	None
Anemone nemorosa	8	0	6	9	6
Conopodium majus	6	3	8	0	2
Euphorbia amygdaloides	10	9	8	8	9
Oxalis acetosella	10	4	10	12	12
Schrophularia nodosa	4	0	0	0	0
Veronica montana	8	1	9	11	8

12 plants of each species were planted into each plot in March 1991.

In the new plantation, there was little difference in the survival of species between the herbicided and mulch plots. However, the survival of all species, except *E. amygdaloides*, was substantially reduced in the control plot. At the young forest site, all of the *O. acetosella* plants survived. The numbers of *A. nemorosa*, *E. amygdaloides* and *V. montana* that were recorded were also high, with few differences between the two treatments. With herbicide, the survival of *C. majus*, however, was considerably lower at the young forest site than in the new plantation.

4.4.2 The performance of the introduced field layer species.

4.4.2.1 The variation of performance of species in the main experiment.

The performance of *Carex sylvatica.*

The bar graphs in Fig. 19 show the variation in the performance of *C. sylvatica* at

different woodland sites. Data are presented for vegetative shoot counts, flowering tiller counts and leaf lengths.

Vegetative shoot counts.

In the control (no treatment) plots, the mean values ranged from 2.2 to 5.7. The highest mean value was recorded in the mature forest site. This was significantly higher than the mean value in the ancient copse, and the mean value in the young forest. The mean number of shoots recorded in the new plantation was significantly lower than that in the young forest, and hence from the mean values at all other sites.

In the herbicided plots, the mean number of shoots per plant ranged from 6.1 in both the young and mature forest sites to 6.3 in the ancient copse. None of the means in the herbicided plots were significantly different from each other, and the differences observed in the control plots were no longer evident.

A comparison of the mean values between treatments within the same site, indicates that significant differences only existed in plots at the young forest and ancient copse. At the young forest site, the mean value in the herbicided plot was significantly higher than the mean value in the control plot. In the ancient copse, the mean number of shoots in the herbicided plot was significantly higher than that in the control plot. At the new plantation, there was no significant difference between the mean values in the herbicide, mulch or control plots.

Flowering tiller count.

In the control plots there was no significant difference between the mean number of flowering tillers at any of the four sites. The mean values ranged from 0.3 in the ancient copse to 0.8 in the new plantation.

In the herbicided plots, the mean values ranged from 0.7 in the young forest to 5.8 in the new plantation. Due to the high variances, there was no significant difference between the mean flowering tiller number at any of the four sites. Only in the ancient copse was the mean number of tillers significantly higher than that in the control plot at the same site.

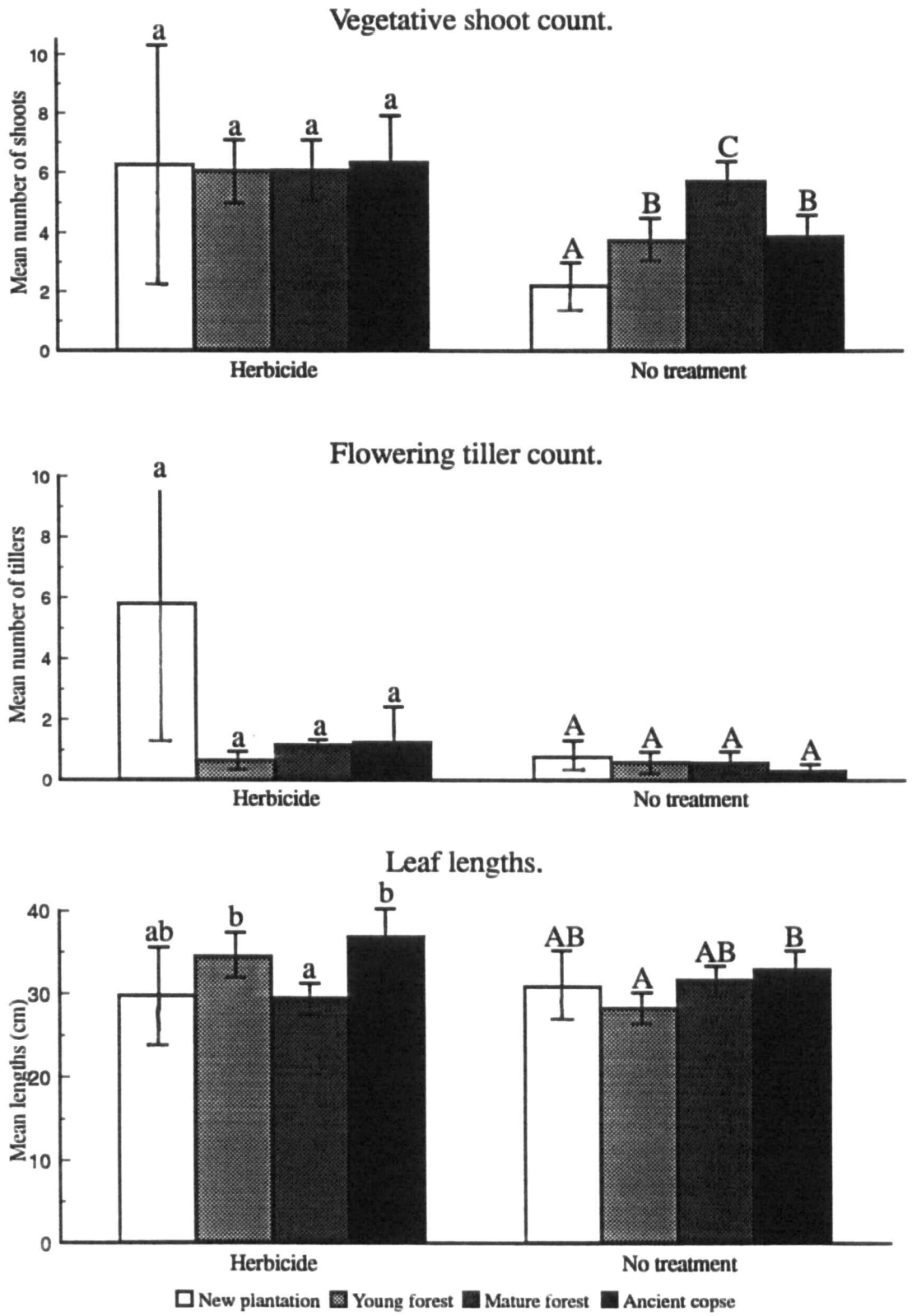


Fig. 19 *Variation in the performance of* Carex sylvatica *at different woodland sites.*
Error bars indicate 95% Confidence Intervals.
a,A *etc.* Indicate significant differences at $P<0.05$. (t-tests.)

Leaf lengths.

In the control plots, the mean leaf lengths at all four experimental sites were similar, and ranged between 28.3cm at the young forest site to 33.0cm at the ancient copse. No distinct trend in the leaf lengths between the four sites was apparent.

In the herbicided plots, the leaf lengths still did not show a pattern. The lowest mean leaf length was in the mature forest, which was significantly different from the mean length in the young forest, and the mean length in the ancient copse.

At the new plantation none of the means from the three treatments were significantly different from each other.

The performance of *Festuca gigantea.*

The bar graphs in Fig. 20 show the variation in the performance of *F. gigantea* in different treatments at the five experimental sites. Data are presented for vegetative shoot counts, flowering tiller counts and mean leaf lengths.

Vegetative shoot counts.

In the control plots, the mean number of vegetative shoots per plant ranged from 1.3 in the new plantation to 4.7 in the mature forest, and these values are significantly different. The mean shoot counts in the oldest and youngest sites were both significantly lower than those in the young and mature forest sites, which were similar to each other.

The pattern of mean shoot counts in the herbicided plots was similar to that in the control plots, with the values at the new plantation and the ancient copse both significantly lower than the values at the young and mature forest sites. The mean value at the young forest site was significantly lower than that in the mature forest. The mean values in the herbicided plots were significantly higher than those in the control plots at all sites except the new plantation.

Flowering tiller count.

In the control plots, the mean number of flowering tillers was very low at all sites,

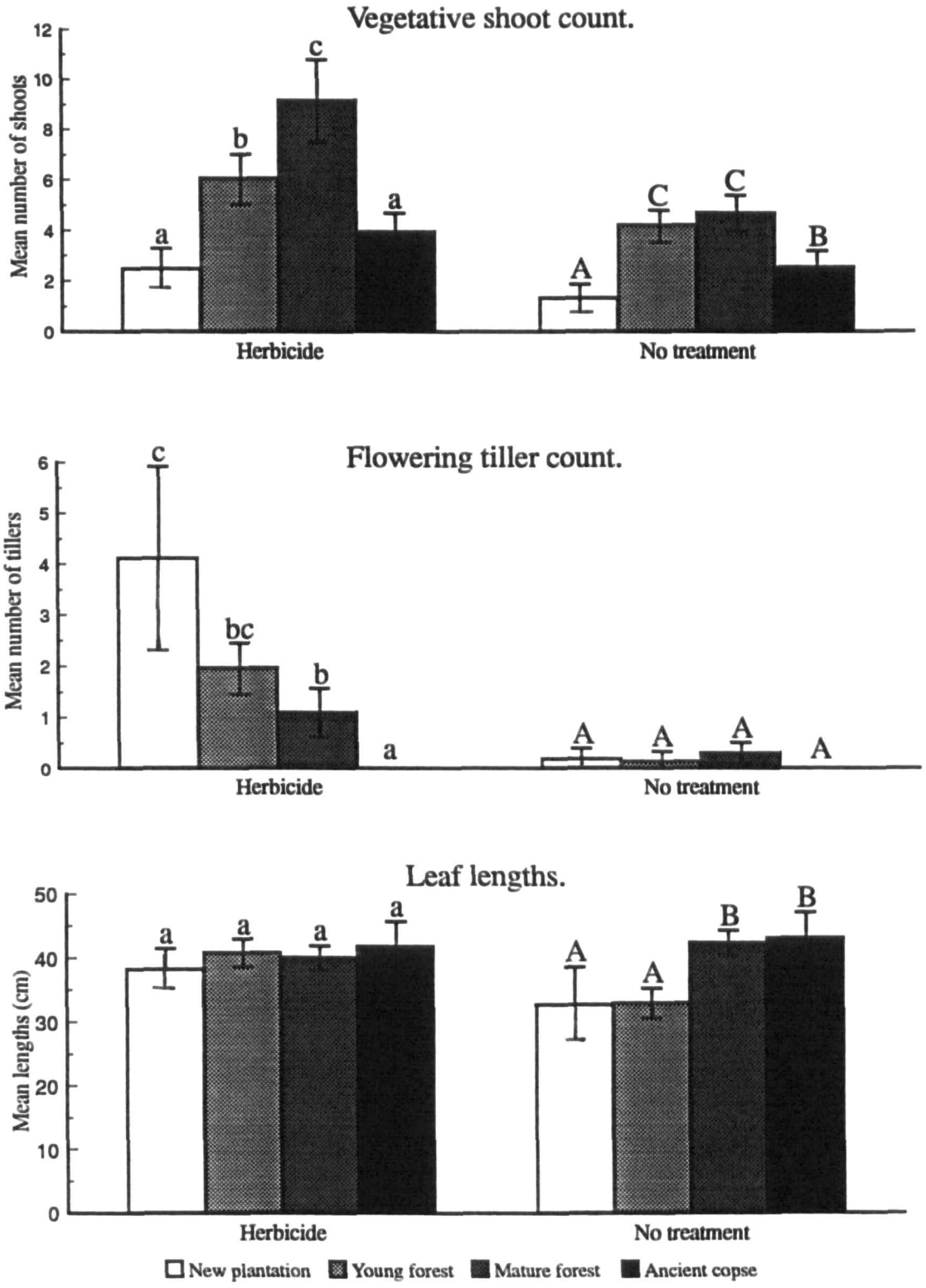


Fig. 20 *Variation in the performance of* Festuca gigantea *at different woodland sites.*
Error bars indicate 95% Confidence Intervals.
a,A *etc.* Indicate significant differences at $P>0.05$. (t-tests.)

ranging from none in the ancient copse, to only 0.3 in the mature woodland, with no significant differences between any of the sites.

In the herbicided ancient copse plot, no flowering tillers were recorded on the *F. gigantea* plants. However, there was a strong trend in the mean values at the other sites, with the mean number of tillers ranging from 1.1 in the mature forest site to 4.1 in the new plantation. The mean values at these sites were all significantly higher than those in the control plots.

Leaf lengths.

In the control plots, the mean leaf lengths ranged from 32.8cm in the new plantation to 43.1cm in the ancient copse. The mean values in the new plantation and young forest plots were both significantly lower than those in the mature forest and the ancient copse.

In the herbicided plots, the mean leaf lengths ranged from 38.3cm in the new plantation to 41.8cm in the ancient copse. None of the means were significantly different in these plots.

A comparison of the mean leaf lengths in different treatment plots within the same sites, indicates that the mean value in the herbicided young forest plot was significantly higher than that in the control plot. At the new plantation the mean leaf length in the herbicided plot was significantly higher than that in the mulch plot.

The performance of *Circaea lutetiana.*

The bar graphs in Fig. 21 show the variation in the performance of *C. lutetiana* at different treatment plots at the five experimental sites. Data are presented for leaf counts per shoot, vegetative shoot counts and leaf lengths.

Leaf counts.

In the control plots, the mean leaf counts ranged from 6.0 in the farm woodland to 8.9 in the ancient copse. The mean value in the ancient copse was significantly higher than those at all other sites.

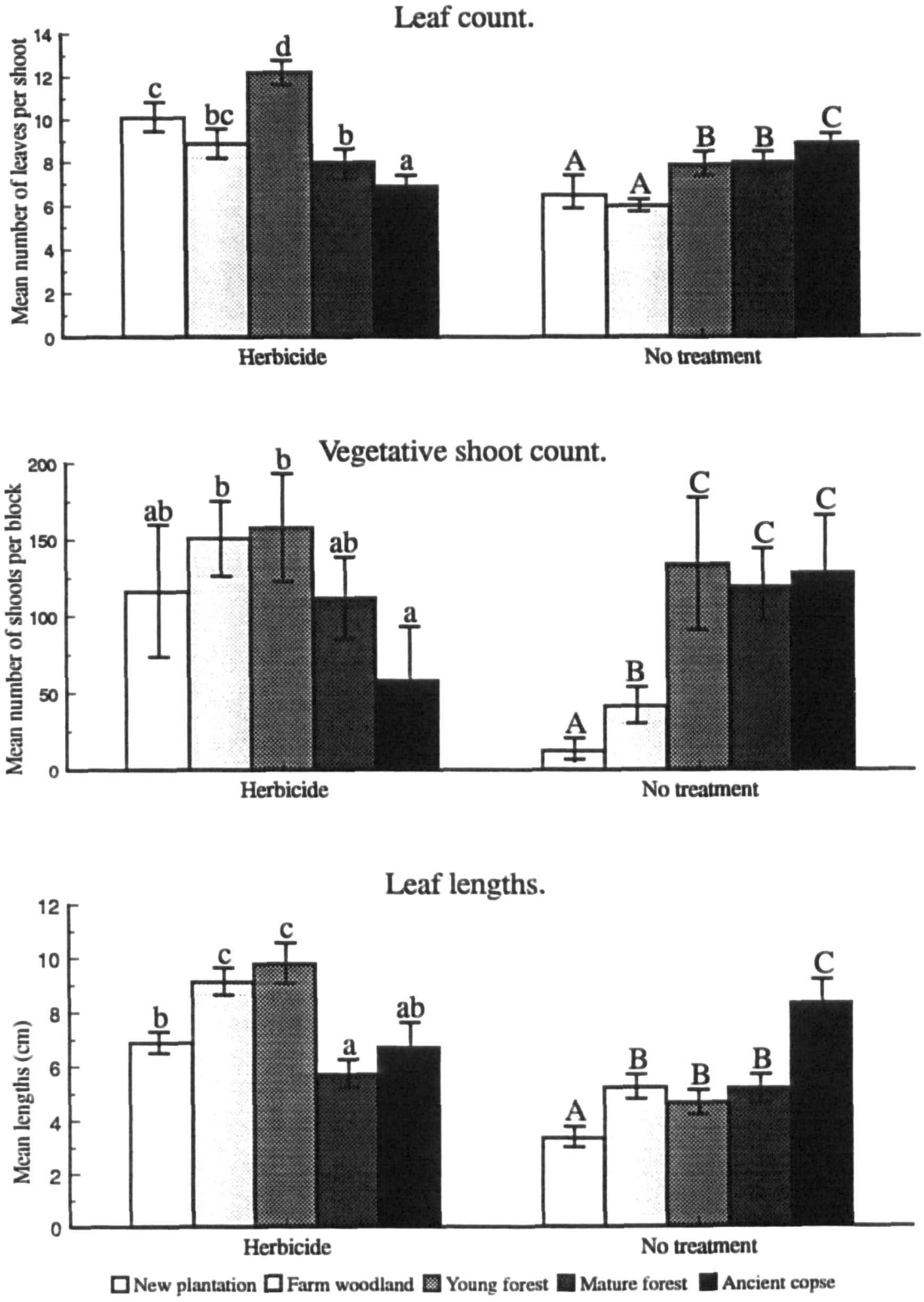


Fig. 21 *Variation in the performance of* Circaea lutetiana *at different woodland sites.*
Error bars indicate 95% Confidence Intervals.
a.A *etc.* Indicate significant differences at $P<0.05$. (t-tests.)

In the herbicided plots, the mean leaf counts ranged from 6.9 in the ancient copse to 12.2 in the young forest. Whilst the mean value in the young forest site was significantly higher than that at all other sites, the value in the ancient copse was significantly lower.

A comparison of the leaf counts between treatments at the same site indicates that the means were significantly different at all sites except in the mature forest. Whilst the mean leaf count in the ancient woodland herbicided plot was significantly lower than that in the control plot at the same site, the values at the three young sites were all significantly higher in the herbicided plots. At the new plantation, the mean value in the control plot was significantly lower than that in the mulch plot.

Vegetative shoot count.

In the control plots, the mean number of vegetative shoots $1.5m^{-2}$ ranged from 12.2 in the new plantation to 134.0 in the young forest plot. The mean value at the farm woodland was significantly lower than that in the mature forest, but significantly higher than that in the new plantation.

Although the mean leaf counts in the herbicided plots were more variable than those in the control plots, the trend in mean shoot counts was quite different, with the lowest counts being recorded in the older woodland sites. Mean values ranged from 58.0 in the ancient copse to 158.0 in the young forest, and these were significantly different.

A comparison of the mean number of vegetative shoots $1.5m^{-2}$ between different treatments within sites, indicates that the values in the new plantation and the farm woodland were significantly higher in the herbicided plots than in the control plots. In the new plantation, the mean shoot number in the herbicided plot was significantly higher than that in the mulch plot, which itself was significantly higher than the value in the control plot.

Leaf lengths.

In the control plots, the mean leaf lengths ranged from 3.4cm in the new plantation to 8.3cm in the ancient copse, and these values were significantly different.

In the herbicided plots the mean leaf lengths ranged from 9.8cm in the young forest to 5.7cm in the mature forest. The mean value at the farm woodland was significantly higher than that at the new plantation, whilst that at the young forest was significantly higher than the value at the ancient copse.

Comparing the mean leaf lengths between treatments within the same sites, the means in the herbicided plots in the three younger woodlands were significantly higher than those in the control plots. There was no significant difference in the mean leaf lengths resulting from the two treatments at the two older woodland sites. At the new plantation, the mean length in the herbicided plot was significantly higher than that in the mulch plot.

The performance of *Lamiastrum galeobdolon.*

The bar graphs in Fig. 22 show the variation in the performance of *L. galeobdolon* in different treatments at the five experimental sites. Data are presented for vegetative shoot counts, flowering stem counts and mean leaf lengths.

Vegetative shoot counts.

In the control plots, the mean number of vegetative shoots per plant were all low, ranging from 2.0 in the new plantation, to 5.3 in the young forest site. The mean at the new plantation was significantly lower than those at all of the other sites.

In the herbicided plots there is a clear relationship between the five means, which ranged from 4.1 in the ancient copse to 12.9 in the new plantation. All means were significantly different from each other, except those at the new plantation and farm woodland sites.

A comparison of the mean vegetative shoot counts between different treatments at the same sites indicates that the means in the herbicided plots were significantly higher than those in the control plots in all sites except the ancient copse. At the new plantation, the mean value in the herbicided plot was significantly higher than that in the mulch plot.

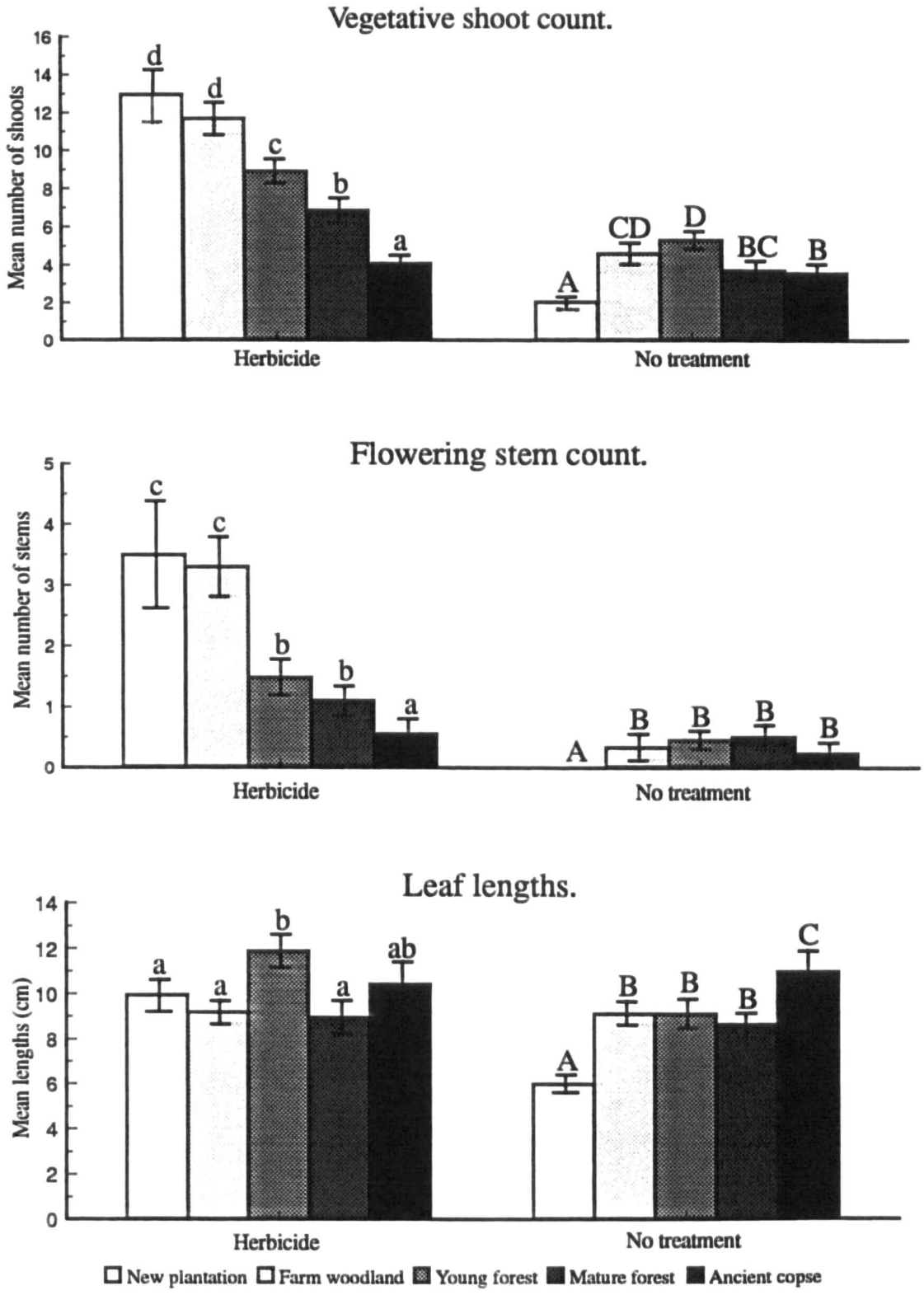


Fig. 22 *Variation in the performance of* Lamiastrum galeobdolon *at different woodland sites.*
Error bars indicate 95% Confidence Intervals.
a,A *etc.* Indicate significant differences at $P<0.05$. (t-tests.)

Flowering stem count.

A very similar pattern to that shown by the vegetative shoot counts is exhibited by the mean flowering stem counts. In the control plots, there were no flowering stems recorded in the new plantation, and the highest mean value was only 0.5 in the mature forest. None of the mean values were significantly different.

In the herbicided plots, there was a marked increase in the mean number of flowering stems, which ranged between 0.6 in the ancient copse to 3.5 in the new plantation. The mean stem number in the ancient copse was significantly lower than that at all of the other sites.

A comparison of the mean flowering stem number between treatments within sites indicates that all of those in the herbicided plots were significantly higher than those in the control plots, except in the ancient copse. In the new plantation, there were no flowering stems recorded in the mulch plots.

Leaf lengths.

In the control plots, the mean leaf lengths ranged between 6.0cm in the new plantation to 11.0cm in the ancient copse, and were significantly different at these sites.

In the herbicided plots, the mean leaf lengths showed no clear trend, ranging between 8.9cm in the mature forest plot and 11.9cm in the young forest plot. With herbicide, the mean values in the new plantation and the ancient copse were not significantly different.

A comparison of the mean leaf lengths between treatments within sites indicates that there were only significant differences at the new plantation and young forest sites, where the mean leaf length was higher in the herbicided plot. In the new plantation, the mean value in the herbicided plot was significantly higher than both that in the control plot, and that in the mulch plot.

Stolon lengths.

Table 19 shows the mean *L. galeobdolon* stolon lengths with 95% Confidence Intervals in both the herbicided and control plots at all five experimental sites in 1991 and 1992.

In 1991, the mean stolon lengths were significantly lower in the new plantation than at all other sites, in both treatments. At the mature forest and ancient copse, stolon lengths were not significantly different in the herbicided and control plots. At the three younger sites, the stolon lengths in the herbicided plots were significantly higher than those in the control plots.

Table 19. *Variation of mean stolon lengths (cm) of* Lamiastrum galeobdolon *in different treatments at five woodland sites between 1991 and 1992. (95% Confidence Intervals are given.)*

	HERBICIDE 1		NO TREATMENT 2	
SITES	**1991** 1	**1992** 2	**1991** 1	**1992** 2
New plantation 1	**42.0** ±4.6 *T2	**90.4** ±7.0 *T2, *Y1	**11.3** ±3.0	**39.1** ±7.4 *Y1
Farm woodland 2	**114.4** ±11.5 *S1, *T2, *Y2	**94.5** ±5.5	**88.0** ± 6.7 *S1,S2	**92.6** ±5.3 *S1
Young forest 3	**116.7** ±16.9 *S1, *T2	**168.9** ±6.0 *S1,S2,S4,S5, *T2,*Y1	**47.2** ±14.7 *S1	**124.1** ±4.3 *S1,S2,S4,S5, *Y1
Mature forest 4	**94.7** ±16.2 *S1	**139.2** ±4.2 *S1,S2,S5, *T2, *Y1	**109.8** ±19.7 *S1,S3	**111.5** ±4.8 *S1,S2
Ancient copse 5	**134.6** ±8.5 *S1,S2,S4, *Y2	**99.5** ± 5.0	**134.6** ±10.6 *S1,S2,S3, *Y2	**101.5** ±6.0 *S1

*: P <0.05.
*S: Significantly higher than different site, same treatment, same year. 1,2,3,4,5 = Site number.
*T: Significantly higher than same site, different treatment, same year. 1 = Herbicide; 2 = No treatment.
*Y: Significantly higher than same site, same treatment, different year. 1 = 1991; 2 = 1992.

By 1992, the mean stolon lengths were significantly higher in the young forest than at all other sites, in both treatments. Only in the control plots was the mean stolon length in the new plantation lower than at all other sites. At the new plantation, and young and mature forest sites, the mean stolon lengths in the herbicided plots were significantly higher than those in the control plots. In the new plantation, there was no significant difference between the control and mulch plots in 1991, but by 1992, the mean stolon length in the control plot was significantly higher than that in the mulch plot.

Comparing mean stolon lengths in the herbicided plots between 1991 and 1992, the

means lengths increased significantly in the second year in all plots except the farm woodland and the ancient copse. At these sites there was a significant decrease in mean lengths. A comparison of mean stolon lengths in the control plots between 1991 and 1992 shows that the mean lengths increased at every site except in the ancient copse, although only in the new plantation and the young forest were these increases significant. At the ancient woodland, as in the herbicided plots, the mean stolon length was significantly lower, decreasing from 1991 to 1992.

The performance of *Primula vulgaris.*

The bar graphs in Fig. 23 show the variation in the performance of *P. vulgaris* at the five experimental sites. Data are presented for leaf counts, flower counts and mean leaf lengths in both herbicided and control plots.

Leaf counts.

In the control plots, the mean number of leaves per plant ranged from 5.6 in the new plantation to 7.1 in the ancient woodland. None of these values were significantly different.

In the herbicided plot, the mean leaf counts ranged from 6.9 in the mature forest to 10.6 at the farm woodland site. The mean leaf counts were variable, and only the value in the farm woodland was significantly higher than that in the mature forest, and that in the ancient copse.

A comparison of the means leaf counts between treatments at the same site indicates that the means in the herbicided plots were only significantly higher than those in the control plots in the new plantation, and in the farm woodland. In the new plantation, the mean value in the mulch plot was significantly higher than that in the control plot.

Flower counts.

In the control plots, the mean flower counts were generally low, and ranged between 2.5 in the new plantation to 7.5 in the young forest.

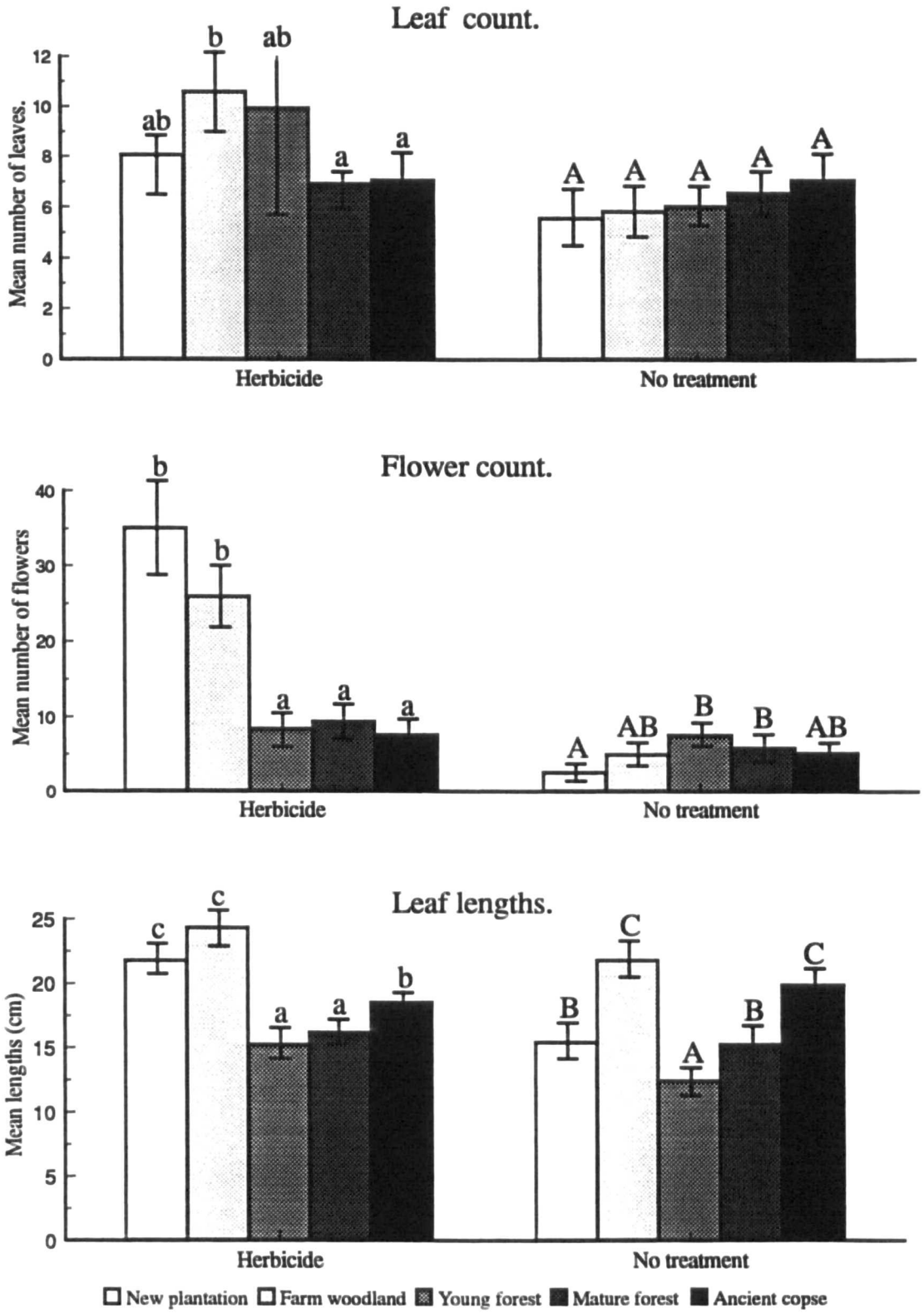


Fig. 23 *Variation in the performance of* Primula vulgaris *at different woodland sites.*
Error bars indicate 95% Confidence Intervals.
a,A *etc.* Indicate significant differences at $P<0.05$. (t-tests.)

In the herbicided plots, the mean flower counts ranged from 7.5 in the ancient copse to 35.0 in the new plantation. The mean value in the new plantation was not significantly different from that of 25.9 at the farm woodland. However, both of these values were significantly higher than the mean flower counts in the three older woodlands.

A comparison of the means from different treatments within sites indicates that the flower numbers in herbicided plots were significantly higher than those in control plots in the new plantation and in the farm woodland. In the new plantation, the mean flower number in the mulch plot was significantly lower than that in the herbicided plot, whilst significantly higher than that in the control plot.

Leaf lengths.

In the control plots, the mean leaf lengths for *P. vulgaris* ranged between 12.4cm in the young forest to 21.8cm in the farm woodland. The mean leaf length in the ancient copse of 19.9 cm was not significantly different from that in the farm woodland.

In the herbicided plots, there was a similar pattern, although mean lengths increased at every site except in the ancient copse. The highest mean leaf lengths were recorded in the two youngest woodlands, and these were no longer significantly different.

A comparison of mean leaf lengths between herbicided and control plots within sites, indicates that the recorded means were significantly different at the three younger sites. In the new plantation, the mean length in the herbicided plot was significantly higher than both that in the control plot and in the mulch plot.

4.4.2.2 The variation of performance of species in the screening experiment.

In the new plantation, the majority of individuals of *A. nemorosa* and *E. amygdaloides* flowered in 1992, whether in herbicide, mulch or control plots. For both *C. majus* and *O. acetosella*, fewer individuals in the control plot flowered. No flowers were recorded on any of the surviving plants of *V. montana*, or the few *S. nodosa* plants.

In the young forest plots, nearly all surviving individuals flowered in 1992. Only the

number of *E. amygdaloides* flowering in the control plot was substantially lower than that in the herbicided plot.

Seed set was observed for *E. amygdaloides* at both sites, and for *O. acetosella* in the young forest plots. *O. acetosella* also spread well at this site, forming good clumps. The most significant amount of vegetative growth was observed for *V. montana*, at the same site, where vegetative shoots of over 35cm were recorded on some plants.

4.4.3 The results of the measuring of environmental factors.

4.4.3.1 Variation of % daylight in different woodland sites.

Figure 24 indicates the relationship between the mean % daylight at each site and the corresponding age of the woodland at the site. Woodland age in years is plotted on a logarithmic scale, and a polynomial (quadratic) regression has been fitted through the five % daylight values. There is a clear relationship between % daylight and woodland age, with high values for % light recorded in young woodlands, falling steeply with the increasing age of the woodland. At an age of approximately 20 years, the mean % daylight within a woodland is less than 20%. This gradually decreases with woodland age.

4.4.3.2 Variation in the % cover of competing vegetation with and without herbicide treatment.

In 1991, less than 5% cover of vegetation was observed in the herbicided plots at planting time. During the year, there was a general increase in the amount of vegetation in plots at all sites, as both grasses and broadleaved weeds recolonised the bare areas around the introduced field layer species. In the ancient copse, the field layer of which was characterised by over 90% *H. non-scripta* prior to the application of herbicide, there was only an estimated 5% cover by *H. non-scripta* in spring 1991. However, the plot soon became recolonised by *G. aparine* which had germinated in the autumn after herbicide application. By summer 1991, *G. aparine* covered an estimated 50% of the plot.

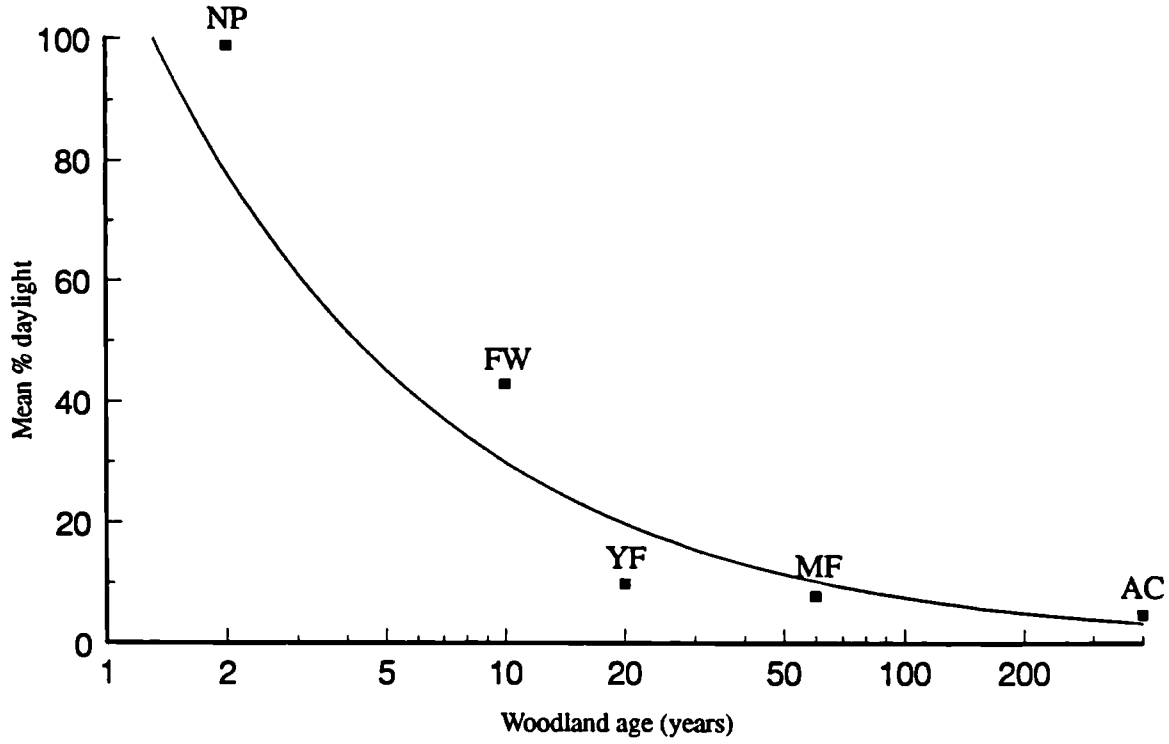


Fig. 24 *The relationship between light and woodland age at the experimental sites, 1991.*
NP: New plantation; FW: F arm woodland; YF: Young forest; MF: Mature forest; AC: Ancient copse.

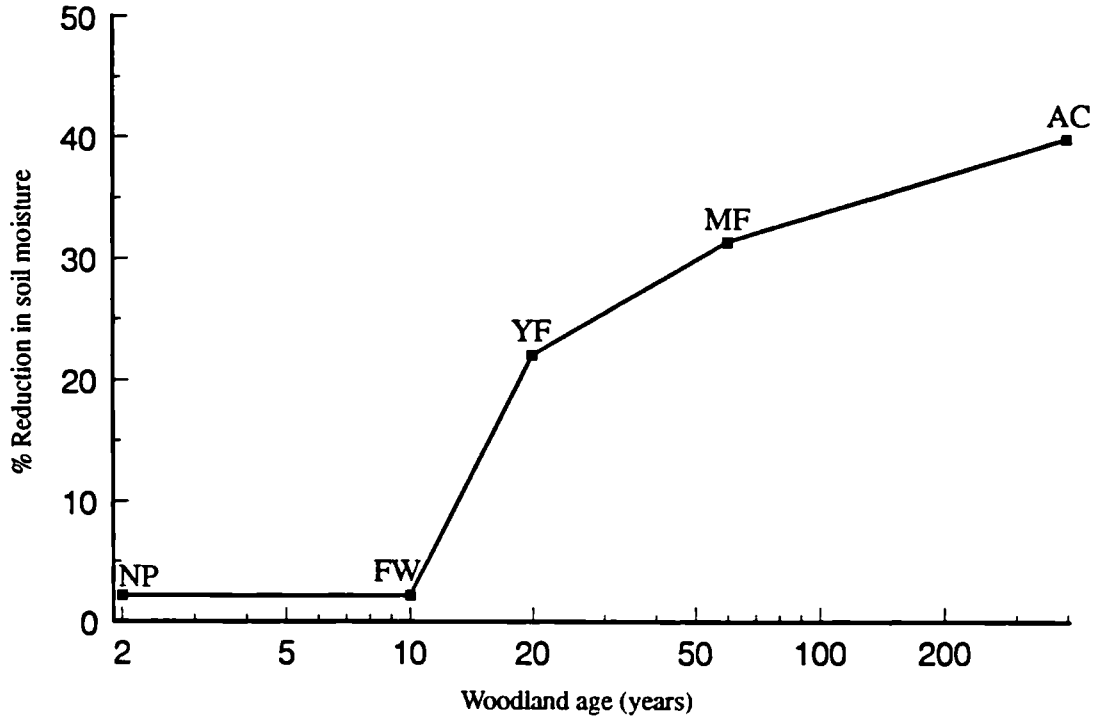


Fig. 25 *The relationship between % soil moisture reduction during the summer and woodland age at the experimental sites, 1992.*
NP: New plantation; FW: Farm woodland; YF: Young forest; MF: Mature forest; AC: Ancient copse.

Table 20 shows the % cover of competing vegetation in plots of all pre-treatments in summer 1992. By this time, the total % cover of competing vegetation in the herbicided plots throughout the experimental sites was generally not significantly different from that in the control plots. The graphs in Fig. 26 indicate the percentage cover of competing vegetation on both herbicided and control plots containing introduced forb species, some two years after herbicide application. These graphs indicate that the composition of the competing vegetation was changed by the application of herbicide, particularly in the sites with higher % daylight. Data for the % cover of vegetation in plots containing introduced grass and sedge species indicated similar changes.

Table 20. *The % cover of competing vegetation in experimental plots with introduced forbs, and grass and sedge species, at different sites two years after different ground pre-treatments.*

PLOTS	SITES	% Cover of Grasses			% Cover of Broadleaved weeds		
		H	N	M	H	N	M
Forbs.	NP	112.0	129.9	45.2	123.9	75.0	195.6
	FW	78.0	100.0	-	49	29.4	-
	YF	5.0	7.4	-	7.0	4.5	-
	MF	0.5	0.5	-	8.5	26.9	-
	AC	2.5	0	-	52.0	69.5	-
Grasses.	NP	67.5	154.0	97.0	143.0	85.0	119.5
	YF	0.5	0	-	2.0	7.0	-
	MF	2.0	25.1	-	8.9	24.6	-
	AC	1.5	3.0	-	91.6	110.0	-

H:Herbicide, N:No treatment, M:Mulch.

NP:New Plantation, FW:Farm Woodland, YF:Young Forest, MF:Mature Forest, AC:Ancient Copse.

As a result of herbicide application, the % cover of broadleaved weed species decreased in the ancient copse, and in the mature forest. However, the % cover of broadleaved weed species increased in the farm woodland, and in the new plantation. In the lighter plots where grass species predominated prior to the application of herbicide, the % cover of grass was still reduced in the farm woodland and in the new plantation two years after herbicide application. Few grass species were present at the shadier woodland sites.

In the new plantation, the mulch reduced the % cover of grass species, but resulted in

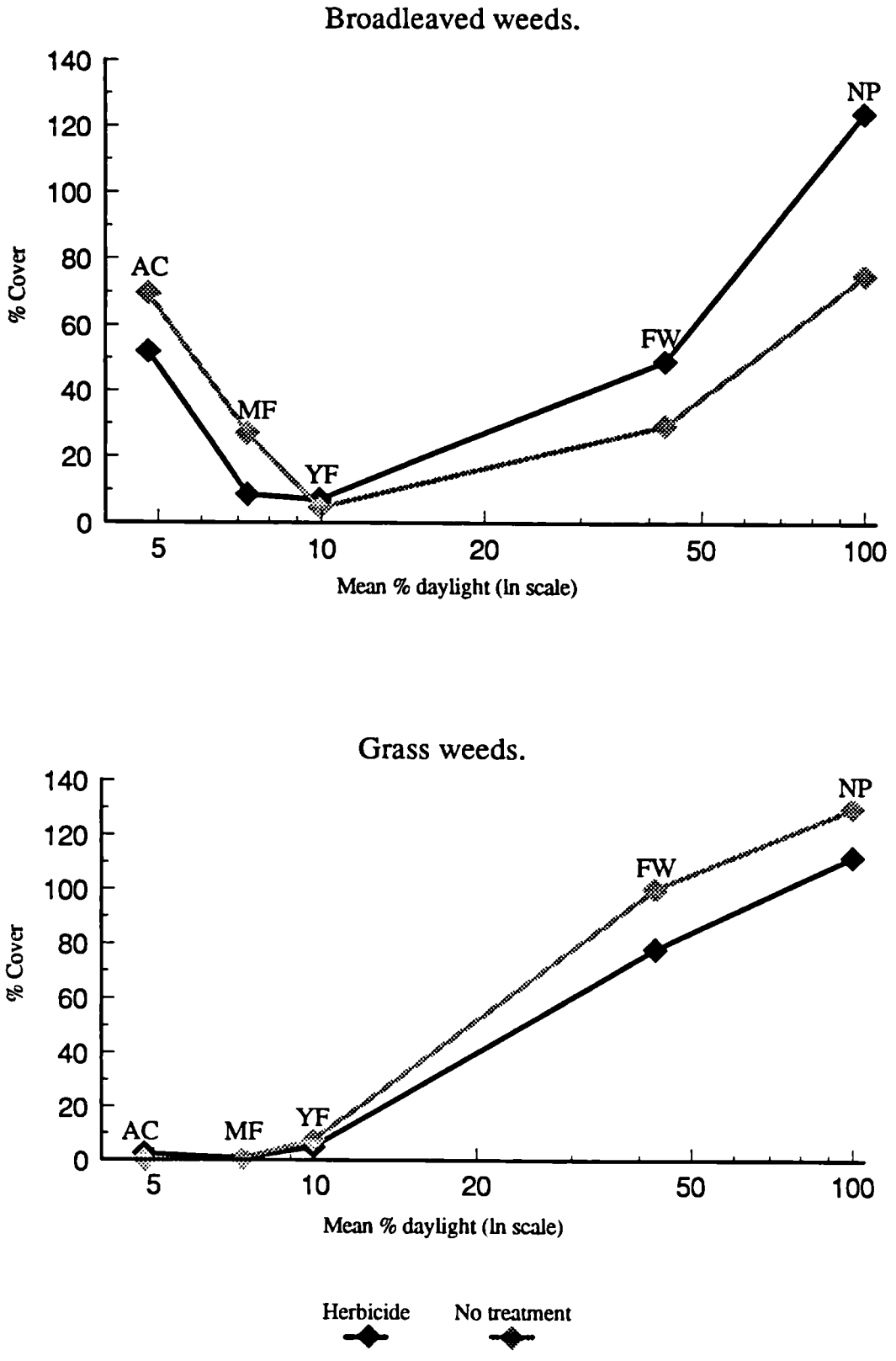


Fig. 26 *% Cover of competing vegetation in herbicided and control plots, containing introduced forb species, two years after herbicide application.*

NP: New plantation, FW: Farm woodland, YF: Young forest, MF: Mature forest, AC: Ancient copse.

an increase in the % cover of broadleaved weeds. This increase was particularly large in the plot where forbs had been introduced, and included species such as *R. repens*, *Achillea millefolium* (Yarrow), and *Stellaria graminea* (Lesser Stitchwort). At the young forest plot the percentage cover of competing vegetation remained very low throughout the experimental period.

4.4.3.3 The soil properties at the experimental sites.

Table 21 gives the results of all the soil analyses that were carried out on soil samples from the five experimental sites. Figure 25 indicates the variation of the percentage reduction in soil moisture between May and September with woodland age.

Table 21. *The analysis of soil properties in woodlands of different ages.*

	Soil texture								% Moisture		
	Age	pH	% Clay	% Sand	% Silt	Type	P_2O_5mg $100g^{-1}$	% Organic Matter	May	Sept	Loss (%)
New plantation	2	5.7	31.8	48.4	19.8	Sandy clay	9.00	7.7	27.9	27.3	2.2
Farm woodland	12	7.5	33.7	47.6	18.7	Sandy clay	18.3	9.2	22.8	22.3	2.2
Young forest	20	4.5	9.4	65.9	24.7	Sandy loam	4.67	15.7	32.1	25.0	22.1
Mature forest	60	4.4	13.0	54.2	32.9	Sandy loam	1.23	11.9	29.0	19.9	31.4
Ancient copse	400	5.4	13.4	59.2	27.4	Sandy loam	1.73	12.9	26.8	16.1	39.9

The five woodland soils all had a high percentage of sand, but the new plantation and farm woodland soils contained more clay than the soils in the older woodlands. The amount of extractable P_2O_5 was higher in the younger woodlands, particularly in the farm woodland. The percentage organic matter was higher in the three older woodlands, than in the young woodlands. The soil pH was alkaline at the farm woodland site, neutral in the new plantation, and acid in the three older woodlands. The percentage soil moisture in May was similar throughout the five sites, but had changed significantly by September. Figure 25 indicates that as woodland age increases, the percentage reduction in soil moisture between May and September also increases.

4.4.4 Relationship of the survival of the introduced field layer species to environmental factors.

The survival data of the introduced field layer species were studied in relation to the light, soil and competition data from the different sites. Most relationships, however, showed no correlations.

4.4.4.1 The relationship of *Circaea lutetiana* survival to the % cover of grass species in 1992.

Figure 27 shows the relationship of *C. lutetiana* survival with the percentage grass cover in 1992 at both herbicided and control plots. In the control plots, percentage grass cover was high in the high light conditions at the farm woodland and new plantation (refer to Fig. 26). The survival of *C. lutetiana* at these sites was greatly reduced, from 60 original plants to 40 in the farm woodland and to 20 in the new plantation. In the herbicided plots, the percentage cover of grass species was reduced and the survival of *C. lutetiana* was significantly higher. The survival of this species was still reduced in the new plantation herbicided plot, where grass cover remained very high at 112%. There is clearly a trend between the survival of *C. lutetiana* and the percentage cover of grasses growing around it.

4.4.4.2 The relationship of *Carex sylvatica* survival to the % cover of broadleaved species in 1992.

Figure 28 shows the relationship of *C. sylvatica* survival to the percentage cover of broadleaved weeds in 1992, at both herbicided and control plots. At sites where the percentage cover of broadleaved weeds was low, *i.e.* below 30% (refer to Table 20), the survival of *C. sylvatica* was not significantly affected. However, in the new plantation and the ancient copse, the percentage cover of broadleaved weeds was high, and in these sites the survival of *C. sylvatica* was significantly reduced in both herbicided and control plots.

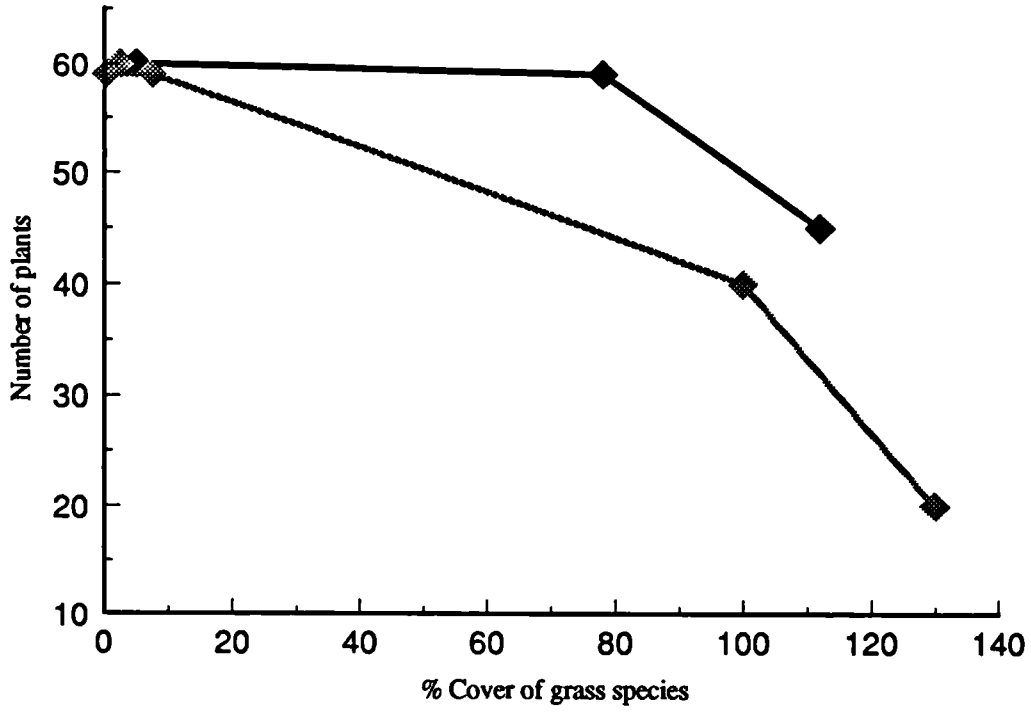


Fig. 27 *Relationship of* Circaea lutetiana *survival to % grass cover in 1992.*

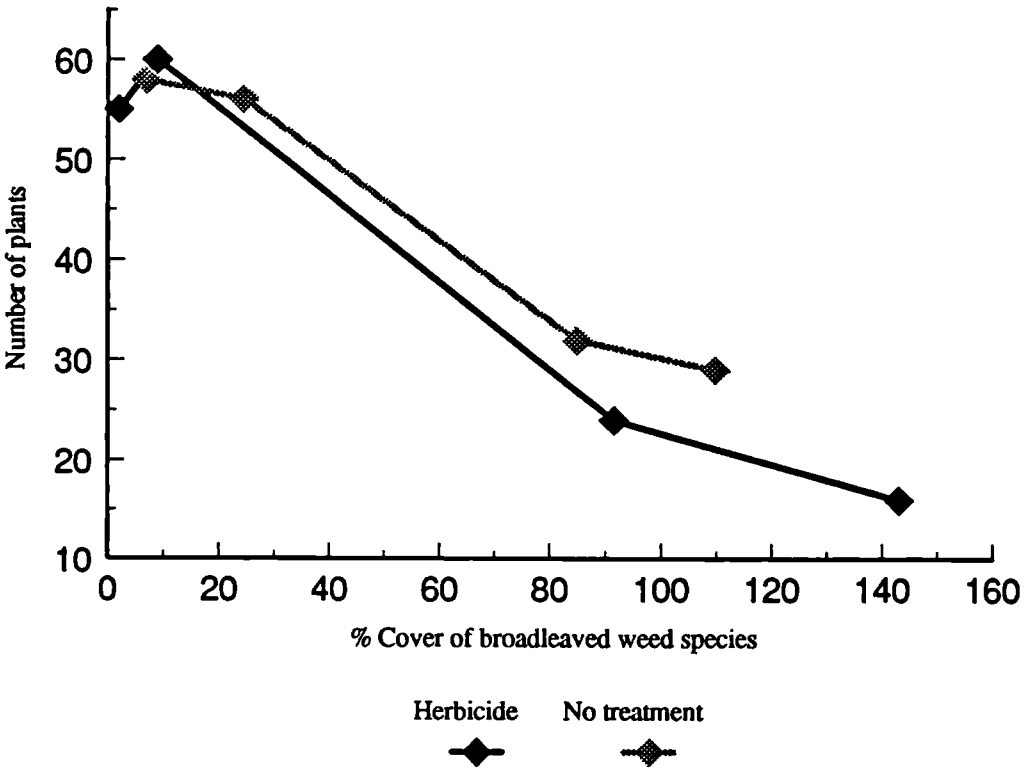


Fig. 28 *Relationship of* Carex sylvatica *survival to % cover of broadleaved weeds in 1992.*

4.4.5 Relationship of the performance of the introduced field layer species to environmental factors.

The growth characteristics data of the introduced field layer species were studied in relation to the light, soil and competition data from the woodland sites. The majority of associations showed no correlation however.

4.4.5.1 The effect of herbicide pre-treatment on flower production under a range light conditions.

Figure 29 shows the variation in flower or flowering stem production by *F. gigantea*, *L. galeobdolon* and *P. vulgaris* at both herbicided and control plots, under a range of light conditions. For each of the three field layer species, the flower counts in the control plots were consistently low and were not dependent on light level. However, in the herbicided plots, the amount of flower production rose steadily as the percentage daylight in the woodland increased. In the herbicided plots, flower production for these three species is positively correlated with percentage daylight. Linear regression lines can be fitted to describe the relationship of the number of flowers produced in the herbicided plots with % daylight. For *F. gigantea*, $r^2 = 0.82$, for *L. galeobdolon*, $r^2 = 0.77$, and for *P. vulgaris*, $r^2 = 0.93$.

4.5 Discussion.

4.5.1 The general success and survival of the field layer introductions.

Eighteen months after being planted into woodlands of different ages, a total of 81.6% of individuals of five field layer species were still present in the experimental plots. This survival figure represented some 2496 individual plants out of 3060 that were planted. Only one species, *B. ramosa*, had failed almost completely.

Three forbs, *C. lutetiana*, *L. galeobdolon* and *P. vulgaris*, were introduced into the experimental sites, and of these a total of 88.6% survived. The percentage survival data

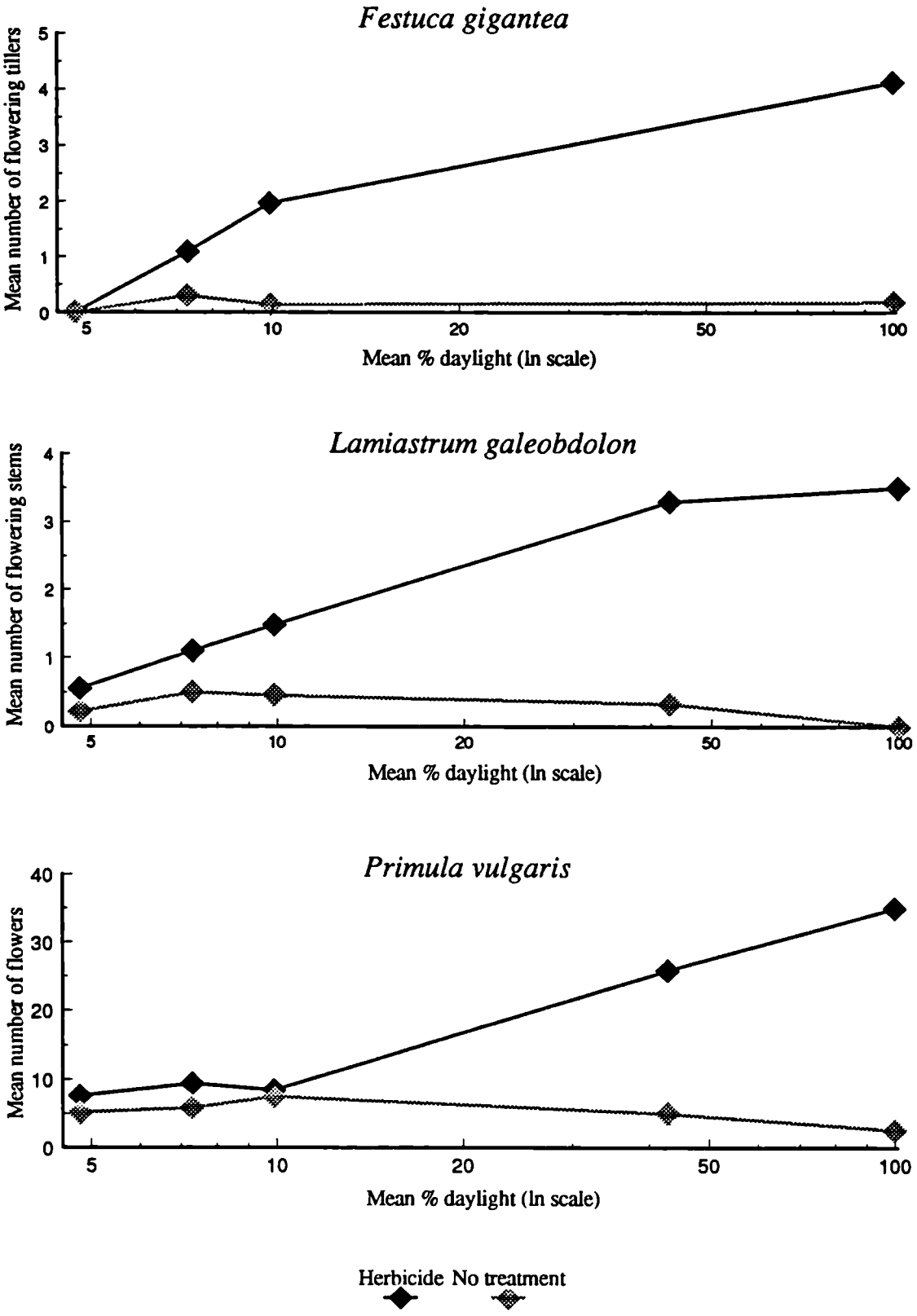


Fig. 29 *Effect of herbicide treatment on flower production for three field layer species under a range of light conditions.*

(Table 16) indicate that these species generally survived well throughout the sites and treatments. One exception to this was *C. lutetiana*, the survival of which was significantly reduced in plots with a high percentage cover of grass species (Fig. 27). The half-life of this species was correspondingly reduced in plots with no ground pre-treatment. This indicates that although this species has a high capacity for vegetative spread in suitable conditions (see also Raven 1963), its capacity to survive and spread is reduced within a grass sward. Similarly, Porter & Nowakowski (1991) found that densities of *V. riviniana*, *V. riechenbachiana* (Pale Wood Violet), and other woodland herbs increased after the application of a graminicide, which reduced the growth of coarse grass species.

Another significant effect of treatment on plant survival was recorded for *L. galeobdolon* in the new plantation mulch plot. Whilst Cohn & Packham (1991) report survival of this species to be enhanced in mulch within young plantations, in the present study *L. galeobdolon* survived very poorly in the mulch plots. Examination of the vegetative shoots revealed indications of herbivory, which was due to slugs (S. McNeill, pers. comm.). This resulted in many completely leafless stems, which rarely recovered. Slugs are known to eat *L. galeobdolon*, particularly in cold frames (Packham 1983). In experiments to investigate the palatability of the leaves of field layer species to slugs (Jennings & Barkham 1975), it was demonstrated that some woodland slug species, (*e.g. Arion ater* and *Agriolimax reticulatus*), preferred to eat *L. galeobdolon* rather than *C. lutetiana* and *P. vulgaris*, amongst other species. This was probably due to the high protein content of the leaves. Since the mulch plot in this experiment was surrounded by grassland vegetation, there were possibly many slugs in the vicinity and the *L. galeobdolon* plants were easily accessible to them (Francis *et al.* 1992b). Another possible cause of the reduced survival of *L. galeobdolon* in the mulch plots is frost damage. This was observed as browning of leaves in late winter 1992. Studies of frost resistance in this species have shown that it can normally withstand heavy frost, without loss of leaves (Packham 1983). Investigating *L. galeobdolon* in Germany, Till (1956) found that whilst overwintering shoots withstood temperatures of -17°C, in spring the hardiness of shoots was reduced, with shoot damage occurring below -8°C. The new plantation is a very open site, which offers no protection from frost, unlike the other woodland sites. It is therefore considered that *L. galeobdolon* may have been damaged

by frost in the mulch plot at this site. Whether such frost action, or the activities of slugs, were more responsible for the poor survival of this species in the mulch plot, is unknown, but in this situation, mulch was not an appropriate ground pre-treatment for this plant species. In contrast, the survival of both *C. lutetiana* and *P. vulgaris* was significantly enhanced in the mulch plot compared with that in the control plot. This was illustrated by the increased half-lives for these species in the mulch plots. Both of these species die back during the winter, and therefore avoid damage by frost. The small rise in the numbers of *P. vulgaris* recorded between 1991 and 1992, indicates that some plants had already died back prior to the monitoring in 1991.

The total half-lives of the woodland forbs ranged between 6.9 years for *C. lutetiana*, and 10.2 years for *P. vulgaris*. These half-lives all increased in herbicided plots, where competition from other field layer species had been reduced at the time of introduction. That for *L. galeobdolon* rose from 10.7 years in the control plots, to 27.3 years in the herbicided plots. This half-life compares favourably with those of two other herbaceous perennials, *Filipendula vulgaris* (Dropwort) and *Sanicula europaea* (Sanicle), growing in well-established natural populations. The half-lives recorded for these species were 18.4 years and 50+ years respectively (Harper 1967, calculated from data of Tamm 1956).

The total survival of the grass, *F. gigantea*, and sedge, *C. sylvatica*, was lower than that of the forbs, at 68.8%. These two species exhibited the most variation in survival between sites. At the young and mature forest sites, where competition was low in both herbicided and control plots, they survived well. However, at both the new plantation and ancient copse, the number of plants remaining after the first 18 months was significantly reduced. For both species, it is possible that the large reduction in soil moisture in the ancient copse during the summer months may have lowered survival at this site.

Figure 28 illustrates the relationship between the survival of *C. sylvatica* and the % cover of broadleaved weed species. There was a marked negative relationship between the survival of this species and the % cover of broadleaved weeds within the plots. It is of interest that in the new plantation, the survival of this species was significantly

reduced in the herbicided plot. Figure 26 indicates changes in the composition of the competing vegetation, particularly at high light levels, where the removal of grass by herbicide, allowed broadleaved weeds, *e.g. Hypochaeris radicata* (Cat's-ear), *Cirsium arvense* (Creeping Thistle), and *Heracleum sphondylium* (Hogweed), to colonise the bare ground. It is likely that *C. sylvatica* cannot survive with strong competition from such species. It is also possible that the survival of this species may have been reduced in the herbicided plot since the bare ground, which resulted from herbicide use, may have become very dry prior to recolonisation by weed species. The increased humidity within the grass sward in the control plot may have helped the young *C. sylvatica* plants to survive. However, though the plants in the control plot were more numerous even in the second growing season, many were very small, and they may in future be ousted by competition from the grass sward. Further, as for *L. galeobdolon*, *C. sylvatica* may have been damaged by frost in the unprotected conditions within the herbicided plot.

F. gigantea also survived poorly in the new plantation, this survival being similarly low in plots of all three treatments. This species survived consistently better in shady conditions, except at very high levels of competition in the ancient woodland control plot. Indeed, its natural distribution is described by Clapham *et al.* (1962) as being in woods and shady hedgebanks, implying that young plants require either shade or low competition levels in order to thrive. However, *F. gigantea* has a score of 4 on Ellenberg's light scale of 1 to 9, which suggests high levels of shade are unnecessary for its survival. It is of interest that the author has observed excellent growth of established *F. gigantea* plants in high light conditions after the application of a selective broadleaved herbicide.

The half-lives for *F. gigantea* and *C. sylvatica* were 3.0 years and 3.5 years respectively. These are similar to that of 2.05 years calculated for *Anthoxanthum odoratum* (Sweet Vernal Grass), which is a perennial grass species (Antonovics 1972).

If the failure of *B. ramosa* had occurred in all sites except the ancient copse, it may have been assumed that it required undisturbed, shady woodland habitats with particular soil conditions for growth, and therefore that it could not occur outside ancient woodland. Although it is naturally distributed in hedges and woodlands (Clapham *et al.*

1962), other researchers (Down & Morton 1980) have been able to transplant this species successfully from woodland areas into nursery beds with little shade. In the present study, the failure of *B. ramosa* occurred throughout the sites, and was quite obvious and pronounced even by the end of the first growing season. It is therefore considered that the reason for the demise of this species is probably due to a factor that was present prior to planting, which weakened the species sufficiently to prevent its establishment. It is suggested that although plants were seen to be coming into growth at planting time, they may have been waterlogged during the previous winter, and hence have had weakened root systems, or they may have been diseased. Alternatively, *B. ramosa* may be a species which is short-lived, and which relies more significantly upon seed for propagation than do other woodland perennials.

It is of interest that the ancient woodland forbs survived the introduction into new areas better than the ancient woodland grass and sedge species. This was illustrated by the total half-lives of the field layer species, which were considerably higher for the woodland forbs than for the grass and sedge species. The study of regenerative strategies in Chapter 5 indicates that the woodland grasses and sedges all reproduce predominantly by seed. Whilst *B. ramosa*, *C sylvatica*, and *F. gigantea* were all successfully propagated prior to introduction, it is possible that they may simply be difficult to transplant. Hence, it is considered that these species may be more successfully introduced into new areas as seed. However, factors such as low seedling survival in areas of high competition would necessitate further research to substantiate this theory.

4.5.2 The variability in the performance of the field layer species.

From the survival data (Table 16) and the species half-lives (Table 17), it could be argued that plant numbers of all species may continue to decline in subsequent years, and hence that long-term survival cannot be assumed from a short-term study. It was for this reason that various growth characteristics for each species were monitored. In this way, the establishment potential of each species in the different woodland conditions could be assessed more realistically, and hence the likelihood of a species to persist under a particular set of environmental conditions could be ascertained. Since the species

half-lives indicate population decay, it is also important to know whether recruitment will sufficiently replenish such population loss.

The results of the monitoring of different growth characteristics used to indicate species' performance did show some clear trends. However, not only were there differences in the response of each species to variable environmental conditions, but also the growth characteristics monitored for any one species often exhibited variable responses. Therefore, each of the five surviving field layer species is considered separately in terms of its performance at different sites. From this, the ability of each species to persist in the woodlands in the long term is appraised.

Soil samples from the five experimental sites were analysed in order to characterise the soils, and to explore any differences found between them. Although some differences were found, none of these are considered sufficiently great to have a significant influence on the performance of the introduced species, particularly because the chosen species had broad ecological amplitudes, not specific soil requirements. No clear relationships were found between the differences in soil characteristics from site to site and the performance of the introduced species.

4.5.2.1 The performance of *Carex sylvatica* at different woodland sites.

The results of the monitoring of vegetative shoot counts, flowering tillers and leaf lengths for this species, indicate that it was generally able to perform just as well in control plots as in those which had been treated with herbicide or mulch. At few sites were there significant differences in the performance of the individuals which survived. The number of flowering tillers produced was low throughout both control and herbicided plots, and mean leaf lengths showed no clear pattern, ranging only from 28.3cm to 36.9cm over all treatments at all sites. It is only the vegetative shoot count, in the control plots that produced significant differences. *C. sylvatica* produced more vegetative shoots in shady areas with low competition levels, and may be expected to persist longest in these conditions. Earlier observations of its poor survival in very light, highly crowded plots also strengthen this conclusion. It is a plant of open woodland, which often grows in rides, and grassland as a woodland relic (Clapham *et al.* 1962), and which does not require deep shade. It should persist well in semi-shaded, weed-free

conditions, but probably will not be easy to transplant into very young plantations where both light levels and competition are high.

4.5.2.2 The performance of *Festuca gigantea* at different woodland sites.

The results for *F. gigantea* showed more marked differences in performance than those for *C. sylvatica*. In the control plots, leaf lengths were significantly longer in the two shadiest sites, whilst the mean number of vegetative shoots was higher in the young and mature forest sites where competition levels were relatively low. In the herbicided plots, there was a marked difference in the performance of *F. gigantea* in terms of both vegetative shoot number and flowering tiller count. The number of flowering tillers, although variable, showed a positive correlation with light, whereas the vegetative shoot count increased in all sites with herbicide treatment, and remained highest in the young and mature forest plots. Taking into account the low percentage survival of *F. gigantea* in the new plantation in all three treatments, it is suggested that this species can be successfully introduced into established plantations, *i.e.* those more than 12 to 15 years old, where increased shade levels reduce the % cover of competing weed species. Indeed, it has been observed within such plantations in Milton Keynes, where it thrives in areas of low competition. The application of herbicide is unnecessary for the successful introduction of this species if it is planted away from existing areas of competing weeds within shady sites.

4.5.2.3 The performance of *Circaea lutetiana* at different woodland sites.

The results for *C. lutetiana* planted into control plots indicated that it generally produced more vegetative shoots and more, longer leaves as shade levels increased. The large increase in leaf length in the ancient copse was possibly due to etiolation in the very low light levels at this site. The performance indicators therefore demonstrate that this species can grow well in any shady area. This is in accordance with the natural distribution of this species in woods and shady places (Clapham *et al.* 1962). In the control plots, leaf lengths and counts, and vegetative shoot counts were significantly reduced in the new plantation, and leaf and vegetative shoot counts were reduced in the farm woodland, *i.e.* both the sites with higher light and competition levels. It has already been explained that high percentage cover of grass species significantly affects the survival of this species in such areas. It is clear that a grass sward also affects the

performance of those individuals that do survive. It is possible that these weakened plants may not survive in the long term.

In the herbicided plots, the general trend is for the performance of this species to be strongly enhanced once the competition levels have been reduced. All of the growth factors that were monitored were significantly enhanced in the new plantation and farm woodland sites. The differences found between the treatments at the young forest site are considered to be because the control plot was much drier than the herbicided plot and did not offer good conditions for growth of this, or indeed any other, species. *C. lutetiana* appeared to benefit from the application of herbicide and was able to perform well in higher light levels once competition was reduced. This species scores 4 on Ellenberg's light scale of 1 to 9 (Ellenberg 1988), indicating that it does not require deep shade once established. Its growth may also have been promoted by high phosphate levels once other weed species were removed. Leaf counts and vegetative shoot counts were also significantly increased in the new plantation mulch plots. It is of interest that in the ancient copse the vegetative shoot count was significantly lower in the herbicided plot than in the control plot. It seems that *C. lutetiana* is able to grow well amongst *H. non-scripta*, but that it produces fewer shoots and spreads less when *G. aparine* becomes dominant, as in the herbicided plot. Packham & Cohn (1990) list it as being a C-R strategist (after Grime 1979), but clearly it cannot compete successfully against very vigorous weed species.

If competition from weed species is reduced either by herbicide or mulch, this species can be introduced successfully into new and very young plantations where it will benefit positively from the increased light levels. It has a high capacity for vegetative spread (Salisbury 1976 and Raven 1963), and should persist until the tree canopy develops sufficiently to increase shade levels and competition is naturally reduced. In sites where shade levels are already sufficient to reduce competition, *C. lutetiana* can be introduced without any site pre-treatments.

4.5.2.4 **The performance of *Lamiastrum galeobdolon* at different woodland sites.**
The results for this species indicate that whilst the number of both vegetative shoots and flowering stems was greatly enhanced by high light and low competition levels, both

leaf lengths and stolon lengths were somewhat higher in shady sites. This was particularly marked in the young forest site. (The exception of the significant increase in mean leaf length in the new plantation herbicided plot is possibly because leaf lengths were monitored in August, by which time a 'canopy' of tall weeds had developed which shaded the *L. galeobdolon* beneath.) As explained for *C. lutetiana*, the young forest control plot did not offer ideal conditions for plant growth, possibly due to dryness. Packham (1983) recorded poor growth of this species in dry areas. It is considered that the differences recorded between herbicided and control plots at this site would have been less if the plots had been more alike.

With no pre-treatment, *L. galeobdolon* performed best in shaded conditions, particularly in the young and mature forest plots, where competition was less than in the ancient copse. Packham and Cohn (1990) measured growth factors for this species in a range of light conditions. They found that plants, in the absence of competition, grew better if light was increased to 20-30% (from 6%) of that found in the open. They considered that high humidity was more important for the successful growth of this species than low light levels. A study in Germany (Werner *et al.* 1982), where *L. galeobdolon* was grown in full daylight and shade, indicated that this species reached light saturation at only just above 20% of full daylight, and was more influenced by light intensity than light quality. Though *L. galeobdolon* shows less photosynthesis in blue light than red light, this reduced efficiency is compensated for by an increase in the size of the photosynthetic apparatus. This is of ecological importance, as in shade this species can produce 2-4 times as much chlorophyll and nitrogen than in full daylight.

By 1992, mean stolon lengths in the ancient copse were significantly lower than at the same site in 1991, and in the young forest plot, in both treatments. This may have been due to the high amount of competition, from *H. non-scripta*, *R. fruticosus*, or *G. aparine*, at the ancient copse. Additionally, severe wilting of stolon leaves was observed in the ancient copse plots, particularly in the drier growing season of 1991. Soil moisture content decreased most between May and September at this site (Fig. 25). This is due to the large uptake of water by roots of trees, which were oldest and, hence, largest in the ancient copse. Al-Mufti (1977) also observed a decline in the percentage cover of this species due to drought-stress, because wilted leaves did not recover. Although *L.*

galeobdolon can endure some water-stress (Packham & Willis 1976), this factor and the high competition levels in the ancient copse probably explains the shorter mean stolon lengths recorded at this site in 1992.

At the young and mature forest sites, vegetative growth of *L. galeobdolon* was remarkable, with many stolons of over 2m in length found at both sites, particularly in the second growing season. Salisbury (1976) recorded mean stolon lengths of 91.5cm in wet years and 59cm in dry years in established populations, which are much shorter than stolons growing in similar conditions in this study. The same author, however, also measured stolons of plants growing in a beech wood during a single, favourable season, the lengths of which ranged from 50-156cm in length. In their work describing the ecological amplitude of this species, Packham & Willis (1976) indicate that *L. galeobdolon* grows between pH 3.8-8.0, but that its growth is poor below pH 4.3. The soil reaction values at the five experimental sites ranged from pH 4.4 in the mature forest to pH 7.5 in the farm woodland. *L. galeobdolon* was therefore growing well within its natural pH range. This species is clearly able to survive and grow well in quite acidic soils with fairly low pH, if conditions of shade, competition and soil moisture are all favourable.

The highest mean leaf lengths, measured from petiole base to lamina tip, were also recorded in the young forest herbicided plot. These are similar to the maximum lengths of *L. galeobdolon* shade leaves, which are described as having 8cm laminas and 3-6cm petioles (Packham 1983).

A feature of all three shady sites in this experiment, was the deep layer of leaf litter on the woodland floor, particularly in the young and mature forest plots. *L. galeobdolon* has an adaptation of shoot structure that enables it to penetrate leaf litter (Sydes & Grime 1981a), and hence can thrive in such conditions, which may be less than optimal for other woodland species. Indeed, Sydes & Grime (1981b) found experimentally that the biomass of *L. galeobdolon* in litter treatments was significantly increased over that in control plots with no leaf litter. They considered that leaf litter helped the development of roots above the mineral soil and hence allowed the exploitation by *L. galeobdolon* of the nutrient release in the decomposing leaf litter. The high humus content in the surface

layers of woodland soils which produces high nutrient status and moisture content is also known to promote high levels of vegetative reproduction in such species as *L. galeobdolon* (Salisbury 1976). That the vegetative growth of this species (as described by leaf and stolon lengths) in the present study was highest in the young and mature forest sites, is thus in accordance with the results of other research.

In contrast to the best conditions for leaf and stolon growth, both the number of vegetative shoots and flowering stems produced by *L. galeobdolon* showed a strong positive correlation with light in plots where competition had been reduced. It is widely accepted that diminished light intensities (in the shade phase) affect flowering in many woodland field layer species (Salisbury 1976). In woodland conditions, *L. galeobdolon* generally flowers more vigorously in hot, dry summers, and produces more stolons in cool damp summers (Packham & Willis 1976). Flower production in this species is reduced in both filtered and dense shade (Mitchell & Woodward 1988), but if plants are well established, they flower well in all but the deepest (*i.e.* 6%) shade levels (Packham 1983). Another woodland herb that is similarly affected by light intensities is *Lysimachia nummularia* (Creeping Jenny). This also spreads almost entirely by runners and produces seed only in very hot summers where shade is slight (Salisbury 1976). The correlation of flowering stem production with increasing light levels in this study was therefore to be expected, but may be due to increased temperature rather than or as well as increased light. Many seedlings of *L. galeobdolon* were noted in the young and mature forest plots, though not at other sites. Packham (1983) noted that seedlings could be found in large populations in late spring, but only beneath moderately dense tree canopies. Whilst flower production was high in the new plantation and young forest sites even in 1991, and successful seed set was observed in the first season, it is considered that the high competition levels recorded in these sites probably hampered seed germination and survival.

That stolon number increased in the lighter plots was rather surprising, as other studies, *e.g.* Salisbury (1976), record more stolon production in cool, wet conditions than warm, dry ones. However, in the very light areas *L. galeobdolon* produced many more short stolons than in the shadier plots. This can be compared with differences observed in the clonal growth of another Labiate *Glechoma hederacea* (Ground-ivy) grown in sand in

a greenhouse experiment (Slade & Hutchings 1987). With high available nutrients, *G. hederacea* produced a high number of stolons with short internode lengths, whereas with no nutrients, it produced few, long stolons, and exhibited more pronounced linear growth. The high phosphate levels at the lighter sites in the present study may therefore be responsible for the increased number of short shoots. Packham (1983) found that when *L. galeobdolon* was grown in pots in 70% and 100% light, plants had to be watered frequently during the summer to be kept alive. Although light levels were similarly high in the new plantation and young farm woodland, the competing vegetation possibly maintained humidity, and hence enabled survival in what would otherwise have been very dry plots.

Generally, this species grows best in shadier places. Indeed, on Ellenberg's shade scale of 1-9, it is given a score of 2. If introduced into shady areas with low competition levels, it will clearly grow well and will flourish even outside ancient woodland habitats. It is also possible to introduce this species into high light areas where its performance will be increased by removal of competing vegetation. Further monitoring will show whether it can persist in such areas once competition levels become high again. Appropriate forms of pre-treatment to reduce competition are herbicide in very grassy areas, or mulch if the surrounding competition is less prevalent.

4.5.2.5 The performance of *Primula vulgaris* at different woodland sites.

It has been demonstrated that *P. vulgaris* survived well throughout the experimental sites in both herbicided and control plots, and in the new plantation mulch plot. The leaf count for this species within the sites and treatments was relatively unaffected by the varying conditions. In the control plots, leaf count per plant altered very little from site to site. It was more variable within the herbicided plots where there was less competition during the first year, but was only significantly higher in the lightest sites. Leaf lengths were variable in the control plots and showed no clear trend. (Leaf lengths in the young forest plot were possibly low due to dryness.) In the herbicided plots, the number of leaves was significantly higher in light situations. Increased photosynthesis during the first growing season probably enhanced the establishment of *P. vulgaris*. This species can occur in both open and shaded habitats, and it exhibits considerable flexibility in its photosynthetic apparatus, enabling utilization of high light levels (Whale

1984).

The flowering performance of *P. vulgaris* correlated positively with increased percentage daylight in the herbicided plots. This indicates that in areas of low competition, this species can flower better in high light levels. Helliwell (1980) studying the species in north-western England, demonstrated that both growth rate and seed production in *P. vulgaris* were related to the amount of light in summer, and to a certain extent to the amount of light in spring. In shading experiments to test these effects, the maximum number of flowers was produced at the highest light levels employed. These were 20% relative illumination in summer and 37% between November and May. Light at a constant 37%, and at 20% in summer preceded by 37% from February to May, also produced very high numbers of flowers. Higher light levels than 37% were not used in Helliwell's experiments. When plants were grown on different woodland soils, the soil with high levels of organic matter, potassium, calcium and phosphate, but at fairly low pH of 4.8, produced significantly more flowers than plants grown on other soils. The number of seeds produced by plants was also highest at the highest light intensities. Helliwell also found that the number of flowers produced correlated very closely with the dry weights of the plants. In the present study, highest flower counts were recorded in plots at high light intensities, where leaf size and number were similarly high. In the present study, good seed set was observed throughout the sites during the first growing season. By 1992, seedlings were very numerous around plants in the young and mature forest plots, and to a lesser extent in the ancient copse. A few seedlings were also seen in the farm woodland, but the majority of these were short-lived. No seedlings were observed in the new plantation; this was probably due to the high competition levels, as for *L. galeobdolon*. These observations are in contrast to those of Helliwell (1980), who recorded that not only were low levels of seeds produced beneath a canopy, but also that there were very few seedlings in the field, or, more usually, none at all. The primroses in this study probably set seed well in the first season as a result of high levels of photosynthesis in the previous year prior to being planted into shadier conditions. Only further monitoring in future years will demonstrate whether the plants that were introduced into different woodland sites will continue to flower and set seed at such high levels.

The poor growth of *P. vulgaris* plants in soil of less than pH 4.7 reported by Helliwell (1980), was not found in this experiment. Whale (1984) grew this species successfully in a culture solution at pH 4.2 and found that germination and growth was good at Madingley Wood, Cambridgeshire at pH 4.1. As for *L. galeobdolon*, it is suggested that given suitable conditions of shade, low competition and moisture, *P. vulgaris* tolerated a slightly more acidic soil.

The study has shown that it is possible to introduce *P. vulgaris* into woodlands of different ages, whether conditions are light or shady. *P. vulgaris* scores 6 on Ellenberg's light scale of 1 to 9, indicating a preference for lighter areas. Primroses are found naturally in woods, hedgerows and banks, and are able to tolerate a range of light levels. Except in areas where the climate is sufficiently rigorous to provide protection, they require the woodland or hedgerow habitats for protection against strong competition (Crawford 1989). This study has shown that in sites with high levels of competing vegetation, this species is able to survive well, certainly in the short-term. However, its performance is significantly increased if this competition is removed by either herbicide application, or by a covering of mulch at very young sites.

4.5.2.6 The performance of the species in the screening experiment.

Five of the six species in the screening experiment generally survived and performed well in the new plantation and young forest plots. All of the species exhibited poor survival and growth in the new plantation control plot, and clearly could not compete successfully against vigorous weed species. *C. majus* was the only species which performed significantly better in the new plantation, where it flowered more profusely than in the young forest plots. Indeed, this species is a component of some unimproved grasslands, as well as old woodlands.

Whilst the performance of both *A. nemorosa* and *E. amygdaloides* was equally good at both sites, that of *O. acetosella* and *V. montana* was enhanced at the shadier site. Both of these species are known to tolerate very high shade levels. Indeed, *O. acetosella* grows better in lower light levels (Packham & Willis 1976), and scores only 1 on Ellenberg's shade scale. Further, in a study of the effects of a conifer nurse crop on an undisturbed woodland flora community (Pigott 1990), *O. acetosella* was the only species

that increased in density in the heavy shade cast by the conifers. It also flourishes on soils which have a pH of less than 4 (Packham & Willis 1976), and so was in almost ideal conditions at the young forest site. *V. montana* is also extremely shade tolerant (Fitter & Ashmore 1974), and can produce prostrate shoots of between 30 to 60cm in shady areas with low competition (Salisbury 1976).

Whilst this screening experiment only dealt with small numbers of plants, it at least demonstrated that a wider range of species can be introduced into woodlands than those investigated in the main experiment. Clearly, given suitable conditions of shade and low competition, a number of ancient woodland field layer species can be introduced successfully into other woodland areas. As in the main experiment, most can also benefit from high light conditions, provided that levels of competing vegetation are first reduced.

4.5.3 A consideration of the experimental objectives.

4.5.3.1 The timing of introductions and the necessity for ground pre-treatments.

The development of a tree canopy controls the shade levels within a woodland. Thus, as a woodland becomes established and matures, the shade levels gradually increase with time. In this way, the growth of vegetation beneath trees in the field layer is controlled. Generally, as shade levels increase, the more competitive weed species gradually decrease, and a woodland field layer develops which is dominated by species that are able to tolerate the shady conditions. Field layer vegetation therefore changes with time, as the tree canopy matures.

This natural control of vegetation by shade frequently poses the habitat restorationist who wishes to enhance woodland field layers with a dilemma: whether to wait until shade increases sufficiently to reduce competition levels or whether to reduce the competition levels artificially. The experimental results presented here have demonstrated that a range of ancient woodland field layer species can be successfully introduced into areas outside ancient woodlands. The species can grow well and become established, particularly in shady conditions with low levels of competing vegetation. In

such conditions, ground pre-treatments, such as the application of herbicide, are unnecessary. It is only in situations with very high levels of competition that a pre-treatment is beneficial to both the initial survival and the subsequent performance of the woodland species. In these conditions, once the existing vegetation cover is reduced, the majority of introduced species clearly benefit from high light levels, as in the coppice cycle, and their performance is better than in established woodland.

The timing of introductions of field layer species and the necessity for ground pre-treatments therefore go hand in hand, and one factor cannot be considered without another. Simply, if a practitioner wishes to enhance a plantation at an early stage in its development when shade levels are low, then a ground pre-treatment is very beneficial, whereas if shade levels are beginning to increase, or are already high, then this study has shown that successful introductions can be made without ground pre-treatments. It may be beneficial in younger plantations to restrict introductions to shadier areas, or to those where leaf litter is beginning to accumulate. Particularly in urban schemes, where trees such as *A. hippocastanum* and *Poplus* species are used extensively, leaf litter very quickly builds up and successfully reduces competition levels. In open areas of high light, both herbicide or mulch are appropriate pre-treatments for the majority of field layer plants; these give field layer species with low competitive abilities the chance to establish. Herbicide may be used to kill existing ground vegetation and leave bare ground for planting, as in this study. Alternatively, a herbicide may be used that is selective for grass species. The impact of grass species on woodland herbaceous species is significant (Sydes & Grime 1981b), as grasses are capable of spreading rapidly to form a dense, elevated canopy composed of numerous shoots, and a comprehensive network of fine roots within the soil. It is therefore considered that competition by a grass sward is a very significant barrier to species survival and subsequent establishment, whereas for most species the more discrete clumps of broadleaved weeds are a much less significant barrier. This selective herbicide technique needs to be investigated further before more specific recommendations can be made. Mulch is also a method of ground pre-treatment which enhances the survival and establishment of some species in high light conditions. However, it is not an appropriate treatment for all species, particularly if applied only to small areas within open grassland. In these circumstances, such a treatment can make the introduced plants susceptible to severe

weather conditions, *e.g.* frost. Further, the use of herbicide can also make the introduced plants accessible to herbivores, by increasing their apparency (Feeny 1976).

4.5.3.2 The choice of species for introduction.

As stressed by Packham & Cohn (1990), the introduction of woodland field layer species into any new area should not only reflect and represent those species in local ancient woodlands, but should also not include rare species with very restricted distributions. Due to lack of availability, the rarer species are less easy to obtain, and this factor alone should curtail their use in restoration schemes. The floras of local woods will give a good indication of those species that will survive within a new plantation, since the meterological influences will be very similar. However, substrates are more variable, particularly if one is dealing with an urban woodland, for example, where soil may have been imported into the site. In such circumstances, the local and natural geological conditions may be quite different from those supporting the young plantation. This study has demonstrated, however, that species were able to grow in a range of soil conditions, and that plants had less exacting requirements in terms of soil conditions than was expected, in the short term at least. Hence, if species are introduced into areas with suitable levels of shade and moisture, most should survive and establish well.

4.5.3.3 The method of species introduction.

Many ancient woodland species produce seed irregularly, in small quantities, exhibit poor germination, and develop from seedling to mature plants only very slowly. (Refer to Chapter 5 for specific details.) Secondly, even if seeds do manage to germinate, as did those of *L. galeobdolon* and *P. vulgaris* in the new plantation, they may very soon be overtaken by more robust and competitive species, particularly in high light levels. In such 'closed' vegetation, it is very difficult for plants of perennial herbaceous species to develop from small seeds to the mature, fertile stage (Tamm 1972). The establishment of many ancient woodland field layer species is therefore enhanced by using young plants, which already have some competitive capacity and the ability to reproduce more quickly. Even if plants cannot persist long enough for shade levels to increase and hence reduce competition, seed may be set at an early stage and can contribute to the seed bank until such a time when conditions become suitable for germination. However, this

study has shown that the survival of ancient woodland grass and sedge species introduced into new areas was rather poor. It has been suggested that such species, which reproduce mainly by seed, may be more successfully introduced as seed. This highlights the importance of a knowledge of species regenerative strategies prior to their introduction. This is discussed further in Chapter 5.

Regarding planting density, plants in this experiment were fairly dense, at $9m^{-2}$. This was successful and allowed seed set. Very low planting densities might discourage cross pollination, and thus reduce reproductive capacity. As demonstrated in planting experiments in Milton Keynes (Chapter 2), plants introduced in moderate to high density clumps have higher seed production. Plants should therefore be introduced in patches to mimic those in natural woodlands and to increase the chances of successful reproduction. Pimm & Gilpin (1989) consider a problem that arises when designing species reintroductions, as to whether to introduce all of the individuals of a species into one place at one time, or whether to separate the individuals into several groups. They suggest that whilst introductions made into one place minimize the problems encountered by very small populations, this may allow all of the individuals to be introduced into the wrong place at the wrong time. The results of the present study and of the introduction of woodland herbaceous species as plants into young plantations (Chapter 2), indicate that with suitable conditions of low light and/or vegetation levels, plants should establish more successfully if introduced in sizeable groups, rather than as discretely dispersed individuals.

4.5.4 Conclusions.

It is possible to make introductions of ancient woodland field layer species into new woods. In their ancient woodland refuges, they tolerate or are adapted to low shade levels to avoid competition. Outside ancient woodlands, their performance can be enhanced, if growing conditions are suitable, and, most importantly, if competition levels are low. It has been demonstrated in this experiment that outside such refuges at least some of the ancient woodland species clearly benefit from increased light levels. Particularly if introduced into shady, dense young plantations, where the field layer is

sparse and often uninteresting, they are capable of filling an empty niche, which they otherwise would colonise only very slowly, perhaps during hundreds of years, or possibly not at all. In light areas, competition must be significantly reduced by herbicide or mulch treatments, if plants are to establish successfully, but elsewhere pre-treatments appear to be unnecessary.

If the enhancement of woodland field layers is to be fully representative of the flora in ancient woodlands, then ancient woodland field layer species must feature in any restoration scheme. Whilst many field layer species associated with woodland edge or margin, hedgerows, and shady banks can be introduced by seed into new woodland areas (see Chapter 2), most ancient woodland species are better introduced as plants. As planted units, they have just enough competitive ability to withstand competition from other species. The introduction of plants also enables species to reach maturity relatively quickly, and so to flower and set seed within their new environment. This should assure their persistence in the long-term.

In general, the survival of the ancient woodland species was good, although this was declining slowly with time. This decline was offset, however, by species' performance, particularly in the young and mature forest sites, which subsequently contributed both to vegetative spread and to the seed bank.

5. The autecology of woodland field layer species.

5.1 Introduction.

5.1.1 The requirement for information about woodland field layer species.

The feasibility of introducing woodland field layer species into new plantations has been demonstrated in Chapter 2. The results of the field trial have highlighted distinctions between the growth strategies of different field layer species, which clearly influenced their ability to establish (Chapter 3). It follows that a source of detailed information about the characteristics of woodland field layer species would be beneficial for practitioners and restorationists, because recognition of the varying growth strategies and requirements of species would both facilitate successful introduction, and would enable their subsequent survival and establishment to be enhanced. Indeed, Packham & Cohn (1990) stress the need for a "gardeners' guide" to the woodland field layer species that may be involved in introduction schemes. They also emphasise that "a detailed knowledge of species' behaviour is essential" for introductions to be made successfully. The purpose of this chapter is to compile details about the autecology of a range of woodland field layer species. Information about the growth and establishment of species has been gathered from literature sources, field observations and experimental work. The amalgamation of such data should provide a useful source of information for reference prior to making introductions of field layer species.

5.1.2 The selection of woodland field layer species.

Peterken (1981a) describes the long-term history of the woodland flora. Using details of pollen analysis from Godwin (1975), the woodland species are placed into four sub-groups, namely 'rapid colonisers', 'wetland-woodland species', 'heathland-woodland species' and 'woodland species'. These groups are distinguished by the development of their habitats through the post-glacial period, and by their presence or absence at the forest maximum. The fourth group of 'woodland species' represent the characteristic

woodland species of the natural Boreal and Atlantic forests. These species are now mainly found in ancient woodlands and have only a limited capacity to colonise recent secondary woodlands. However, with their woodland associations, species of all four groups are shade-tolerant to some extent.

In today's woodlands, these species can be separated into two main groups by their degree of shade-tolerance. Some are light-demanding, marginal or woodland edge species, whilst others are true woodland species, tolerant of deep shade. For this study, thirty field layer species which are characteristic of English Nature South region woodlands have been selected. Both the marginal species and deep shade species are encompassed. These species include forbs, grasses and sedges, and are considered to be representative of woodland field layer species within the region. The chosen species are interesting and attractive, are readily available for introduction, and are not sufficiently rare or limited in distribution for their introduction to raise ethical concerns. One of the species, *G. aparine*, is a secondary woodland species (Peterken 1981a), and has been selected as a contrast to the others. The introduction of this species into new woodlands is neither suggested, nor probably necessary!

5.1.3 The importance of different characteristics and growth strategies.

Whether the components of a woodland field layer can be described as marginal or deep-shade species, they possess other characteristics which are distinctive and diverse. It is these characteristics, which concern aspects of growth and reproduction that are relevant to species introduction into new woodlands. For example, *S. dioica* sets copious amounts of highly viable seeds, whereas *A. reptans* sets few, poorly germinating seeds yet reproduces well in a vegetative manner. Such information clearly has an important bearing on the method of introduction for these two species. (*S. dioica* could be introduced as seed, whilst *A. reptans* may be more successfully introduced as young plants.)

The method of reproduction, or regenerative strategy, is, perhaps, the most important characteristic about which information is gathered, as this is so clearly linked to the

method by which any species is introduced into a new area. Features such as the seed to flower time period, the amount of seed production, seed weight and method of seed dispersal are also linked to information on the method of reproduction. Germination characteristics such as requirements for chilling and/or light, and whether the species forms part of a seed bank or maintains a persistent seedling bank are also of interest. The ability of a species to reproduce vegetatively and to remain winter-green are investigated. Species details such as soil type and habitat requirements, which give an indication of site suitability are noted.

There is a need to investigate such characteristics to gain a wider comprehension of the autecology of the field layer species. The compilation of this information provides a knowledge source which clearly has practical uses. In addition, it enables both comparisons and distinctions to be made between species with different strategies, and is therefore of ecological interest.

5.1.4 The sources of autecological information.

The majority of the information presented in this chapter has been gathered from existing literature. Many of the references which have been used present some autecological details about just one, or, at most, a few woodland field layer species, and then often about only one aspect of growth, *e.g.* germination requirements. Hence, the references are many and varied.

Two small-scale investigations have also been carried out to elucidate two aspects of the growth of woodland field layer species, dispersal and germination. The first is an investigation of the dispersal capacity of ancient woodland field layer species into a plantation. The 43 year old plantation, which is surrounded by ancient woodland, provides an ideal opportunity to study the natural dispersal of ancient woodland field layer species from an existing and established habitat into a newly created one. The second study is an experiment which was designed to investigate the germination potential of ancient woodland field layer species. Seeds of 14 species were tested for a chilling requirement prior to germination. The influence of soil type on germination was

incorporated into the experiment by sowing seed into both a proprietory seed compost and an ancient woodland soil.

5.2 Site details.

5.2.1 An investigation of the dispersal capacity of ancient woodland field layer species into a plantation.

This investigation was carried out within Linford Wood, which is situated to the north of the city centre of Milton Keynes (SP 847405). The wood, which covers 38ha, has records dating back to 1283, and is at least 700 years old. The underlying geology is chalky boulder clay, which has given rise to a clay loam soil (Casey 1982). The wood has a high mixed canopy of *F. excelsior*, *A. campestre* and *Q. robur* standards, with a few tall trees of *M. sylvestris* and *C. monogyna* beneath. The shrub layer consists primarily of *C. avellana*, *F. excelsior*, *Ulmus procera* (English Elm), and *P. spinosa.* The field layer is diverse, and includes 14 ancient woodland species. The composition of the field layer varies according to the drainage. In wetter areas, *Deschampsia cespitosa* (Tufted Hair-grass), *Filipendula ulmaria* (Meadowsweet), and *Cirsium palustre* (Marsh Thistle) are frequent, whereas in drier areas, *H. non-scripta* and *M. perennis* predominate (Casey 1982). The wood is very actively managed, being within the city and surrounded by urbanisation.

The plantation is an area of 2.58ha within the ancient woodland, separated from it only by a hard core path about 2m in width. It was a meadow until 1949, when it was planted with *Picea abies* (Norway Spruce). During the intervening years the trees have been thinned, and the spacing is now about 5m. The field layer has been allowed to develop naturally and no deliberate species introductions have been made. Species such as *Primula veris* (Cowslip) are present within the field layer, indicating its previous meadow nature. There has been open access to the plantation from the ancient woodland, and well-worn paths exist across the site which are regularly used by the general public.

5.3 Materials and methods.

5.3.1 An investigation of the dispersal capacity of ancient woodland field layer species into a plantation.

5.3.1.1 The monitoring of the field layer.

In July 1992, the field layer vegetation within the 1949 plantation was recorded and all existing species were listed. A list of the ancient woodland field layer species within neighbouring compartments of the ancient woodland was also compiled from a report entitled 'Vegetation survey of Linford Wood' (Cobham Resource Consultants 1984).

5.3.1.2 The monitoring of the distribution of ancient woodland field layer species within the plantation.

Within the plantation, four ancient woodland field layer species, *C. sylvatica*, *C. lutetiana*, *F. gigantea* and *S. europaea*, were identified from the list of species recorded in 5.3.1.1. In August 1992, twenty five individual plants of each of the first three species were chosen at random whilst walking through the plantation. The distance of each plant from the edge of the plantation was measured as accurately as possible, and was recorded. Only 7 plants of *S. europaea* were found, and the distance that they were growing from the edge of the plantation was also measured. From the measurements obtained for each species, the mean distance of the species from the edge of the plantation was calculated.

5.3.2 An investigation of the germination potential of ancient woodland field layer species.

5.3.2.1 The collection of seeds.

Between June and September 1991, approximately 1000 seeds of each of 10 ancient woodland field layer species were collected from wild plants. Table 22 shows the date and place of collection for each of the species. In addition, 4 species were ordered from John Chambers seed merchants. Seed was requested to be as fresh as possible, but this could not be guaranteed. Only 115 *O. acetosella* seeds and 100 *Vicia sepium* (Bush

Vetch) seeds were collected from wild plants, and no further seed was available for either of these species. All seeds were kept in paper bags until required.

Table 22. *Details of ancient woodland field layer species seed collection.*

SPECIES	Date	Place	No.
Allium ursinum	7/91	Green lane, Hawkley, Hants.	1000+
Campanula trachelium	8/91	Hedgebank, Ropley, Hants.	1000+
Conopodium majus	6/91	Old pasture, Charlwood, Hants.	1000+
Euphorbia amygdaloides	8/91	Silwood Park, Berks.	1000+
Galium odoratum	7/91	Woodland, Charlwood, Hants.	1000+
Hyacinthoides non-scripta	9/91	West's Copse, Berks.	1000+
Melica uniflora	7/91	Woodland, Charlwood, Hants.	1000+
Oxalis acetosella	8/91	West's Copse, Berks.	115
Sanicula europaea	7/91	Woodland, Charlwood, Hants.	1500
Vicia sepium	8/91	Hedgebank, Charlwood, Hants.	100
Lamiastrum galeobdolon	2/92 1000+ of all species purchased from John Chambers seed merchants.		
Milium effusum			
Primula vulgaris			
Viola odorata			

5.3.2.2 **The collection of soil.**

In March 1992, approximately 50kg of soil was dug from West's Copse, Berkshire and put into plastic sacks. The soil was sieved, using a 2mm sieve, to remove large roots, bulbs and other pieces of undecayed organic matter. Prior to use, the soil was kept in open sacks to allow aeration. A sufficient quantity of Arthur Bowyer's multi-purpose seed compost was also obtained.

5.3.2.3 **The seed sowing.**

In mid March 1992, 1000 seeds of each of 12 ancient woodland field layer species were counted into 20 groups of 50, placed into paper bags and labelled. For *O. acetosella* and *V. sepium* 10 groups of 10 seeds were counted and stored.

Between the 17th and 19th of March, 4.5" diameter plastic pots were 4/5 filled with either woodland soil or seed compost, and watered. For each field layer species, 10 groups of 50 seeds were mixed with a little woodland soil and scattered onto the 10 pots of the moist woodland soil. This was repeated with another 10 groups of 50 seeds, using 10 pots of compost. This made a total of 20 pots for each species. For *O. acetosella* and *V. sepium*, 5 groups of 10 seeds were sown into woodland soil, and 5 groups were sown into compost.

For each of the field layer species, 5 pots of each soil type were placed outside and covered with plastic netting to prevent disturbance by birds or small mammals. The remaining 5 pots of each species in both soil types were placed in a 5°C Controlled Temperature (CT) room. For *O. acetosella* and *V. sepium*, 3 pots of each soil type were placed outside, and 2 pots of each soil type were placed in the 5°C CT room. All of the pots were checked regularly and kept damp by misting with water. As a control, 2 pots of each soil type, but without any seed, were placed both outside and in the CT room. These were treated in exactly the same way as those pots into which seed had been sown.

After 1 month, the pots were removed from the CT room, placed next to those outside, and covered with plastic netting.

5.3.2.4 The monitoring of seed germination.

From mid April onwards, the pots were checked every 2 weeks and germination was recorded. The number of seedlings of each of the sown species was carefully recorded. In the sown pots, and in the control pots, those species which germinated but had not been sown were removed from the pots, identified and listed.

5.3.3 The sources of autecological information.

Information about the ecological characteristics of the 30 woodland field layer species was gathered from the following sources: Baker (1947), Beattie & Lyons (1975), Bierzychudek (1982), Brown & Oosterhuis (1981), Buckley (1987), Buckley & Knight

(1989), Cavers (1979), Clapham *et al.* (1962), Culver & Beattie (1980), Daft *et al.* (1980), Ernst (1979), Grime (1979), Grime *et al.* (1981), Grime *et al.* (1984), Handel (1978), Helliwell (1980), Knight (1964), Merryweather (1991), Packham (1978), Packham (1983), Packham & Willis (1976), Read *et al.* (1976), Salisbury (1976), Shirreffs (1985), Slade & Causton (1979), Stace (1991), Thompson & Grime (1979), Thompson (1980), Thompson & Cox (1978), and Yanney Wilson (1959).

5.3.4 The data analysis.

5.3.4.1 An investigation of the dispersal capacity of ancient woodland field layer species into a plantation.

From the distance measurements obtained for each of the four field layer species, the mean distance and corresponding 95% Confidence Intervals of the species from the edge of the plantation were calculated.

5.3.4.2 An investigation of the germination potential of ancient woodland field layer species.

For the five replicates in each of the four sowing treatments, mean seedling numbers, with associated 95% Confidence Intervals, were calculated for each of the woodland field layer species.

5.4 Results.

5.4.1 An investigation of the dispersal capacity of ancient woodland field layer species into a plantation.

5.4.1.1 The composition of the field layer.

The list in Appendix C shows the field layer species that were recorded within the 1949 plantation. Species have been grouped according to whether they are generally confined to ancient woodland; species usually found in ancient woodland, but which tolerate other

habitats; and shade-tolerant species, including weeds. Only one species, *P.vulgaris*, that is a poor colonist and is mostly confined to ancient woodland was found within the plantation.

Using the Vegetation Survey of Linford Wood (1984), ancient woodland field layer species were identified which were growing in compartments neighbouring the plantation. Some, *e.g. C. lutetiana* and *S. europaea*, were also growing in the plantation, but 7 species were not found in the plantation. These were *A. nemorosa*, *Epipactis helleborine* (Broad-leaved Helleborine), *F. vesca*, *L. galeobdolon*, *O. mascula*, *Potentilla sterilis* (Barren Strawberry), and *S. nodosa*.

5.4.1.2 The distribution of ancient woodland field layer species within the plantation.

Table 23 shows the mean distance (with 95% Confidence Intervals) that four of the field layer species found within the plantation were growing from the edge of the plantation.

Table 23. *The mean distances (m), with 95% Confidence Intervals, of field layer species growing within the 1949 plantation.*

SPECIES	Distance (m)
Carex sylvatica	16.29 ±5.12
Circaea lutetiana	16.62 ±5.86
Festuca gigantea	18.10 ±6.55
Sanicula europaea	4.50 ±1.39

The mean distance that *S. europaea* was found within the plantation was significantly lower than that for the other three species. There was no significant difference in the distances at which the other three species were growing within the plantation.

5.4.2 An investigation of the germination potential of ancient woodland field layer species.

Table 24 shows the mean number of seeds that germinated for each of the sown species. Five of the species failed to germinate with any of the treatments, and germination was generally low throughout the treatments. The highest number of seedlings recorded was for *C. trachelium* growing outside in woodland soil. There was no significant difference between the germination in any of the four treatments for this, or indeed, any other of the field layer species. A few seedlings of *H. non-scripta* were recorded in May 1992,

Table 24. *Mean seedling numbers, with 95% Confidence Intervals, of a range of woodland field layer species sown into different soils and with different chilling treatments.*

	Outside		Constant 5°C	
SPECIES	Woodland soil	Compost	Woodland soil	Compost
Allium ursinum	0	0	0	0
Campanula trachelium	**27.0** ±6.6	**22.8** ±5.4	**20.0** ±4.1	**22.2** ±6.0
Conopodium majus	0	0	0	0
Euphorbia amygdaloides	**4.0** ±3.2	**5.4** ±4.5	**3.0** ±2.9	**5.8** ±5.4
Galium odoratum	0	0	0	0
Hyacinthoides non-scripta	**1.0** ±1.2	**2.8** ±1.0	**3.4** ±4.5	**1.0** ±0.9
G	**14.8** ±4.2	**10.0** ±5.6	**11.0** ±3.9	**15.4** ±5.3
Lamiastrum galeobdolon	0.6	0	0	0
Melica uniflora	0.6	0.8	0	1.0
Milium effusum	**5.8** ±2.4	**11.0** ±4.9	**5.8** ±4.5	**7.8** ±6.4
Oxalis acetosella *	0	0	0	0
Primula vulgaris	0.8	**3.2** ±2.8	0.2	0.4
Sanicula europaea	0	0	0	0
Vicia sepium *	0.3	0.7	0	0
Viola odorata	0.2	1.2	1.0	3.6

Number of seeds sown per pot = 50. * Number of seeds sown per pot = 10.

G: Seedlings counted October 1992.

but the majority of seedlings of this species were not recorded until October of the same year.

Over all of the treatments, significantly more seeds of *C. trachelium* germinated than those of any other field layer species. Significantly more *H. non-scripta* seeds germinated than those of *E. amygdaloides* and *Milium effusum* (Wood Millet), which germinated significantly better than *Melica uniflora* (Wood Melick), *P. vulgaris* and *V. odorata.*

Appendix D lists 23 species that germinated within the pots of woodland soil, but which were not sown.

5.4.3 The characteristics of woodland field layer species.

Detailed information about a range of characteristics of thirty woodland field layer species is presented in Tables 25, 26 and 27.

Shade-tolerant and woodland marginal species.

Nineteen of the species are present on the English Nature South Region ancient woodland vascular plant list (Appendix A). These species are all tolerant of deep shade in woodlands. The other species are woodland edge or marginal species, which can grow and compete successfully in areas of higher light.

Seed to flower time period.

The time taken for each species to reach flowering maturity varies from a few months to over 10 years. All of the woodland marginal species are able to set seed in their first or second growing seasons. Eight of the 20 deep shade species develop slowly from seed, taking two or more years to reach flowering maturity.

Pollinators.

All of the shade-tolerant field layer species, except for the wind-pollinated grass and sedge species, are pollinated by insects. Some of the insect pollinators are rather

Table 25. *Characteristics of ancient woodland field layer species.* I

SPECIES	South Region Ancient Woodland Indicator	Shade-tolerant, or marginal species	Seed to flower time period (years)	Pollinators	Seed production	Seed weight (mg)	Seed dispersal vectors	Seed bank type	Chilling requirement for germination	Light requirement for germination	Persistent seedling bank	Regeneration strategy	Vegetative expansion	Tolerance of leaf litter	Wintergreen	Mycorrhizal association	Soil type	Habitat	Poisonous	Additional information
Allium ursinum	Y	S	4-5	Insects	C	4.78	Shake (up to 2-5m)	II	Y	N	Y	S (V)	(Bulb)	Y	N	Y	Damp	Shady, woods	Y	Pollinated by insects and selfed. Up to 9000 seeds m^{-2}. Plants live for about 8 years.
Anemone nemorosa	Y	S	10-15	Bees & flies	F	0.99	Shake (up to 130mm)	II	In	N	N	V (s)	Rhizome	Y	N	Y	Moist clay; (all)	Damp woods, hedges	Y	Vernal geophyte. Intolerant of very wet soils. Cold treatment reduces germination time. Life: 100+ years.
Bromus ramosus	Y	S	1	Wind	M	7.37	Animals, clothing	II	Y	N	N	S	None	N	N	-	Base-rich	Woods, hedges	N	Rather less mobile than *F. gigantea*. Can persist in areas that were originally wooded.
Campanula trachelium	Y	S	1-2	Insects	C	0.25	Shake	II	Y	N	N	S	None	N	N	-	Clay, base-rich	Woods, hedges	N	
Carex sylvatica	Y	S	1-2	Wind	M	1.65	Shake, insects	II	Y	Y	N	S	Rhizome	Y	Y	N	Damp clay	Woods, scrub	N	Found as a garden relict.
Circaea lutetiana	Y	S	2-3	Small *Diptera*	M	0.88	Animals, clothing	II	Y	N	N	V (S)	Rhizome	Y	N	Y	Moist, base-rich	Woods, shade	N	Self-compatible. Rapid local dominance in secondary woodlands.
Conopodium majus	Y	S	3-4	Flies, beetles	M	2.26	Shake	II	Y	N	N	S	Tuber	N	N	Y	All -not chalky	Woods, fields	N	Rarely reproduces vegetatively. Associated with old habitats.
Euphorbia amygdaloides	Y	S	2	Flies, beetles	F	4.00	Explosive	II	Y	N	N	(S)	(Short rhizome)	M	Y	Y	Moist clay	Damp woods, hedges	N	Stems biennial, inflorescences arising in the second year.
Festuca gigantea	Y	S	1	Wind	M	3.12	Animals, clothing	II	Y	Y	N	S	None	N	N	N	Moist, base-rich	Damp woods, hedges	N	Self-compatible. Long awns; can be dispersed by water. Colonises 2° woods.
Galium odoratum	Y	S	3	Bees & flies	F	7.10	Animals, clothing	?	Y	N	N	V (S)	Rhizome	M	Y	Y	Damp, base-rich	Woods	N	

S: Shade-tolerant; M: Marginal; Y: Yes; N: No; C: Copious; M: Moderate; F: Few; In: Increased; S: Seed; V: Vegetative; B_s: Persistent seed bank; I, II, III, IV: Seed bank types (Thompson & Grime 1979).

Table 26. *Characteristics of ancient woodland field layer species.* II

SPECIES	South Region Ancient Woodland Indicator	Shade-tolerant, or marginal species	Seed to flower time period (years)	Pollinators	Seed production	Seed weight (mg)	Seed dispersal vectors	Seed bank type	Chilling requirement for germination	Light requirement for germination	Persistent seedling bank	Regeneration strategy	Vegetative expansion	Tolerance of leaf litter	Wintergreen	Mycorrhizal association	Soil type	Habitat	Poisonous	Additional information
Hyacinthoides non-scripta	N	S	4-5	*Bombus* spp.	M	6.17	Shake, (animals)	II	Y	N (I)	N	S (v)	Bulb	Y	N	Y	Light acid	Woods, hedges	N	Dominant in woods on light acid soils. Also grows in open, grassy areas.
Lamiastrum galeobdolon	Y	S	2	Insects, self	F	1.98	Ants	II	Y	N	N	V (S)	Stolon	Y	Y	Y	Rather heavy soils	Woods, hedges	N	*L. g ssp. montanum*. Robust, long stolons, able to exploit gaps. Roots at stolon nodes. Lives for decades.
Melica uniflora	Y	S	1	Wind	M	2.78	Ants?	I, II, IV	Y	N	N	S, V	Rhizome	N	N	N	Base-rich	Woods, shade	N	Seed may be undispersed, or heavily predated, as stands often v. localised. A poor coloniser.
Milium effusum	Y	S	1	Wind	M	1.20	Birds, mammals	III	In	Y	N	S (V)	None	N	Y	Y	Moist, humus -rich	Damp, shady woods	N	Very limited capacity for vegetative spread. Also grows on calcareous soils with humus.
Oxalis acetosella	Y	S	1	Self, (insects)	F	1.01	Explosive (up to 1m)	II	Y	N	N	V, S, B_s	Rhizome	Y	Y	Y	Moist -esp. acid	Damp woods	Y	Patch-forming chamaephyte. Most seeds produced from cleistogamous flowers.
Primula vulgaris	Y	S	1-2	Insects	M	1.75	Shake, ants	II	Y	N	N	S (v)	Rhizome	M	N	Y	Moist clay	Woods, hedges	N	Found in grassy places in the west. Low palatability to most herbivores.
Sanicula europea	Y	S	8-16	Flies, beetles	F	2.97	Animals, clothing	II	Y	N	Y	S, V	Rhizome	M	Y	Y	Chalk clay, loams	Woods	N	Also self-pollinated. Can colonise 2° woodland. Stress-tolerator that can live for 360+ years.
Tamus communis	Y	S	1	Insects	M	18.33	Animals	II	?	N	N	S	Tuber	N	N	Y	Moist fertile	Wood margins, hedges	N	Perennial tubers with annual climbing stems. Produces berries. Grows on well-drained soils.
Veronica montana	Y	S	1?	Insects	F	0.34	Poor	IV?	Y	N	Y?	V (B_s)	Creeping stems	Y	Y	_	Moist clay	Damp woods	N	The creeping stems, with adventitious roots, form clonal patches. Spreads by means of regenerating shoot fragments.
Vicia sepium	Y	S	?	Insects	M	26.0	Poor	?	N	N	N	V (B_s?)	_	N	N	Y	Moist	Wood margins hedges	N	Hard-coat dormancy prevents germination. Has a limited capacity for vegetative spread. Semi-shade plant. Root nodules.

S: Shade-tolerant; M: Marginal; Y: Yes; N: No; C: Copious; M: Moderate; F: Few; In: Increased; S: Seed; V: Vegetative; B_s: Persistent seed bank; I, II, III, IV: Seed bank types (Thompson & Grime 1979).

Table 27. *Characteristics of woodland marginal species.*

SPECIES	South Region Ancient Woodland Indicator	Shade-tolerant or marginal species	Seed to flower time period (years)	Pollinators	Seed production	Seed weight (mg)	Seed dispersal vectors	Seed bank type	Chilling requirement for germination	Light requirement for germination	Persistent seedling bank	Regeneration strategy	Vegetative expansion	Tolerance of leaf litter	Wintergreen	Mycorrhizal association	Soil type	Habitat	Poisonous	Additional information
Ajuga reptans	N	M	2	Bees	F	1.47	Shake, (?ants)	II	N	Y	N	V (s)	Rhizome, stolons	Y	Y	Y	Moist, clay	Damp woods, fields	N	Self-pollination possible.
Alliaria petiolata	N	M	2	Self, (insects)	C	2.25	Explosive	?II	N	Y	N	S (v)	Root buds	M	Y	N	Moist, fertile	Hedges, wood margins	N	Automatically self-pollinated. Grows in lightly-shaded habitats. Food of Orange-Tip larvae.
Digitalis purpurea	N	M	2	Self, insects	C	0.07	Wind, shake	III	N	In	N	S B_v (V)	None	N	Y	Y	Acid	Shady, disturbed	Y	Limited capacity to form daughter rosettes. Polycarpic, or, more rarely monocarpic, perennial.
Galium aparine	N	M	1	Self	C	7.25	Animals, clothing	II	Y	N	N	S	None	Y	Y	Y	All, fertile	Most, not aquatic	N	Seed only briefly persistent in soil, as germination occurs in autumn/winter. Capable of winter growth. Annual.
Galium mollugo	N	M	1	Flies	C	0.67	Shake	II	N	N	N	S	None	M	Y	Y	Base-rich	Hedges, woods, scrub	N	*G. mollugo ssp. mollugo*
Geum urbanum	N	M	2	Self, insects	C	0.73	Animals, clothing	II	N	Y	Y?	S	Short rhizome	N	Y	Y	Moist	Hedges, wood margins	N	Little capacity for vegetative spread. A semi-shade species, often growing in 2° woodland.
Glechoma hederacea	N	M		Insects	F	0.69	Poor	-	N	In	N	V	Creeping stems	Y	Y	Y	Fertile	Hedges, woods, rides	N	Germination increases with dry storage. Grows in light, patchy shade, and is rather characteristic of 2° woodland.
Silene dioica	N	M	1	Insects	C	0.69	Shake	III	N	Y	N	B_v	Short stolons	N	Y	N	Moist, fertile	Hedges, woods, scrub	N	Vegetative spread is largely ineffectual. A mesophytic, long-day plant.
Stachys sylvatica	N	M	1	Insects	M	1.40	Poor	?IV	Y	In	N	V B_v	Rhizome	M	N	Y	Moist, fertile	Hedges, wood margins	N	Forms clonal patches as a result of rhizomatous growth. Rapidly colonises 2° woodland.
Stellaria holostea	N	M	1	Insects, self	F	3.70	Poor	-	N	N	N	V	Rooting shoots	N	Y	N	Moist, rather infertile	Hedges, scrub, woods	N	Freshly collected seed is dormant. Low tolerance of heavy shade.

S: Shade-tolerant; M: Marginal; Y: Yes; N: No; C: Copious; M: Moderate; F: Few; In: Increased; S: Seed; V: Vegetative; B_v: Persistent seed bank; I, II, III, IV: Seed bank types (Thompson & Grime 1979).

specialised. Only *O. acetosella* is predominantly self-pollinated, producing cleistagamous flowers more frequently than chasmogamous ones (Packham 1978). In contrast, half of the woodland marginal species are capable of self-fertilisation, though only one, *G. aparine*, is exclusively self-pollinated.

Seed production.

The majority of the shade-tolerant field layer species, 11 out of 20, produce moderate amounts of seed. Only two produce seed in copious amounts, whilst seven produce little seed. Whilst three of the woodland marginal species produce few seeds, the majority produce seeds in large quantities.

Seed weight.

The seed weights of the woodland field layer species range between 0.07mg for *D. purpurea* to 26.00mg for *V. sepium*. More than half of the shade-tolerant species have seed weights over 2.0mg, compared with only three of the 10 woodland marginal species. The mean seed weight for the shade-tolerant field layer species is 4.75mg $\pm$3.01, whilst that for the woodland marginal species is 1.89mg $\pm$1.54.

Seed dispersal vectors.

About half of the shade-tolerant species and the majority of the woodland marginal species have no specific vectors for seed dispersal, relying on shake of the flowering stem, or perhaps rain splash, for seed distribution. A further three species, *A. petiolata*, *E. amygdaloides* and *O. acetosella*, have explosive mechanisms of seed dispersal. Only a third of all species have animal or human vectors. The seed of *D. purpurea*, which is very light, can be dispersed by wind.

Seed bank type.

Species were classified according to the seed bank types described by Thompson & Grime (1979). Seed banks Types I and II are both transient, with Type I present in the summer, and Type II present in the winter. Seed banks Types III and IV are both persistent. In Type III, many of the seeds germinate immediately after release, but some fail to germinate directly and are incorporated into a seed bank. In Type IV, a few of the seeds germinate directly after release, and the rest are incorporated into a seed bank.

Of those species for which such seed bank Types are described, 20 have Type II seed banks. Three species, *D. purpurea*, *M. effusum* and *S. dioica*, have seed banks Type III. Two species, *S. sylvatica* and *V. montana*, have seed banks Type IV. *M. uniflora* possesses seed banks Types I, II and IV.

Chilling requirement for germination.

Seventeen of the shade-tolerant field layer species require chilling to break dormancy prior to germination. The germination time of *M. effusum* is decreased by a chilling treatment. In contrast, only two of the woodland marginal species, *G. aparine* and *S. sylvatica* require a chilling treatment prior to germination.

Light requirement for germination.

Only three of the shade-tolerant field layer species, *C. sylvatica*, *F. gigantea* and *M. effusum* require light for germination. This is in contrast to the requirements of the woodland marginal species, where light is either required for, or increases, germination in seven of the 10 species.

Persistent seedling bank.

Only four of the woodland field layer species have persistent seedling banks. These are *A. ursinum*, *G. urbanum*, *S. europaea* and *V. montana*.

Regeneration strategy.

Whilst reproduction by seed is the main regenerative strategy for 13 of the shade-tolerant field layer species, about half are capable of vegetative regeneration. Six of the woodland marginal species reproduce predominantly by seed, and four rely on vegetative reproduction.

Vegetative expansion.

Twenty two of the woodland field layer species are able to regenerate in a vegetative manner. Twelve of the 30 species have rhizomes, three have stolons, and four have bulbs or tubers.

Tolerance of leaf litter.

Eight of the shade-tolerant species and three woodland marginal species are able to tolerate leaf litter. Another seven species show a moderate tolerance of leaf litter.

Wintergreen.

Only eight of the shade-tolerant field layer species are wintergreen, compared with nine of the 10 woodland marginal species.

Mycorrhizal association.

There are records of mycorrhizal associations for the majority of the woodland field layer species.

Soil type.

The woodland field layer species grow on a wide range of soil types, and few have very specific soil requirements. The majority of species need moist or damp soils, which links with their requirement for shady and humid habitats.

Habitat.

The majority of the shade-tolerant field layer species grow in woodlands and other shady areas. Their growth outside woodlands, *e.g.* in hedgerows, is usually associated with relict habitats. The woodland marginal species are found predominantly in hedgerows, woodland rides and margins, and scrub.

Poisonous.

A. ursinum, *A. nemorosa*, *D. purpurea* and *O. acetosella* are poisonous if eaten in sufficient quantity.

5.5 Discussion.

5.5.1 The dispersal capacity of ancient woodland field layer species into a plantation.

The brief study of the field layer vegetation within the 1949 plantation indicated that it was dominated by shade-tolerant species, such as *A. sylvestris*, *D. glomerata*, *P. trivialis* and *U. dioica*, rather than ancient woodland species. However, 23 woodland species were recorded within the plantation, six of which were ancient woodland vascular plant species, and two, *C. lutetiana* and *M. perennis*, were deep-shade species. Only *P. vulgaris* is regarded as a poor colonist, which is mostly confined to ancient woodland.

Of the four woodland species that were studied in more detail, three had colonised well into the plantation and were found growing at mean distances of 16-18m from the edge of the plantation. Two of these, *C. lutetiana* and *F. gigantea*, are both characteristic members of undisturbed communities in ancient woodlands, but are present in secondary woodlands on former cultivated ground (Peterken 1981). They are dispersed by both animals and humans, and have the ability of rapid colonisation. *C. sylvatica* is effectively dispersed by ants. It is possible that, as for some *Viola* spp. (Culver & Beattie 1980), the activities of the ants may promote germination and seedling survival in this species. It can also be dispersed on stockings, or in the mud on boots (Woodruffe-Peacock 1918). These three field layer species all reach maturity within two growing seasons, which is considered beneficial to their colonisation of new sites. They have been able both to disperse into the plantation, and to establish successfully.

Plants of *S. europaea* were found at a mean distance of only 4.5m from the plantation edge. This species, which produces hooked fruits, is clearly capable of dispersal by animals or humans. It therefore was able to colonise into the plantation. In contrast to the other species, *S. europaea* establishes very slowly, and only reaches flowering maturity at approximately 8-16 years old (Inghe & Tamm 1985). Indeed, plants have been recorded in Swedish forests that did not flower until 23 years old, and one plant produced no flowers during a 39 year period (Inghe & Tamm 1985). Although

established populations of this species in forest conditions have a persistent seedling bank, seedlings are produced only irregularly (Inghe & Tamm 1985). Further, it is considered that any seedlings produced either from the initially dispersed seeds, or from mature plants, could easily have been ousted by competition in the weed and grass-dominated swards within the plantation. As for *A. nemorosa*, it is difficult for fruit that does reach a new area to establish a population when surrounded by existing competing vegetation (Peterken 1981b). Also, horizontal clonal expansion of this and another long-lived woodland species, *Hepatica nobilis* Miller (Round-lobed Hepatica), has been estimated at only 0.5cm per year (Inghe & Tamm 1985). It is therefore suggested that whilst *S. europaea* possesses a good dispersal mechanism, it is very slow to colonise a new area. It is considered that if this species reaches areas that are shady and that have low cover of existing vegetation, its colonisation potential may be increased. Indeed, it is listed as a fast-colonising woodland species by Peterken (1981a). However, with strong competition from other species, as in the 1949 plantation, its very slow growth and long time period before flowering appear to reduce the ability of successful colonisation.

Seven ancient woodland species growing in compartments neighbouring the plantation were not recorded in the plantation. Apart from *F. vesca*, which is dispersed well by birds (Woodruffe-Peacock 1918), these are characterised as having poor dispersal mechanisms. This has clearly been a barrier to their colonisation into the plantation, despite the short distance between it and the nearby compartments. Similar observations about the colonisation of ancient woodland field layer species were made in a study of an ancient woodland situated beside a recent secondary woodland of about 100 years old in Essex (Webster & Kirby 1988). Here, even after 100 years, only four of the nine ancient woodland species present in the ancient woodland were recorded in the recent woodland.

A few plants of *P. vulgaris*, a poor colonist, which is mostly confined to ancient woodland or woodland relict habitats, were growing in the plantation. This species is mainly ant-dispersed (Keith-Lucas 1968). Rain-splash may also move seed away from plants (Helliwell 1980), but only over short distances. It is reported that only a small number of *P. vulgaris* seedlings survive even in very favourable circumstances in

woodlands (Helliwell 1980). Also, despite vigorous flowering and good subsequent seed-set, very few seedlings were observed amongst competing vegetation in the new plantation or farm woodland plots in the experiment described in Chapter 4. It is therefore considered that this species can only disperse over short distances into new areas, and then is slow to colonise, particularly within an existing sward.

The development of a woodland field layer in the plantation has been steady, but rather slow. A wide range of woodland species is now present, but these species are recognised as having good dispersal mechanisms, and/or as being rapid colonisers, *e.g. A. maculatum*, *C. lutetiana* and *G. urbanum*. Some species, *e.g. P. vulgaris* and *S. europaea*, have been dispersed into the plantation, but have subsequently colonised only very slowly. Half of the South Region ancient woodland vascular plant species recorded in Linford Wood have failed to colonise into the plantation after 43 years, despite their proximity to it. This demonstrates their poor capacity to disperse even very short distances. Further, it is possible that even if seeds of these species do reach the plantation in the future, they will be very slow to spread and colonise successfully.

5.5.2 The germination potential of ancient woodland field layer species.

Throughout the treatments, the germination of the ancient woodland field layer species was low, with five species failing to germinate. Only one species, *C. trachelium*, produced about 50% seedlings, and for only three other species, *E. amygdaloides*, *H. non-scripta* and *M. effusum*, was germination above 5%. It is considered possible that the time length of the tests was rather short, as many woodland species have characteristically slow germination. *C. majus*, for example, did not germinate until the second spring in the tests described in Chapter 2.

The results for the germination of *H. non-scripta* were similar to those obtained in Chapter 2, as the majority of seedlings were not observed until October. By this time, the seeds had received the required heat and then chill necessary to break seed dormancy (Thompson & Cox 1978). However, a small proportion of the seeds in this test germinated in late April. Having been collected in September of the previous year,

(somewhat later than in the other experiment), they had already been subjected to a period of high temperatures in the wild. Although, in these tests, they were not chilled until some months later, some had the capacity to germinate.

The two treatments to which the seeds were subjected were found to have no significant effect upon subsequent germination. It was thought that the use of woodland soil, containing mycorrhizal fungi, may help to promote germination and seedling survival. This was not observed, as seedling numbers were not significantly different whether sown into woodland soil or compost, and those seedlings that were recorded grew well in both soil types. It is considered possible that mycorrhizal fungi may help seedling development in very low nutrient soils, but clearly the seed compost contained sufficient nutrients for seedling growth.

The different chilling treatments also had no effect upon the germination of the field layer species. As shown in Tables 25 and 26, and in the germination tests described in Chapter 2, the majority of true woodland species do require chilling to break dormancy prior to germination. Here, the constant chilling in a 5°C CT room was compared with intermittent chilling during periods of low temperatures outside. For those species that did germinate, it appears that intermittent chilling was sufficient to break dormancy, and that storage at constantly low temperatures was unnecessary. In laboratory experiments, woodland species that require chilling to break dormancy, are often subjected to periods of moist storage at low temperatures (*e.g.* Grime *et al.* 1981). It may be of practical value that seeds sown into natural conditions are capable of germination after intermittent chilling.

Generally, even freshly collected seed of ancient woodland field layer species appears to have low germinability, certainly in the short term. It is possible that this germinability may increase with dry storage, as for *V. sepium* (Grime *et al.* 1979), or that germination may just be slow, as for *C. majus*. It is also considered that a longer chilling period, whether constant or intermittent, may lead to increased germination in these species. The low germination of ancient woodland species in this test, and in that described in Chapter 2, helps to explain the very low densities at which some of the field layer species, such as *C. majus*, *G. odoratum* and *P. elatior*, were recorded in the experimental sites in

Chapter 2. In contrast, the majority of marginal species in the germination test in Chapter 2 had germination rates of 20% and more, and produced high numbers of seedlings in the field. The species list in Appendix E indicates the 23 species that germinated in pots of woodland soil, but were not sown. These species are components of the seed bank in the ancient copse. It is of interest, that only three of these species, *C. sylvatica*, *F. vesca* and *P. vulgaris*, are ancient woodland species. Eight of the species are woodland marginal species, whilst the rest are shade-tolerant weed species.

5.5.3 The characteristics of woodland field layer species.

The compilation of many detailed characteristics for 30 woodland field layer species enables comparisons to be made between true woodland species which are tolerant of the shade produced by a closed woodland canopy (Peterken 1974), and woodland edge, or marginal, species, which can grow in woodland conditions or other shady places, *e.g.* hedgerows, outside woodlands (Peterken 1981a).

Whilst the two groups of species are not wholly dissimilar, with features such as regeneration strategies, pollinators, and seed dispersal vectors in common, clear trends are apparent by which they can be distinguished. The woodland marginal species are all quick to reach maturity, and produce seeds in their first or second growing seasons. Many are self-pollinated. They produce copious amounts of relatively light seeds, *e.g.* *D. purpurea*, or have very successful vegetative methods of reproduction, *e.g.* *A. reptans*. The marginal species are able to persist as seeds for many years prior to germination (Salisbury 1924). The majority of seeds require light for germination, but not chilling, and have moderate to good germination rates. Most of the marginal species are wintergreen. In general, they have a wide habitat range, in wood margins and rides, hedgerows and scrub. The Ellenberg light scores for these species range from 4 to 7, in the scale of 1, deep shade, to 9, full light, (Ellenberg 1988). This indicates that they can grow successfully, and hence must have some competitive ability, in fairly open conditions. Benefitting from higher light levels, they are able to grow and flower quickly, which enables them to spread and colonise into new areas.

Whilst *G. aparine* is not a species that is considered necessary to introduce into new woodlands, it has been included in this study for comparison with other woodland field layer species. It is a widely-distributed weed, found in both shaded and unshaded communities, and in arable situations (Grime *et al.* 1979). It is recognized as being a very successful plant, and this is partly due to its ability to exist in "tall-herb communities and ephemeral assemblages of disturbed land" (Grime *et al.* 1979). It shares a heavy seed weight, and a requirement for chilling, but not light, to break dormancy with many of the shade-tolerant field layer species. However, it produces large numbers of hooked, bristly seeds (Grime *et al.* 1979), which are dispersed very effectively. With predominantly autumn germination, it has the ability to grow during mild winter periods. Although an annual, *G. aparine* is therefore at an advantage over other plants by spring.

Many of the shade-tolerant field layer species are slow to reach flowering maturity, and then may have rather specialised insect pollinators. In a study of the flowering ecology of a range of woodland herbs in North America (Schemske *et al.* 1978), it was found that seed production was possibly pollinator limited for several field layer species which flowered in early spring. This was because few days were suitable for pollinator visits to flowers, and some pollinators were rare. It was demonstrated that hand pollination was more successful than natural pollination for some vernal species. The present study and others, (such as Salisbury 1942), have found that the shade-tolerant species produce fewer, heavier seeds than the woodland marginal species. The North American work also showed that the seed set was low for most species. The production of large seeds by most shade-tolerant species is to ensure adequate energy supplies for seedling establishment in woodland conditions. Indeed, the height to which seedlings grow in shade is directly related to seed size and shade-tolerance (Crawford 1989). The seeds of the shade-tolerant species tend to lack mechanisms for widespread and rapid seed dispersal (Webb 1966), and have poor viability. The requirement for large seeds, and their subsequent limited dispersal, has caused the shade-tolerant woodland species to be very poorly represented in the British flora in comparison with that of Continental Europe. This is due to the barrier to migration produced by the English Channel at the end of the last ice-age (Crawford 1989). Most seeds of shade-tolerant species require chilling to break dormancy, but do not need light for germination. Germination rates,

both in the field (Chapter 2) and in germination tests (Chapters 2 and 5), are generally poor.

Some shade-tolerant species have excellent methods of vegetative expansion, *e.g. L. galeobdolon*, but others, even with low production of viable seed, do not, *e.g. E. amygdaloides*. The shade-tolerant species are more confined to shady areas with relatively high humidity, *i.e.* woodlands. The Ellenberg light scores for these species range between 1 to 6, but the majority score 4, or less (Ellenberg 1988), indicating that they grow in shady conditions. Shade-tolerant species do not have the ability to compete well in conditions of increased light. Many of the shade-tolerant species are very long-lived. For example, individuals of *A. nemorosa* may live for hundreds of years (Shirreffs 1985), and plants of *S. europaea* have been estimated to be more than 360 years old (Inghe & Tamm 1985). Overall, their characteristics mean that they are both poorly dispersed, and slow to colonise new areas. Once they are established, however, they have the ability to persist for many years.

Woodland field layer species that are tolerant of deep-shade may be divided into three groups (Barkham 1992). These are:

i. Those that produce high amounts of seed and have limited clonal growth, such as *A. ursinum* and *H. non-scripta.*

ii. Those with rhizomatous clonal growth, such as *A. nemorosa* and *M. perennis.*

iii. Those which have neither of the above capacities, such as *Narcissus pseudonarcissus* (Wild Daffodil).

With suitable conditions for growth, the first two groups of species are capable of completely covering considerable areas of ground. In contrast, the third group, which includes the majority of woodland shade species, can only slowly colonise areas between existing clumps, and generally exhibit high mortality in seed reproduction (Barkham 1992). Thus, the demographic characteristics of the shade-tolerant woodland field layer species determine their ability to establish and spread within a woodland.

In relation to the methods for species introductions into new areas, the shade-tolerant species that are capable of successful reproduction by seed, and those that exhibit predominantly vegetative reproduction have already been distinguished in Chapter 2. The

woodland marginal species, the characteristics of which have been described, form another group of species with good reproduction from seed. The recognition of these differences in regenerative strategies are very important when making species introductions for enhancement purposes. The distinctions in introduction methods, *i.e.* whether by seeds or plants, are used in the production of a decision support system (Chapter 6) to give practical advice for the successful introduction of woodland field layer species into new areas.

5.5.4 Conclusions.

Woodland marginal species are fast-growing and quick to reach maturity. This, combined with the production of small, easily-dispersed seeds with good germination rates, or good vegetative regeneration, enables them to colonise into new areas.

Shade-tolerant woodland species tend to have heavy, poorly dispersed seeds, which have low, or slow, germination. In all but the most favourable conditions, seedling development is slow, and plants may take many years to reach flowering maturity. Once established, however, these species are able to persist for many years, even in vegetative states in deep shade, and are very long-lived.

The characteristics of many of the woodland field layer species, particularly those which are shade-tolerant and that are associated with ancient woodland, indicate their very poor colonisation capacity. These species clearly have very limited abilities to reach new woodland areas, especially if such areas are isolated. Hence, field layer introductions are considered necessary for the enhancement of new plantations, if representative and interesting woodland field layers are to be established.

The information that has been presented about the characteristics of a range of woodland field layer species can be used prior to the introduction of such species into new areas. Details of habitat requirements should ensure that suitable species are selected for a particular site. The method by which species are introduced, *i.e.* whether by seeds or as plants, can be determined from the information concerning regeneration strategies.

6. The development of a decision support system for the enhancement of field layers in new plantations and young woodlands.

6.1 Introduction.

6.1.1 Decision support systems.

A decision support, or expert, system is a computer programme that summarises information and knowledge, and imitates a human decision-making process. In this way, it performs functions that are normally carried out by a human expert. The programme usually requires input from the user, which it obtains by a series of questions that would normally be asked by the expert. Depending on the information that is input by the user, the programme then makes a series of decisions based on the specific details, whilst complying with pre-set rules. Then the programme gives answers or advice in order to solve the problem.

Generally the user needs some basic details about and knowledge of the problem, whether it concerns insect pests in a stored crop, control of a weed species, or the establishment of a woodland. Input, however, should be minimal, and a good programme should guide the user towards a solution after a series of fairly straightforward and simple questions.

In recent years, there has been much progress both in the development of methods to produce expert systems, and in the advancement of the necessary computer software (Holt 1987). Thus, a useful, prototype system can now be developed within a relatively short time period of a few weeks or months. Once the initial version of the system has been written, input from users and experts can help to refine the prototype. This is an essential part of the development strategy of any decision-making system. However, even though a system can soon become functional, it is never really finished, since further refinement and addition of more knowledge can continue almost indefinitely. One important aspect of a decision support system is that it not only enables the user

to solve a problem, but also often enables the experts to approach problems in a more systematic manner (Holt 1987).

6.1.2 The appropriateness of a decision support system for the enhancement of new woodlands with field layer species.

During the course of the research presented in this thesis, the author has frequently been approached for advice on practical methods for field layer enhancement in plantations and new woodlands. As explained in Section 1.2, the case for introductions is strong, if diverse and attractive woodland field layers are to be re-created. In the urban environment, large-scale tree planting has taken place, such as in Milton Keynes, and is still continuing with the proposed Community Forests. Particularly in these situations, where plantations are often isolated and may be surrounded by roads and housing developments, there is a growing awareness that field layer introductions are simply a logical step after tree planting. It is the urban habitat managers and wildlife officers that request advice on methods for the successful introduction of woodland field layer species. The compilation of information gathered in this research into a decision support system is considered an appropriate way in which to present the knowledge for practical use.

As a result of the experimental work, literature reviews, and field observations that have been reported in Chapters 1 to 5 of this thesis, much detailed information now exists concerning the characteristics of woodland field layer species, and practical methods for their successful introduction into young plantations and newly planted woodlands. The field trials in Milton Keynes (Chapters 2 and 3), and the newly implemented experiment in Berkshire (Chapter 4), have led to the identification of key variables that are considered to be essential to the problem of field layer establishment. These are the degree of canopy development at a site, which governs the average % daylight that reaches the plantation floor, and the amount of existing vegetation at the site. Further, the study of species characteristics (Chapter 5) presents important information, such as species preferences for soil types, tolerance of shade, and reproductive strategies, which should be considered prior to making field layer introductions.

Some of the species information gathered from literature sources, such as Biological Floras, is the result of some years of experimentation and research. While it was intended that the results presented in this thesis should be incorporated into the expert system, some experiments, such as that described in Chapter 4, have only been implemented for 2 years. It is therefore considered that certain results give only a short-term indication of the species reactions to new environments. Coupled with field observations in other sites, it is felt that there is a danger in extrapolating these to long-term situations. For this reason, some decisions presented in the system err on the side of caution, and do not necessarily reflect all of the short-term experimental results.

The main criteria on which the decision to write an expert system is based, are whether sufficient expertise is available at the outset, and if the problem is fully comprehended. It is considered that the 3 year research programme which has been undertaken, and the results and conclusions that have been drawn from it, meet these requirements.

6.1.3 **The objectives of the support system.**

The purpose of the work presented in this chapter was to develop a preliminary expert system for woodland field layer enhancement. It was proposed that the following information and advice should be provided in the decision support system:
i. The suitability of the site for making field layer introductions.
ii. The selection of species appropriate for the site conditions.
iii. Information regarding introduction techniques and methods, to ensure successful establishment of field layer species.

With knowledge of a few details concerning the proposed site for enhancement, practitioners, restorationists, farmers and others, should have to answer a few simple questions, and then be given advice and information about woodland field layer introductions. As long as certain site conditions are fulfilled, the system should produce a list of field layer species that are suitable for the particular characteristics of the site. In addition to this list, information that is necessary to make successful introductions should be available. At the end of the procedure, the user should be able to introduce

field layer species into the site, which have been chosen specifically for the conditions at the site. Further, with the additional advice on introduction techniques, these species should establish and persist to develop into a permanent field layer.

6.2 Methods.

6.2.1 The components of a decision support system.

A decision support system consists of two main components, namely a **knowledge base**, to which is linked an **inference engine** (Waterman 1986). The knowledge base contains stored knowledge within the computer system. The inference engine is the part of the computer programme that controls the structure of the expert system. This enables the computer system to apply a 'reasoning' mechanism to the knowledge base, and to solve the problem effectively. A third essential component of the system is the **user interface.** This is the part of the computer programme that enables the user to communicate with the programme, and is also controlled by the inference engine.

There are four other key roles in the development of an expert system. These are:
i. The domain expert.
ii. The knowledge engineer.
iii. The expert-system building tool.
iv. The user. (Waterman 1986)

The domain expert is the person who provides the knowledge for the system, which is contained in the knowledge base. The knowledge engineer is the person who structures and creates the support system. In this instance, the author is both the domain expert and the knowledge engineer. The expert-system building tool is the programming language used to create the system, and its support package. For this decision support system, KnowledgePro (Thompson & Thompson 1987) was selected as the programming language. This is a rule-based expert system shell, which contains an in-built inference engine. Though rather less flexible than lower level programming languages, such a shell

requires less technical expertise, as the engineer has only to build the knowledge base. Since the decision support system that is presented is just a part of the entire thesis, and is only intended to be a preliminary attempt at system creation, it was considered that the use of a shell was appropriate here.

6.2.2 An explanation of the programming language.

Human expert logic generally takes the form of **'if'** (a condition is true), **'then'** (do action) statements (Holt 1987). KnowledgePro is based upon such if--then rules, as are many other system shells. The expert knowledge is represented by a series of these rules within the knowledge base. The user must provide answers to questions that are asked by the system. Then the rules are searched by the system, using a decision tree. By following certain 'branches' of the decision tree, some conditions will be satisfied, but not others. Thus, the user's answers evaluate the conditions, and the system uses a series of such conditions within a set of rules to provide a particular solution. Examples of such rules, conditions and solutions are given in Section 6.3.1. KnowledgePro employs a system of 'backward chaining', which begins with a hypothesis, and endeavours either to substantiate or revoke this using the available data.

6.2.2.1 The use of decision trees.

A decision tree is the main structure of the computer programme written by the knowledge engineer. It enables the expert knowledge to be presented in a clear and succinct manner. This is known as 'knowledge representation'. The decision tree is arranged in a hierachical way, and contains the rules in which the decisions are made. It is the organisation of information into such a hierarchy, that forces even the experts to approach the problem systematically. For instance, it is soon apparent even to a novice engineer, that a rule which influences the entire outcome of the system, should be placed at the top of the decision tree, whilst one that merely provides information about a particular subject is best positioned as part of a lower branch. For clarification it is possible to arrange complex problems as groups of sub-problems. It is important that the branches of all such groups are defined fully, so that system failure is avoided.

6.2.2.2 The use of topics within the knowledge base.

Topics are used for both structural organisation and information storage, and are central to the KnowledgePro environment (Thompson & Thompson 1987). Each topic is a particular subject, or 'piece of knowledge' that is relevant to the problem. Topics may consist of commands to run a procedure, may give information and/or advice, or may evaluate a variable. Topics can be arranged hierarchically, whereby a 'child' topic is nested within a 'parent'. In this way, the overall structure of the decision tree is designed. The order in which topics are defined within the system is not as important as the level of nesting of one topic within another. However, topics should be arranged so that the system proceeds in a logical manner, and questions do not have to be repeated unnecessarily.

6.2.2.3 The use of hypertext within the knowledge base.

Hypertext is text that is marked within the computer programme, displayed as highlighted text to the user, and which has additional text linked to it. It enables the end user to receive more information about the questions being asked and the statements being made. Thus, the system is able to cater for different levels of expertise amongst users. For instance, hypertext is available on demand from the user, and whilst someone with a comprehensive knowledge of the problem may not need to call upon it, a user with less knowledge may benefit from the extra information that it contains.

6.2.3 The system design procedure.

There are three main constituent stages in the design of a decision support system. They are:

i. The structuring of the problem.

ii. The compilation of expert knowledge.

iii. The incorporation of appropriate knowledge into the system.

6.2.3.1 The structuring of the problem.

Essentially, the decision support system should follow the same procedures that are

involved in a consultation with an expert. An expert initially acquires certain details about the specific problem from the user. Then, based on the expert's knowledge, decisions are made from the information provided by the user, and finally a solution to the problem is found. Thus, the problem is solved. To mimic this procedure, the decision support system first evaluates conditions, by asking the user questions. The logical rules within the decision tree are pursued depending on the value of the conditions, and so a solution is reached.

The decision support system for woodland field layer enhancement first assesses the suitability of a site for field layer enhancement. Certain conditions have to be satisfied by the user's answers in order for the system to proceed further. If the site is considered to be suitable, then the next section of the system evaluates more detailed site characteristics in order to arrive at a list of field layer species appropriate for introduction into the site. After this, the user can request information concerning introduction methods and techniques for successful species establishment.

6.2.3.2 The compilation of expert knowledge.

The preceding chapters in this thesis are the main source of expert knowledge used in this system. Information used for assessing the overall suitability of a site for field layer introduction, and the site characteristics that determine species selection are based upon the results and conclusions presented in Chapters 2, 3, and 4. Observations within many, varied young plantations and newly planted woodlands during the research have also enabled reasoned judgements to be made concerning site suitability. The use of specific conclusions from the thesis within the expert system will be demonstrated and explained in Section 6.3.

One of the main objectives of the system is to select woodland field layer species that are suitable for introduction into the site to be enhanced. For this purpose, data have been compiled for a group of 50 woodland field layer species. In this preliminary system, only species that are representative of the South East, South, and South West English Nature regions have been chosen. These are both marginal and deep-shade species, which are considered to be attractive, interesting, not limited to very specialised habitats, and which can be propagated fairly easily. The information gathered about a

range of field layer species in Chapter 5 has been used for this, as have other sources, such as Clapham *et al.* 1962, Stace 1991, and Grime *et al.* 1979. All of the species are known to be available from suppliers as either seeds or plants. Information which is considered necessary for species selection has been compiled as a data file which is external to the expert system. This file is loaded into the system at the start, so that the species data is available when required by the programme. For each species, the information contained on the data file consists of:

i. The Latin name.

ii. The English name.

iii. The degree of shade-tolerance of the species.

iv. The main regenerative strategy, *i.e.* seed or plant.

v. The required soil moisture level.

vi. The soil type in terms of pH range.

6.2.3.3 The incorporation of knowledge into the system.

Expert knowledge is built into the system in two ways. In the first two sections of the system, it is incorporated into the questions that are put to the user. In this way, necessary information is extracted from the user enabling site assessment and species selection. In addition, the user may be given important details by means of hypertext. In the final section of the system, once field layer species have been selected, the user is presented with expert knowledge and advice that is considered necessary for the successful introduction of field layer species into new woodlands.

6.3 Results.

6.3.1 The structure of the expert system.

The structure of the expert system is illustrated by the decision tree shown in Fig. 30. The system has four main parts, the last three of which correspond to the original objectives.

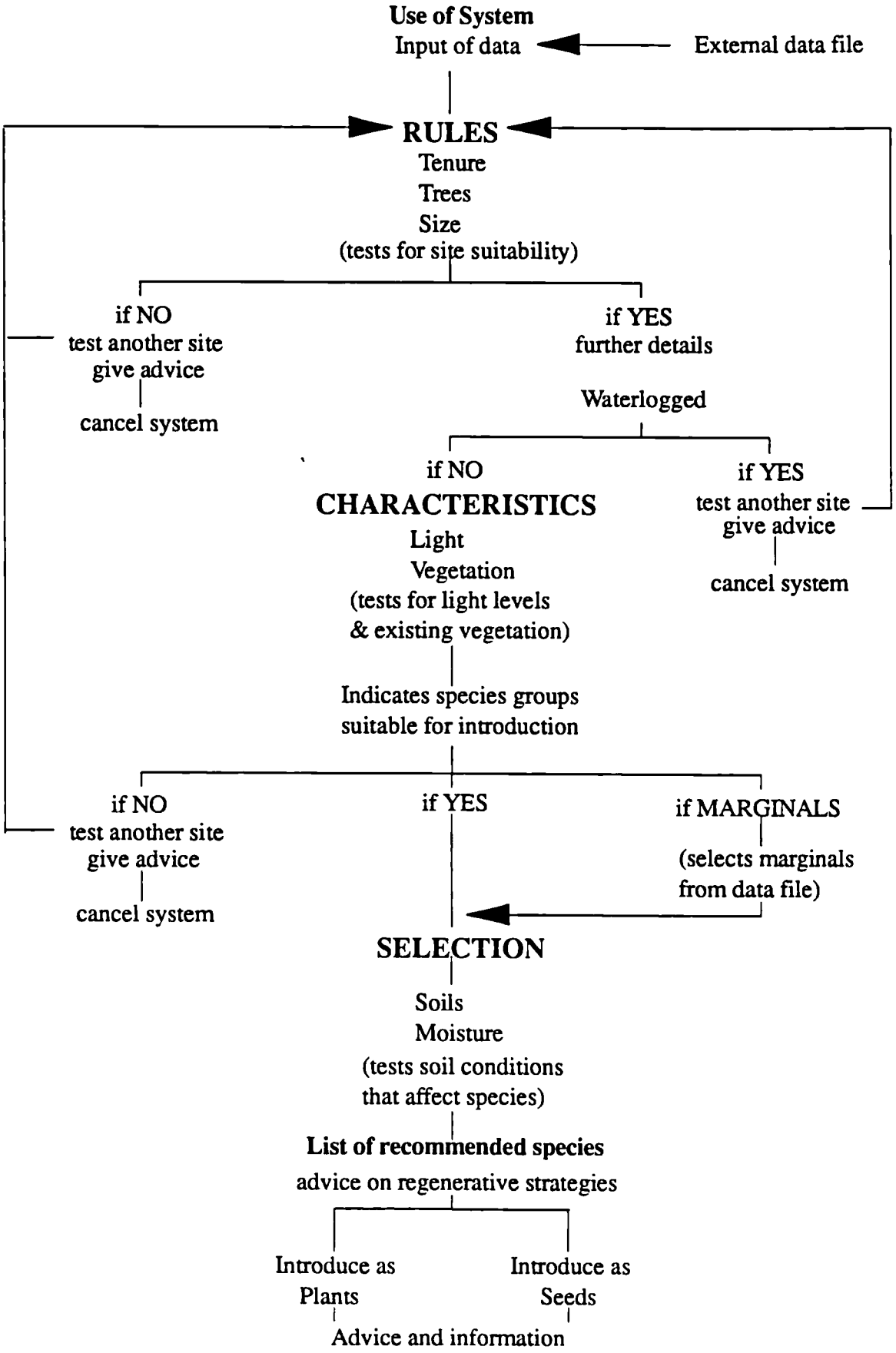


Fig. 30 *A decision tree for the enhancement of young plantations and new woodlands with field layer species.*

These components are:

i. The use of the system and input of data.

ii. The assessment of overall site suitability for field layer enhancement.

iii. The selection of field layer species that are appropriate for the site conditions.

iv. The presentation of practical techniques and methods for successful field layer introduction and establishment.

The components of the decision support system are now presented and explained. They will be discussed later.

6.3.1.1 **The use of the expert system and input of data.**

Topics: Initialise, Species data, Start, Use.

At the beginning of the expert system variables are defined that are used later in the programme. The external data file, containing information about 50 woodland field layer species, is then loaded into the system, so that it is ready for use whenever required by routines within the programme. This initialisation is essential to the running of the system and occurs automatically, prior to the system being introduced to the user.

The decision support system, 'Enhance', is then introduced to the user. The purpose of the system is clearly explained, and the objectives are set out. At this stage, the user is advised that a certain amount of knowledge of the site is necessary if the system is to be used to good effect. Specific variables, such as the size of the site and the soil pH, are listed, so that the user is aware of the input that is expected. Someone with very little knowledge of a site could then evaluate the variables before proceeding any further.

6.3.1.2 **The assessment of site suitability.**

Topics: Rules (Tenure, Size, Trees), Reassess, Water (Waterlogged), Comment.

In this section, the feasibility of enhancing the field layer at the proposed site is decided. The conditions of the topic 'Rules' are determined by asking the user:

i. The duration of site tenure.

ii. Whether trees have established on the site.

iii. The size of the site.

In this preliminary version of the decision support system, the user is asked simply whether the duration of site tenure is indefinite, or not. Next, the presence of established trees on the site is ascertained. The hypertext topic 'Established' defines established trees as those which are at least 5 years old, and which are putting on good growth. Finally, the suitability of the size of the site is determined with the question 'Is the site at least 30m wide?'. The user's responses to these questions are then evaluated and tested to determine the site's suitability for enhancement. If all of the answers are 'Yes', then the site is considered to be suitable for enhancement, whereas an answer of 'No' to any of the 3 questions leads to a recommendation that the site is unsuitable for field layer introductions.

If the site is rejected as being unsuitable for field layer enhancement, the user is given advice in the topic 'Reassess'. This presents the option of whether to test the conditions at another site, or to cancel the system entirely. A practitioner who has more than one potential site for enhancement can therefore re-evaluate the 'Rules' conditions for another site.

It is also important to know if a site is waterlogged, prior to selecting field layer species for introduction. The user is questioned about this, and can only proceed further if the site is not waterlogged. Whilst a waterlogged, or very wet site, *e.g.* an alder carr, could support both trees and field layer species, it is beyond the scope of this preliminary expert system to recommend species for such conditions. If the site is waterlogged, then the user is again given the option to test the conditions at another site, or to cancel the system.

All of the criteria for site suitability must therefore be satisfied before the system continues.

6.3.1.3 **The selection of field layer species.**

The identification of species groups for introduction.

Topics: Characteristics (Light, Vegetation), Yes, No, Target, Marginals.

A decision tree for the evaluation of site characteristics to determine species groups for introduction is given in Fig. 31. The user is asked whether the mean daylight in summer

is 40% or more, and whether the amount of existing vegetation at the site is between 0-10%, 10-40%, or more than 40%. The rules within the topic 'Characteristics' are evaluated by the user's answers in the topics 'Light' and 'Vegetation'. The evaluation of these topics is shown in Fig. 31.

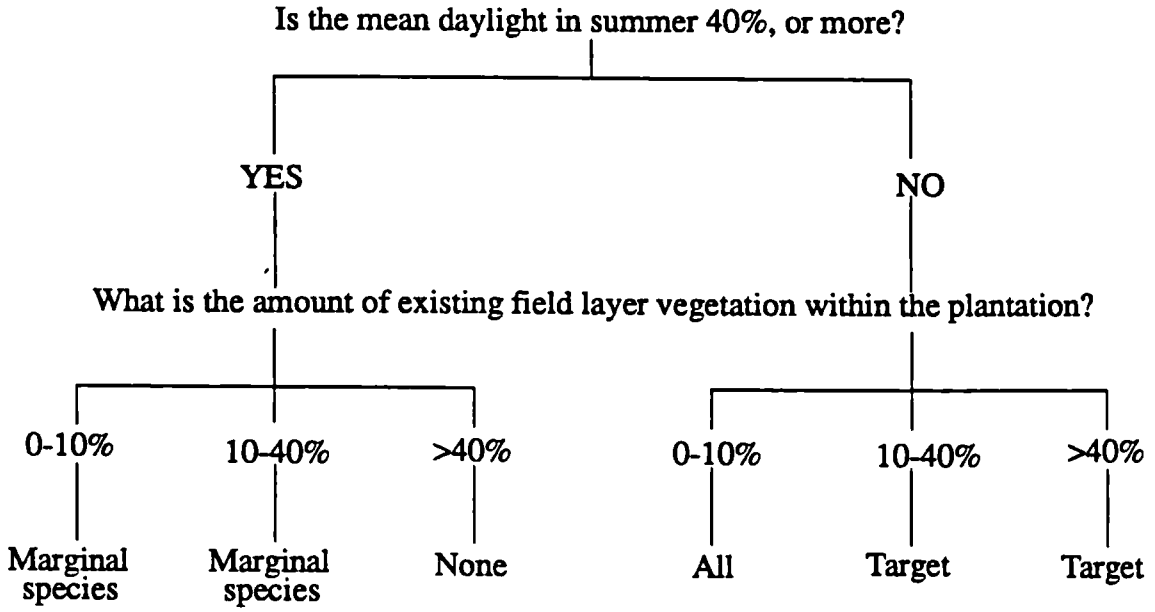


Fig. 31 *A decision tree for the evaluation of site characteristics to determine species groups for introduction.*

The site is only considered to be unsuitable for field layer introductions, if there are high light levels accompanied by a substantial amount of existing field layer vegetation. In this case, the system can, once again, be either re-run, or cancelled. If there are high light levels at a site, with either 10-40% or no existing vegetation, then the user is recommended to introduce woodland marginal species into the site until shade increases. At this point, the topic 'Margin' automatically sorts through the species data set, and removes the deep-shade species, retaining only those which are woodland marginals.

If light levels are less than 40%, it is considered that a full range of both woodland marginal and deep-shade field layer species can be introduced into the site. However, if the existing field layer is 40% or more, then the user is advised to target the introduced species into shady areas, and away from existing patches of vegetation. The

justification for the particular thresholds of light and vegetation cover used in the system is discussed later in Section 6.4.

The differentiation of species into the groups 'all species', 'target species', or 'marginal species' is important to the survival and subsequent establishment of the introduced field layer species. These groups are retained from now onwards, and all advice that is given later in the system refers back to the results of this section.

The selection of species to suit soil type.

Topics: Selection, Soils, Moisture, Common names, Advice.

This section of the decision support system selects species that are appropriate for the soil type at the site. In the topic 'Soils', the user is asked if the pH at the site is acid, neutral, or alkaline. Information on methods for obtaining accurate pH readings, and a definition of each pH range with examples of soil types, is provided by a hypertext topic. The topic 'Soils' is evaluated by the user's answer, and species that are incompatible with the soil type are removed from the species list. In the topic 'Moisture', the soil moisture conditions at the site are determined by asking whether the soil is 'dry, moist, or wet'. Depending on the evaluation of this topic, any more species which are unsuitable for the site are removed from the species list.

By this stage, the species list has been reduced to contain only those species which are suitable for the particular light conditions, level of competition from existing vegetation, pH, and soil moisture at the site. The Latin names of these species are shown to the user at the end of the topic 'Moisture'. There is then an option to view the common names of the selected species, which may benefit those less familiar with woodland field layer species. At the end of this section, the user is advised of the number of species that are suitable for introduction into the site, and is reminded about which species group they belong to.

6.3.1.4 The presentation of techniques and methods for field layer introduction.

Topics: Techniques, Methods, Seeds (Edge, All, Specific), Plants, Print.

The final section of the decision support system gives advice to the user to enable the successful introduction of the species which have been selected for the site. The topic 'Techniques' emphasises the importance of introduction techniques for the successful establishment of woodland field layer species. The user is advised that the different regenerative strategies of the species must be taken into consideration prior to attempting their introduction into a new site. A hypertext topic, 'Regenerative strategies', provides additional information for a user who is unfamiliar with plant reproductive strategies. The system then splits the selected species into two lists, using information about their main reproductive strategies, which is contained in the species data file. The lists indicate which species are best introduced as young plants, and which as seeds. They are displayed to the user beneath the headings 'Plants' and 'Seeds'.

In the topic 'Methods', the user is asked whether information is required about the use of seeds or plants, and a choice of 'seeds, plants, both, neither' is made available. Both of the topics 'Seeds' and 'Plants' give comprehensive information about methods for field layer introduction. Within the topic 'Seeds', information is given about the seed production capacities of marginal and deep-shade field layer species, and sowing rates are suggested. These details are tailored to the species groups that were identified in 'Characteristics', by using the sub-topics 'Edge', 'All', and 'Specific'. Practical advice is also provided about species germination requirements, the preparation of seed mixtures, and the recommended time and method of sowing. Finally, the user can choose to see a list of seed suppliers. The topic 'Plants' provides practical details for the introduction of woodland field layer species as young plants. The user is advised of the importance of planting density for successful establishment, and given recommendations about the time and suggested rate of planting. If requested by the user, a list a plant growers is displayed.

At the end of this section, the user has the opportunity of printing the lists of species to be introduced as seeds and plants to a file, in order to create a record of the species that have been selected for introduction into the site.

6.3.2 The decision support system on disc.

The decision support system is supplied to the user on a 3.5" floppy disc. This also contains a runtime version of KnowledgePro, the species data file, and a batch file for system installation. The user simply types 'Install' in the same drive as the floppy disc. This command creates a directory called GARDEN in the C drive, and then copies all the relevant files from the floppy disc into this directory. The user can then run the decision support system. A copy of this software is supplied on a 3.5" disc at the back of this thesis.

6.4 Discussion.

6.4.1 The determination of criteria for use in the decision support system.

The aim of the work presented in this chapter was to develop a decision support system that is straightforward to use, and gives sound, uncomplicated recommendations about field layer enhancement, yet which contains a sufficient level of detail to result in successful introductions, and, hence, achieves the enhancement of an existing field layer. To accomplish this, it was necessary to translate both experimental results and field observations into 'rules' and 'conditions' that governed a decision-making process. Some careful and considered judgements were therefore made in order to distinguish the factors that were likely to be most influential upon the growth of woodland field layer species within young plantations and newly planted woodlands.

The selection of the criteria upon which the decisions in each section of the expert system were based, is explained and discussed below.

6.4.1.1 Site suitability.

During the research period, many young plantations and newly planted woodlands were visited and evaluated. The conditions at such sites were found to be extremely variable, both between and within the sites. The four plantations described in Chapter 2, for

example, which were all within the city of Milton Keynes, were found to be very changeable, in terms of canopy species, tree establishment, drainage, light levels, competing vegetation, and disturbance. In this respect, it is suggested that two sites are rarely the same, and thus the criteria on which the suitability of a site was based should, by necessity, be rather broad and unspecific.

In this prototype expert system, indefinite site tenure was considered necessary to make field layer introductions worthwhile, since the establishment phase of some species takes many years. Some woodland marginal species, such as *A. petiolata*, *D. purpurea*, *G. urbanum*, and *S. dioica*, are, however, very quick to mature and establish, even from seed. It is considered that species such as these could be recommended for sites without indefinite tenure, where they would be useful and attractive.

So that it was possible to recommend simple and practical methods for field layer enhancement later in the system, the presence of established trees was used as a second criterion on which to determine site suitability. The experiment described in Chapter 4 demonstrated the feasibility of introducing woodland species into areas with newly planted trees, particularly if weed control was practised to increase establishment. However, the results presented were only for the first two years after field layer introduction. It is considered possible that due to very high light levels in new plantations, the competing vegetation may eventually oust the less competitive woodland species. Where trees are about 8-10 years old, (such as in the farm woodland site in Chapter 4), the development of the canopy has reduced light levels sufficiently to allow the woodland field layer species to persist. If a practitioner was prepared to regularly hand-remove competing vegetation within a high light area, then any introduced woodland species would probably thrive and establish successfully. This is only considered practical, however, on a very small scale, and is much too labour intensive for the majority of schemes. Hence, the presence of established, healthy trees of at least 5 years old was required as one of the criteria on which to base site suitability.

Finally, the minimum size of the site was also considered to be important to the establishment of field layer species. This is because the light regime within a very small site may be dominated by edge effects. Whilst woodland marginal species benefit from

increased light, shade levels within the site should be sufficient for the growth of shade-tolerant species, but reduce that of competing vegetation. Although some authors, (*e.g.* Cole 1982), recommend a minimum site width of 40m to reduce edge effects, many of the grid road plantations in Milton Keynes are only 30m wide. Since successful introductions of woodland field layer species have been made within such sites, a minimum site width of 30m was considered to be sufficient.

6.4.1.2 Species selection.

The results of the field trials in Milton Keynes that are presented in Chapters 2 and 3, have clearly demonstrated differences in the establishment strategies of woodland marginal and deep-shade species. The marginal species are quick to reach flowering maturity, and rapidly colonise bare ground if conditions are favourable. The deep-shade species establish much more slowly, some growing vegetatively for many years before flowering. Whilst both groups of species benefit from high light levels, only the woodland marginal species have sufficient competitive ability to thrive and persist in such conditions for any length of time. Thus, the light levels at a site are extremely important when selecting species groups for introduction. In addition, the amount of existing field layer vegetation at a site, which itself is partially controlled by the light level, also influences species selection. Hence, both light levels and the amount of existing vegetation at a site were identified as criteria on which to select species groups.

The results of the survival and performance of introduced species in woodlands of different ages (Chapter 4), and those of the distribution of shade-tolerant species in the young plantations in Milton Keynes (Chapter 3), have indicated that grass species in particular exert a considerable competitive effect on establishing populations of woodland field layer species. The analysis of the relationship of % cover of grass species with % daylight has indicated that grasses can be dominant within a field layer until light levels are less than 20%. However, the results in Chapter 4 showed that grass species were mainly dominant in the more open sites where % light levels were 40% or more. Competition exerted by any of the components of vegetation, such as grasses, and perennial and annual weeds, has been identified as being important to the survival and persistence of introduced field layer species. Such competition is particularly detrimental to the establishment of slow-growing, shade-tolerant species, which

themselves are poor competitors. Thus, high levels of shade are beneficial to introductions by reducing competition. However, it has also been recognised that introduced field layer species can benefit from light, which increases species' performance and hence promotes establishment and spread. Further, it is known that many practitioners do not always wish to wait for light levels to decrease, as this may take some years. It was therefore considered that the summer light levels at a site needed to be less than 40% of daylight before the introduction of field layer species could be recommended. The selection of this light level not only allows the introduced field layer species to benefit from light and does not require the development of full canopy cover, but should also reduce the possibility of dominance by competing vegetation, and grass species in particular. In addition, it is considered that once a woodland canopy has developed to produce 40% light conditions, it is likely to develop considerably lower light levels than this within a few years.

The experiment reported in Chapter 4 also demonstrated that the existing field layer vegetation at a site exerted considerable competitive influence on species that had been introduced as young plants, and significantly affected both their survival and subsequent performance. Further, field observations made within young plantations in Milton Keynes indicated that where species had been sown into plantations with substantial amounts of existing vegetation, both germination and seedling survival rates were reduced. Hence, it is important that the levels of existing vegetation at a site must be taken into consideration prior to the introduction of field layer species. For the time being, the three levels of existing vegetation have been determined mainly from field observations, and are rather subjective. It was considered that if the amount of existing vegetation was less than 10%, then this would have little effect on any introductions. However, if the existing vegetation level was 40% or more, then this would exert considerable competitive pressure on any introduced species, particularly as rapid colonisation could soon increase the vegetation level further.

The use of species groups ensured that unless site conditions were very unsuitable for species introductions, *i.e.* with high light levels and much existing vegetation, there was always an option to enhance the field layer to some extent, albeit possibly just in some areas of the site, or with a limited range of species. Thus, a practitioner with a very light

site, but low levels of existing vegetation, would at least be able to introduce woodland marginal species into the site. Such species, though not fully representative of a natural woodland field layer, would add to the interest and attraction of an impoverished field layer. Once shade levels at such a site increased, deep-shade species could then be introduced.

As a result of the field trials reported in Chapter 2, the widespread sowing of woodland field layer species has continued throughout young plantations in Milton Keynes. Though largely successful, experience has shown that the survival rates of field layer species are reduced if there is existing vegetation, even in a shady site. This is most probably because small seedlings and even young plants, particularly of the deep-shade species, are not able to compete successfully with established vegetation. Hence, in such conditions, it is recommended that a full range of woodland field layer species can be introduced, but should be targeted into shady areas away from existing vegetation. Species should therefore survive in patches from which they can spread out once established.

By using the criteria of light and vegetation levels at a site, it was possible to determine whether a full range of species could be introduced throughout the site, or targeted into certain areas, or whether marginal species alone were suitable for introduction.

Having distinguished such groups, species were then further selected depending on the soil conditions at the site. Since field layer species with specialised habitat requirements had been excluded from the species data set, it was thought sufficient to match species with soil conditions in terms of soil pH range and moisture level. This method was simple for the user, yet stringent enough to remove species that were unsuitable for a particular site. The soil types listed in Chapter 5, and additional information from Clapham *et al.* (1962), and Grime *et al.* (1979), were the sources of information for the soil details in the species data set.

6.4.1.3 **The recommendation of introduction techniques.**

The large-scale field trials in Milton Keynes involved the introduction of woodland field layer species into young plantations using both seeds and young plants. The extensive

monitoring of these trials, described in Chapter 2, demonstrated which species established best when introduced as seed, and which as young plants. Further, it was clear that the most successful introduction methods largely depended on the main regenerative strategies of the field layer species. (See also Francis *et al.* 1992a.) Thus in general, the woodland marginal species were best introduced as seeds, whilst the majority of deep-shade species established more successfully if introduced as plants. As a result of the field trials, experimental work in Berkshire, and germination tests, it was recognised that some of the deep-shade species, such as *A. ursinum*, *C. trachelium*, *E. amygdaloides*, and *H. non-scripta*, could also be introduced as seeds. All of this information was incorporated into the species data set, so that introduction techniques could be recommended for the list of selected species.

For those species best introduced as seeds, information was provided about germination requirements and the timing of sowing. The germination tests reported in Chapters 2 and 5, and other details gathered about germination in Chapter 5, gave useful information concerning the need for chilling and light to break dormancy in some species. With practical experience of large-scale sowing in Milton Keynes, it was considered essential to recommend introduction methods that were simple, yet successful. The advice given by the expert system therefore recommended that seeds were all mixed together, and sown at such a time that those seeds which required chilling would receive it. Further, due to the inherent variability observed and recorded at most sites, specially prepared 'seed beds' were judged unnecessary. It was considered that a proportion of the seeds of each species within the seed mixture were likely to fall in areas suitable for their particular light and moisture requirements.

Sowing rates were also suggested for seed mixtures. These varied depending on whether a full range of field layer species was to be introduced throughout a site, or just targetted into suitable areas, or whether only woodland marginal species were to be sown. Experience of sowing rates was gained from the monitoring of the large-scale field trials implemented in 1987 (see Chapter 2). Here, sowing rates were approximately 20kg ha^{-1} at high sowing density. The results of this sowing demonstrated that after 3 years marginal species were found in higher densities than deep-shade species. This was partially due to their generally higher germination rates, and to their ability to reach

flowering maturity more quickly. The resultant densities of many of the woodland marginal species, such as *G. urbanum*, *S. dioica*, and *T. japonica*, were considered to be too high. Francis *et al.* (1992a) therefore suggested a sowing rate of 10kg ha^{-1} for a seed mixture which contained both woodland marginal and deep-shade species. Further, the species characteristics studied in Chapter 5 showed that deep-shade species have a tendency to produce rather heavier seeds than the woodland marginal species. So, it was also recommended in the expert system that the deep-shade species should make up a higher proportion of the seed mixture than the woodland marginal species.

For those sites with substantial levels of existing field layer vegetation, it has been recommended that seed is targeted into suitable areas away from the competing vegetation. The seed mixture used in such circumstances would cover considerably less area than the mixture sown throughout the site. Hence, it is suggested in the expert system that the sowing rate for targetting such areas of the site should be reduced to 5kg ha^{-1}. This mixture would still contain both marginal and deep-shade field layer species.

The continuing introduction of woodland field layer species as seed into young plantations in Milton Keynes has provided further information about sowing rates. At present, the sowing rate used in Milton Keynes is approximately 2.8kg ha^{-1}, though this may vary slightly depending on species availability (Milton Keynes internal document 1991). Due to cost and species availability, this seed mixture contains predominantly woodland marginal species. Though germination rates are generally low (see Section 2.4.2), this sowing rate appears to introduce sufficient individuals to allow subsequent establishment and colonisation of a field layer. Hence, the expert system suggested a sowing rate of 3kg ha^{-1} for the introduction of woodland marginal species.

Information was also provided in the decision support system for the introduction of field layer species as young plants. The use of young plants was recommended for those species which produce few seeds, but which are capable of vigorous vegetative reproduction. Such advice results from the outcome of experimental work with field layer plants in Milton Keynes and Berkshire. In trials, some species, such as *T. scorodonia*, established more successfully when planted than when sown, and other species, such as *A. reptans* and *L. galeobdolon*, had to be introduced as plants, since

seed was not available. The study of the regenerative strategies of woodland field layer species made in Chapter 5, demonstrated which species had predominantly vegetative reproduction. Clearly, if such species are to be successfully introduced into new woodlands, then it is necessary to use young plants.

The expert system recommends that plants are grouped together, rather than introduced as discrete individuals, as this better mimics the mosaics of woodland field layer species that are observed in naturally colonised areas (Francis *et al.* 1992a). Further, the results of plantings in Milton Keynes showed that some species, such as *P. vulgaris*, established more successfully at high rather than low planting densities (Chapter 2). Though plant availability is likely to dictate planting densities, these were recommended to be 9 plants m^{-2}, which is the same as the high density planting rate used in the Milton Keynes trials and that in the Berkshire experiment.

6.4.2 The decision support system: its success, and further development.

The development of a preliminary decision support system for the enhancement of woodland field layers is considered to be relatively successful. Within a few months, the results of research have been compiled into a system for the introduction of field layer species into a new site. This gives practical recommendations and advice to practitioners and habitat managers, which should enable them to make successful field layer introductions. In order to develop the system, it was necessary to identify the key variables governing the growth and establishment of woodland field layer species.

Whilst a useful method has been produced by which to impart expert advice, the preliminary decision support system could be improved upon, and supplemented with additional advice and information. The variability of sites has been mentioned as one potential difficulty in the initial testing of site suitability. The criteria used for determining site suitability in the present system could be more critically defined in the future.

The selection of field layer species that are appropriate for introduction into a site could

also be made more carefully. Factors such as existing canopy species, the accumulation of leaf litter, slope and aspect of a plantation could be incorporated into the species selection procedure. Soil nutrient levels, which are recognised as playing an important role in the determination of field layer species, could also be included. Further, the range of field layer species for which data are held currently could be extended to contain species from other regions of the country. Information in the species data file could be supplemented to include details of specific germination requirements, flowering times, and insect visitors, for example. All such information could be displayed to the user if it was needed.

Where sites have high levels of existing vegetation, such as a rough grass sward, beneath the establishing trees, they have been rejected as unsuitable by the present system. Enhancement of such sites is considered difficult, as removal of competing species is labour intensive and expensive. Graminicides have been used to manipulate existing field layers, and thereby encourage the growth of desired species (Porter & Nowakowski 1991). Although insufficient research has been carried out in this area, it is suggested that selective herbicides may be very useful for the introduction of field layer species into existing vegetation. The expert system could be further developed to include recommendations for the use of such herbicides in the future, following suitable experimental work.

6.4.3 Conclusions.

The development of a preliminary decision support system has helped to define the important variables governing the establishment of woodland field layer species that have been introduced into young plantations and new woodlands. In addition, the resulting system should enable practitioners to select field layer species for a new site, and, using the information and advice, to introduce them successfully.

7. Conclusions and general discussion.

7.1 Practical aspects of field layer enhancement.

The success of the field trials in Milton Keynes (Chapter 2), and of the experiment implemented in Berkshire (Chapter 4), has demonstrated that it is possible to introduce woodland field layer species into recent woodlands and young plantations. Although the initial survival rates of the introductions were variable, it is considered that the introduced species have survived in sufficient numbers to enable their establishment and spread. Further, from the study of the regenerative strategies, and other autecological details of the field layer species (Chapters 2, 3, and 5), effective, yet practical, methods of species introduction have been identified. The importance of the use of both seed and plant material in order to introduce a representative group of species into new areas has been recognised in this, and other studies (Buckley 1982, Cohn & Packham 1991). The study reported here has distinguished three distinct groups of species. These are:

i. Woodland marginal species, which can be introduced as seeds, *e.g. S. dioica* and *A. petiolata*;

ii. Shade-tolerant species, which produce high amounts of seed, have low vegetative ability, and can be introduced as seeds, *e.g. H. non-scripta* and *A. ursinum*;

iii. Shade-tolerant species, with a predominantly vegetative strategy, which can be introduced as plants, *e.g. A. reptans* and *L. galeobdolon.*

The recognition of these groups is considered to be fundamental to the success of the introductions. Many of the deep-shade species will not establish successfully if they are introduced as seed. Not only is their germination poor, but seedling growth is slow, and there is a possibility that such species may be ousted by competition during their establishment period.

The studies have also highlighted the importance of certain site factors to the success of survival and establishment of the field layer species. The introduction of ancient woodland field layer species into woodlands of different ages was largely successful (Chapter 4). This study demonstrated that soil conditions are less crucial than was considered previously, particularly for those species with a wide ecological amplitude.

However, the light levels at a site, which specifically control vegetation levels, are of paramount importance. The majority of woodland species are known to have poor competitive capacities, and having adapted to tolerate shade, grow in the woodland refuge. Hence, it is usually recommended (Buckley 1982, and Emery 1986) that species are not introduced until shade levels have increased sufficiently to reduce the amount of competitive species which inevitably colonise new areas. It is suggested, however, that if competition is controlled by other means, then species can be effectively introduced prior to canopy closure. The introduction of ancient woodland species into woodlands of different ages (Chapter 4) has shown that species actually benefit from high light levels, if competition from existing vegetation is reduced.

To control competition, the use of herbicide is very effective. If used repeatedly beneath establishing trees, it can substantially reduce the buried seed bank of non-target species to acceptable levels (Buckley & Knight 1989), whereas if used only a single time on an existing field layer, it may be effective in changing the structure of the competing vegetation (Chapter 4). Foresters have long advocated the use of herbicides to ensure good tree establishment. By reducing the pool of potential weed competitors, ideal conditions are created for the introduction of field layer species once the trees have established, and the herbicide regime has ceased. Further, use of herbicide also enables earlier introduction of species, when light levels are still relatively high, and from which the field layer species can benefit and establish well. The use of mulch for weed reduction has also been tested, but is not an appropriate form of control in some circumstances (Chapter 4), and is less applicable to large-scale schemes. Some, (Cohn & Packham 1991), however, have advocated the use of mulch, and have found it suitable in particular circumstances.

Unless practitioners wishing to make introductions are prepared to wait many years until shade has increased sufficiently to reduce the growth of invasive weeds, an effective ground pre-treatment is extremely beneficial. In this way, the field layer introductions can be an integral component of young woodland management, being complementary to the techniques used in tree establishment (Francis *et al.* 1992a).

The practical details about ground pre-treatments, the timing and methods of

introduction, and species choice have been encompassed into a decision support system for the enhancement of new woodlands by the addition of field layer species. This preliminary system has been written in a straightforward, 'user-friendly' manner, and should allow practitioners and restorationists to enhance woodland areas in a practical way, whilst simultaneously ensuring the successful establishment of the introduced field layer species.

7.2 The benefits and ethics of field layer enhancement.

Research has shown that species which colonise recently developed secondary woodland are not the same as those which characterise semi-natural woodlands, in the short-term (Peterken 1974). The poor natural colonising ability of woodland field layer species, and the isolation of newly planted woodlands, may result in field layers that are low in species diversity. In order to prevent this, and to enhance such field layers, it is considered that introduction of field layers species may be necessary (Chapter 1). In addition to this, the introductions are also beneficial to the developing communities into which they are introduced. Many of the woodland species are attractive and interesting, and they enhance the appearance of the young plantations, particularly in urban areas, such as in Milton Keynes, where these plantations are in close proximity to housing developments. Here, they are perceived positively by the inhabitants, many of whom expect to see colourful woodland wildflowers beneath the trees (M. Street, pers. comm.). The establishment of such attractive naturalistic areas for recreation and education may help to reduce visitor pressure on the few remaining natural ancient woodlands (Cohn & Packham 1991).

The effects that the field layer species have on other elements of the developing ecosystem are also important. Many of the field layer species are attractive to insects, whether as sources of nectar and pollen, such as *H. non-scripta*, *L. galeobdolon* and *P. vulgaris*, or as larval food plants, such as *A. petiolata*. Within the plantations at Milton Keynes, a large variety of insects have been noted in association with the field layer species. Studies on the use of farm woodlands by *Bombus* species (Saville *et al.* 1992)

have demonstrated that such areas are important nesting and foraging sites for these, and other crop pollinators. Further research into the identification of field layer species as good nectar sources, showed that many components of the woodland field layer, such as *A. reptans*, *G. hederacea* and *L. galeobdolon*, were important for the bumblebees. Other studies have indicated the importance of field layer species for attracting butterflies and pheasants (Ludolf *et al.* 1989). In general, if the field layer species enable populations of insects to establish in the developing woodlands, then other components of the ecosystem, such as birds and small mammals, will also be encouraged.

Another study in farm woodlands (Rushton & Whiteley 1991) identified the capability of field layer vegetation to reduce nitrate leaching in soil water. This important effect was recorded after a low maintenance set-aside mixture was sown between young trees. It was therefore suggested that the inter-rows between trees should be sown with suitable wild flower mixtures to alleviate the problem of nutrient leaching. Trials already implemented by the Forestry Commission, incorporate the sowing of meadow species between rows of establishing trees in farm woodlands (Williamson *et al.* 1992). Since few of these species will persist once shade levels increase, it is suggested that more appropriate mixtures of woodland field layer species could be developed for such purposes. Further, their poor colonising ability would ensure that they could not become a weed problem in nearby crops.

Despite their obvious benefits, the introduction of woodland field layer species into new woodlands and young plantations is mostly for enhancement purposes. The addition of this one component of the entire woodland ecosystem into a new area is not considered to be an attempt at ancient woodland re-creation. Indeed, ancient woodlands cannot be re-created, but only mimicked to some extent (Kirby 1992). Their fascination is that each is different from the other, making "a statement of society and culture" (Sutherland & Gibson 1988). In the new woodlands, the elements of old forests will develop very slowly, possibly over centuries rather than decades. Some of these elements, such as the trees and field layer species, can be introduced or encouraged by providing a suitable framework for their development (Kirby 1992).

Generally, attitudes towards field layer enhancement have altered during the last 10

years (J. Packham, pers.comm.), and it is now acceptable to introduce "common species into new woods within the existing range of these species" (Kirby 1992). However, in urban areas, the attitudes towards woodland habitat creation still range from extreme tolerance, to complete opposition. Some, (Spray & Spray 1984 and Peterken 1986), encourage species introductions where appropriate, and recognise that the manipulation of such communities can greatly serve conservation interests. Indeed, the aim of woodland habitat creation can be to alter the natural process of succession, rather than waiting many years for species to invade naturally (Emery 1986), and it is possible to accelerate this by tree planting and field layer enhancement. Others, however, believe that urban woodlands should be left to be colonised naturally, often by a mix of exotic and alien species that have adapted to the urban situation, and then should be protected and managed accordingly (Hare 1988). Strongly against introductions of any type, Hare writes of natural urban woodlands that "there are continued attempts to replace them with native species in the name of ecology....Is it ecologically sensible to attempt to impose on urban localities an imitation of the distant countryside?" when "In town 'the aliens' are the natural inhabitants....People cannot be expected to appreciate the environment around them in the city if they are only encouraged to enjoy a distant, almost mythical countryside which is all too often unavailable to them."

Some still oppose the introduction of species into new areas completely. In the wider context of species translocations outside the urban environment, some, (C. Chatters, pers. comm.), are particularly concerned with the introduction of the ancient woodland indicator species (*sensu* Peterken 1974) into new areas, as they consider that this will affect their distribution and present confinement to old woodlands. Further, it is regarded that "such activities cloud the study of the distribution and natural spread or decline of species" (Payne 1992). Indeed, writing of the past centuries of unintentional changes in plant distributions by farmers and traders, Payne (1992) concludes that "to try to arrest these global trends by petty measures such as parochial translocations of plants seems to me to be a misuse of ingenuity".

Fortunately, these are the extreme views of a minority. The majority are aware that the earth is now "in the midst of an environmental emergency. And emergencies require extraordinary responses" (Berger 1990). To encompass genuine concerns about plant

genetics and distribution patterns, it is necessary that there are clearly-defined rules for the way in which habitat creation is managed. Introduced vegetation should conform to local natural or semi-natural patterns. It is important that species introductions are recorded permanently, and that such records are made available. Species of British origin should be used for introductions, as there is concern that if species of dubious origin are introduced, native populations may be altered, and loss of genetic integrity may occur (Anon 1989). The recent and successful opposition by Britain to an E.E.C. requirement for free access to markets for continental wild flower seeds (Stokes 1993) is very important in this context. Ideally, only local races of native species should be introduced into new areas. Perhaps ultimately, "the species used, the nature of the material, the source of the stock, the location and the time of the introduction(s) should be recorded, and the information sent to the local Biological Records Centre" (Anon 1989). It is clearly important, that introductions of any species into new areas are adequately recorded. Further, if possible, such introductions should be regularly monitored. Hence, their initial survival, subsequent establishment and persistence can be studied. In this way, the species introductions can lead to valuable experiments and can contribute to an understanding of the ecology of woodland plants.

7.3 The ecology of woodland field layer species.

The results of the field trials, experiments, germination tests, and literature searches carried out in this study have not only had practical value, but have also given an important insight into the ecology of the woodland field layer species. Many of the field layer species, particularly those which are tolerant of deep shade conditions, are associated with old, undisturbed woodland habitats as a refuge in which they avoid competition from more robust species. The majority of the field layer species do not have a requirement for the shady conditions, but have adapted to tolerate them. This study has clearly demonstrated that if competing vegetation levels are reduced, woodland species can grow well in open areas, and can actually benefit from high light conditions. The introduction of ancient woodland species into woodlands of different ages (Chapter 4) showed an increase in the performance of *F. gigantea*, *L. galeobdolon*, and *P.*

vulgaris in terms of flower or flowering stem production. Such enhanced reproductive success is very important to the persistence of these species, particularly in new areas.

The research has also highlighted the differences between the marginal and shade-tolerant species. The autecological characteristics of 30 field layer species were investigated (Chapter 5), and with germination tests (Chapters 2 and 5), and the monitoring and analysis of species survival and subsequent establishment after introduction into young plantations (Chapter 2), the distinctions between them have been thoroughly examined. The woodland marginal species are quick to reach flowering maturity, and produce copious amounts of small, easily-dispersed seeds, which have moderate to high germination rates. These light-demanding species show high initial survival when introduced into new areas, and have rapid establishment rates if conditions are suitable. In contrast, the deep-shade species are slow to flower, and many exhibit predominantly vegetative growth. They produce few, heavy seeds, with poor dispersal and low viability. When introduced into new areas, their establishment, although enhanced by the introduction of young plants, is slow, and they may be ousted by competing vegetation in high light conditions. These fundamental differences in the ecology of woodland marginal and deep-shade species have been related to introduction techniques (refer to Section 7.1).

The work has also indicated that, at least for the species studied, ancient woodland species must be mainly limited in their colonising ability, not by site conditions, such as soils, but by poor seed production and dispersal. This conclusion is also reached by Peterken & Game (1984) in their study of the distribution of woodland species in the woodlands of central Lincolnshire.

The field trials and experiments have demonstrated that the introduction of field layer species into new areas is feasible. Survival rates from seeds, though generally rather low, are considered to be adequate to ensure the subsequent establishment and persistence of species in the new environments. An attempt was made to study the patterns of establishment of the introduced field layer species within the young plantations in Milton Keynes (Chapter 3). The introductions were made 5 years ago, and detailed monitoring and analysis showed some clear trends in species establishment.

There were indications that some species, such as *H. hirsutum* and *T. japonica*, were establishing predominantly in lighter areas, whilst others, such as *H. non-scripta*, were more restricted to shady conditions. Further, there were distinct differences in reproductive rates, with some species populations, such as *G. urbanum* and *S. dioica*, being dominated by seedlings, whilst other species, such as *G. odoratum* and *H. non-scripta*, had yet to reproduce, and exhibited mostly vegetative growth.

Apart from these trends, patterns of establishment were difficult to characterise. It was concluded that this was due to the heterogeneity of the sites and of the initial sowing, and to the dominance of transient dynamics in these mid-successional communities. It is considered that within another few years, as shade levels increase further with canopy development, and thus competing vegetation is reduced, more distinct species assemblages will emerge, and the field layer will stabilise.

7.4 Further considerations and future developments.

It is important that the young plantations and woodlands into which introductions have been made, and which have already been recorded in detail, should be studied in the future, as there is, undoubtedly, more valuable information to be gained from them. Although the introduced field layer species have survived and subsequently established, their persistence in the long term is not guaranteed. It is possible, that some species, particularly those with poor competitive ability, will not be able to withstand competition from more robust field layer species in the long term. Despite the use of weed control, natural colonisers will inevitably invade the sites until shade levels have increased substantially (Chapter 4). Even in shady areas, shade-tolerant weed species, such as *A. sylvestris* and *G. aparine*, may exert strong competitive pressure on the introduced species. In addition, if unmanaged, the plantations may develop towards a 'thicket stage' (Kirby 1992), characterised by a dense, shrubby understorey. During this time, it is possible that some of the establishing field layer species may be eliminated due to a decrease in light levels. It can be argued, however, that as in neglected coppice, the majority of species would survive in a vegetative state until light increased once

again.

A commitment to the management of such areas will therefore be important to the development of the woodland field layer. The timing of this management must be considered carefully, as it will affect species establishment. Ideally, thinning of trees and shrubs within the plantations should occur once the slower, deep-shade species have established, and they will then benefit from increased light levels. If, on the other hand, thinning is carried out during the establishment phase of these species, then the increase in light levels may encourage the growth of natural colonisers and woodland marginal species to such an extent that they oust the deep-shade species.

In future years, the continued monitoring of the field layer species in young plantations will help to elucidate the effect of such management regimes upon field layer establishment. With little experience of their outcome, only suggestions can be made at this stage. It is important to consider that each situation may possibly be different, and accompanied by a knowledge of species behaviour, the management of each new woodland may have to be tailored accordingly.

Further monitoring of field layer development should also clarify whether the rates of spread of the introduced species, and the patterns of species distribution and abundance are equivalent to those in natural colonies. In this way, the behaviour of the field layer species can be compared between natural and created populations. It is of interest, that a study of woodland herbaceous species introduced into an American arboretum, demonstrated that although establishment was good, the dispersal of some species was often slow, or insignificant (Woods 1984). Species, such as *Sanguinaria canadensis* L. (Bloodroot) and *Asurum canadense* L. (Wild Ginger), which are both ant-dispersed, grew into unnaturally large patches, and failed to colonise their new site effectively. This unnatural distribution correlated well with low ant populations in the arboretum. In nearby natural forests, where there were approximately 200 times more ants, species dispersal followed natural patterns. The study suggested that the absence of a small member of the biotic community may have long-lasting and large-scale effects on efforts to restore it successfully. Such a conclusion has important implications for woodland habitat creation.

It is considered that the mycorrhizal associations which the majority of woodland field layer species have with soil fungi (Read *et al.* 1976), may also play a very important role in their growth and survival. Enabling the plants to increase the uptake of nutrients, particularly phosphates, these fungi are essential to their growth in old woodlands. It is unknown whether such associations develop when field layer species are introduced into new areas, as the correct vesicular-arbuscular species of fungi may not be present in the soils at these sites. It may be that higher fertility levels reduce the need for the nutrient supplementation, but there has, as yet, been little, or no, research into this subject. If mycorrhizae are necessary for the long-term survival of the field layer species, then this would be very important when introducing them into new areas.

The full extent to which herbicides can be used in the manipulation of field layers has yet to be developed sufficiently, and requires further research. The benefits of herbicide use in establishing populations has already been mentioned. Other studies, (Putwain & Mortimer 1991), have demonstrated the use of graminicides during the establishment of direct-seeded broadleaved woodland. Whilst enabling good tree growth, it was also found that herbicide increased the ecological diversity in the herbaceous plant community. Research into the management of existing field layers with graminicides (Porter & Nowakowski 1991, and Haggar *et al.* 1991), has shown that woodland herbs may be allowed to recolonise and increase within impoverished and grass-dominated field layers after herbicide application. Thus, biodiversity is enhanced. Since bare earth policies, such as that used in Milton Keynes (Chapter 2), are neither widely used nor accepted, it is considered that there may be many occasions when the enhancement of existing field layers will be necessary. Techniques for the introduction of woodland field layer species into such areas using selective herbicides could usefully be developed for this purpose.

In Britain, there are currently ambitious plans for the creation of new forests (Chapter 1), and there is continued interest in the enhancement of woodland field layers. Indeed, this aspect of habitat enhancement is now receiving attention from organisations such as the Department of Transport, who forsee the benefits of woodland field layer introductions into the linear copses along Britain's trunk road network (Sangwine 1992). If successful introductions are to be made on such a large scale, it is important that the

study of field layer introductions into secondary woodland continues in the future. As the advantages of field layer enhancement are further perceived, it will be necessary both to continue the development of practical and successful methods for such introductions, and to fully understand their ecological implications.

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Personal communications.

Gerald Dawe 40, Milford Road, Birmingham. B17 9RL

Stuart McNeill Imperial College, Silwood Park, Ascot, Berks. SL5 7PY

John Packham Wolverhampton Woodland Research Group, University of Wolverhampton, Wolverhampton. WV1 1SB

Ian Trueman School of Applied Sciences, University of Wolverhampton, Wolverhampton. WV1 1SB

Appendix A.

ANCIENT WOODLANDS SURVEY–SOUTH REGION

SITE	NO.	Grid Ref	O.S. Sheet	County
Locality	Ha.	Recorder/s		Date/s

WOODLAND VASCULAR PLANTS – those species which in South Region: (a) seldom occur outside woodland; or (b) when they occur in woodland, are indicative of long continuity; or (c) in at least part of the region, act as ancient woodland indicators.

	A	B
Acer campestre*		
Adoxa moschatellina		
Agropyron caninum		
Allium ursinum		
Anemone nemorosa		
= Aquilegia vulgaris*		
= Arum italicum neglectum		
Blechnum spicant		
+ Bromus benekenii		
Bromus ramosus		
+ Buxus sempervirens*		
Calamagrostis epigejos		
+ Campanula latifolia*		
Campanula trachelium		
= Cardamine bulbifera		
= Cardamine impatiens		
+ Carex digitata		
Carex laevigata		
Carex pallescens		
Carex pendula*		
Carex remota		
= Carex strigosa		
Carex sylvatica		
= Cephalanthera longifolia		
= Chrysosplenium alternifolium		
C. oppositifolium		
Circaea lutetiana		
= Colchicum autumnale		
Conopodium majus		
= Convallaria majalis*		
= Corydalis claviculata		
Crataegus oxyacanthoides		
Daphne laureola		
+ Daphne mezereum		
= Dipsacus pilosus		
= Dryopteris pseudomas		
Epipactis helleborine		
= Epipactis leptochila		
+ Epipactis phyllanthes		
= Epipactis purpurata		
+ Epipogium aphyllum		
= Equisetum sylvaticum		
Euphorbia amygdaloides		
Festuca gigantea		
= Frangula alnus		
= Gagea lutea		
Galium odoratum		
Geum rivale		
= Gnaphalium sylvaticum		
= Helleborus foetidus		
= Helleborus viridis		
Holcus mollis		
= Hordelymus europaeus		
Hypericum androsaemum		
= Hypericum montanum		
Ilex aquifolium*		
Iris foetidissima		
Lamiastrum galeobdolon		
Lathraea squamaria		
Lathyrus montanus		
= Lathyrus sylvestris		
= Luzula forsteri		
Luzula pilosa		
Luzula sylvatica		
Lysimachia nemorum		
Malus sylvestris*		
Melampyrum pratense		
Melica uniflora		
+ Melittis melissophyllum		
Milium effusum		
= Monotropa hypopitys		
Myosotis sylvatica*		
Narcissus pseudonarcissus*		
Neottia nidus-avis		
= Ophrys insectifera		
Orchis mascula		
= Ornithogalum pyrenaicum		
Oxalis acetosella		
Paris quadrifolia		
Phyllitis scolopendrium*		
Platanthera bifolia		
Platanthera chlorantha		
Poa nemoralis		
Polygonatum multiflorum		
= Polygonatum odoratum		
= Polygonum dumetorum*		
Polypodium vulgare		
= Polystichum aculeatum		
Polystichum setiferum		
Populus tremula		
+ Primula elatior*		
Primula vulgaris*		
Prunus avium*		
= Pulmonaria longifolia		
+ Pyrola minor		
+ Pyrus communis*		
Quercus petraea*		
Ranunculus auricomus		
Ribes nigrum*		
Ribes sylvestre*		
= Ruscus aculeatus		
Sanicula europaea		
Scrophularia nodosa		
Sedum telephium		
= Solidago virgaurea		
Sorbus aria*		
Sorbus aucuparia*		
= Sorbus torminalis		
= Stellaria neglecta		
+ Thelypteris oreopteris		
+ Tilia cordata*		
= Ulmus glabra		
Vaccinium myrtillus		
Veronica montana		
Viburnum opulus*		
= Vicia sylvatica		
Viola odorata*		
Viola reichenbachiana		
+ Wahlenbergia hederacea		

+ Rare
= Restricted

Column A: current records
Column B: old records

* Only tick these species if they occur well within the wood and do not appear to have been planted.

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Appendix B.

B1. Results of 2-way ANOVA for *C. sylvatica* vegetative shoot counts.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	3	14.5	4.8	1.4
TREATMENT	1	52.8	52.8	14.8**
ERROR	35	124.6	3.6	-
TOTAL	39	192.0	-	-

$F_{.05[3,35]} = 2.87$ $F_{.05[1,35]} = 4.13$

B2. Results of 2-way ANOVA for *C. sylvatica* flowering shoot counts.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	3	64.8	21.6	2.8**
TREATMENT	1	35.4	35.4	4.5**
ERROR	35	273.4	7.8	-
TOTAL	39	373.6	-	-

$F_{.05[3,35]} = 2.87$ $F_{.05[1,35]} = 4.13$

B3. Results of 2-way ANOVA for *C. sylvatica* maximum leaf lengths.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	3	125.5	41.8	1.9
TREATMENT	1	20.2	20.2	0.9
ERROR	35	778.7	22.3	-
TOTAL	39	924.5	-	-

$F_{.05[3,35]} = 2.87$ $F_{.05[1,35]} = 4.13$

B4. Results of 2-way ANOVA for *F. gigantea* vegetative shoots.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	3	152.0	50.7	21.6**
TREATMENT	1	39.3	39.3	16.7**
ERROR	35	82.3	2.4	-
TOTAL	39	273.7	-	-

$F_{.05[3,35]} = 2.87$ $F_{.05[1,35]} = 4.13$

B5. Results of 2-way ANOVA for *F.gigantea* flowering shoots.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	3	17.3	5.8	6.3**
TREATMENT	1	21.6	21.6	23.8**
ERROR	35	31.8	0.9	-
TOTAL	39	70.6	-	-

$F_{.05[3,35]} = 2.87$ $F_{.05[1,35]} = 4.13$

B6. Results of 2-way ANOVA for *F.gigantea* leaf length.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	3	327.2	109.1	6.7**
TREATMENT	1	81.1	81.1	5.0**
ERROR	35	567.1	16.2	-
TOTAL	39	975.5	-	-

$F_{.05[3,35]} = 2.87$ $F_{.05[1,35]} = 4.13$

B7. Results of 2-way ANOVA for *C. lutetiana* shoots per block.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	4	36633.0	9158.3	4.8**
TREATMENT	1	12832.0	12832.0	6.7**
ERROR	44	83881.0	1906.4	-
TOTAL	49	133347	-	-

$F_{.05[4,44]} = 2.61$ $F_{.05[1,44]} = 4.08$

B8. Results of 2-way ANOVA for *C. lutetiana* leaf lengths.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	4	50.9	12.7	4.8**
TREATMENT	1	65.2	65.2	24.3**
ERROR	44	118.1	2.7	-
TOTAL	49	234.2	-	-

$F_{.05[4,44]} = 2.61$ $F_{.05[1,44]} = 4.08$

B9. Results of 2-way ANOVA for *C. lutetiana* leaf count per shoot.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	4	40.3	10.1	4.9**
TREATMENT	1	38.7	38.7	18.8**
ERROR	44	90.5	2.1	-
TOTAL	49	169.4	-	-

$F_{.05[4,44]} = 2.61$ $F_{.05[1,44]} = 4.08$

B10. Results of 2-way ANOVA for *L. galeobdolon* shoot counts.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	4	116.3	29.1	4.9**
TREATMENT	1	309.2	309.2	52.0**
ERROR	44	262.0	6.0	-
TOTAL	49	687.4	-	-

$F_{.05[4,44]} = 2.61$ $F_{.05[1,44]} = 4.08$

B11. Results of 2-way ANOVA for *L. galeobdolon* flowering stem counts.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	4	15.1	3.8	4.9**
TREATMENT	1	38.2	38.2	49.3**
ERROR	44	34.1	0.8	-
TOTAL	49	87.4	-	-

$F_{.05[4,44]} = 2.61$ $F_{.05[1,44]} = 4.08$

B12. Results of 2-way ANOVA for *L.galeobdolon* leaf lengths.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	4	56.6	11.3	6.3**
TREATMENT	1	20.6	20.6	11.5**
ERROR	44	78.7	1.8	-
TOTAL	49	155.9	-	-

$F_{.05[4,44]} = 2.61$ $F_{.05[1,44]} = 4.08$

B13. Results of 2-way ANOVA for *P. vulgaris* flower counts.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	4	1249.0	312.3	5.5**
TREATMENT	1	1842.0	1842.0	32.3**
ERROR	44	2511.5	57.1	-
TOTAL	49	5603.1	-	-

$F_{.05[4,44]} = 2.61$ $F_{.05[1,44]} = 4.08$

B14. Results of 2-way ANOVA for *P. vulgaris* leaf counts.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	4	13.1	3.3	1.3
TREATMENT	1	40.5	40.5	16.3**
ERROR	44	109.0	2.5	-
TOTAL	49	162.6	-	-

$F_{.05[4,44]} = 2.61$ $F_{.05[1,44]} = 4.08$

B15. Results of 2-way ANOVA for *P. vulgaris* maximum leaf lengths.

SOURCE OF VARIATION	df	SS	MS	F_S
SITE	4	487.4	121.9	26.6**
TREATMENT	1	56.7	56.7	12.4**
ERROR	44	201.5	4.6	-
TOTAL	49	745.5	-	-

$F_{.05[4,44]} = 2.61$ $F_{.05[1,44]} = 4.08$

Appendix C.

The composition of the field layer within the 1949 plantation.

Species confined to ancient woodland, poor colonists.

Primula vulgaris (Primrose)

Species found in ancient woodland, but which tolerate other habitats.

Bromus ramosus (Hairy-brome)
Carex sylvatica (Wood-sedge)
Festuca gigantea (Giant Fescue)
Hyacinthoides non-scripta (Bluebell)
Hypericum hirsutum (Hairy St John's-wort)
Mercurialis perennis (Dog's Mercury)
Sanicula europaea (Sanicle)

Woodland species which are good colonisers.

Ajuga reptans (Bugle)
Arum maculatum (Lords-and-Ladies)
Brachypodium sylvaticum (False Brome)
Circaea lutetiana (Enchanter's-nightshade)
Epilobum montanum (Broad-leaved Willowherb)
Geranium robertianum (Herb-Robert)
Geum urbanum (Wood Avens)
Glechoma hederacea (Ground-ivy)
Hedera helix (Ivy)
Poa trivialis (Rough Meadow-grass)
Rubus sect. *Glandulosus* (Bramble)
Stachys sylvatica (Hedge Woundwort)
Stellaria holostea (Greater Stitchwort)
Tamus communis (Black Bryony)
Urtica dioica (Common Nettle)

Shade-tolerant species, including weeds.

Anthriscus sylvestris (Cow Parsley)
Arctium minus ssp. *pubens* (Lesser Burdock)
Bellis perennis (Daisy)
Cardamine hirsuta (Hairy Bitter-cress)
Cirsium arvense (Creeping Thistle)
Dactylis glomerata (Cock's-foot)

Shade-tolerant species, including weeds (cont.).

Dactylorhiza fuchsii (Common Spotted-orchid)
Deschampsia cespitosa (Tufted Hair-grass)
Elytrigia repens ssp. *repens* (Common Couch)
Filipendula ulmaria (Meadowsweet)
Galium aparine (Cleavers)
Heracleum sphondylium (Hogweed)
Holcus lanatus (Yorkshire-fog)
Lapsana communis ssp. *communis* (Nipplewc)
Myosotis sylvestris (Wood Forget-me-not)
Plantago major (Greater Plantain)
Primula veris (Cowslip)
Ranunculus repens (Creeping Buttercup)
Rumex obtusifolius (Broad-leaved Dock)
Senecio jacobea (Common Ragwort)
Stellaria media (Common Chickweed)
Taraxacum sect. *Ruderalia* (Dandelior
Torilis japonica (Upright Hedge Pars /)
Veronica chamaedrys (Germander S edwell)
Viola hirta (Hairy Violet)

Appendix D.

Species which germinated in pots of woodland soil.

Ajuga reptans (Bugle)
Cardamine hirsuta (Hairy Bitter-cress)
Carex sylvatica (Wood-sedge)
Cerastium arvense (Field Mouse-ear)
Cirsium arvense (Creeping Thistle)
Cirsium vulgare (Spear Thistle)
Digitalis purpurea (Foxglove)
Fragaria vesca (Wild Strawberry)
Geranium robertianum (Herb-Robert)
Glechoma hederacea (Ground-ivy)
Juncus effusus (Soft-rush)
Poa trivialis (Rough Meadow-grass)
Polygonum spp. (Knotweed spp.)
Primula vulgaris (Primrose)
Prunella vulgaris (Selfheal)
Rubus sect. *Glandulosus* (Bramble)
Senecio vulgaris (Common Ragwort)
Silene dioica (Red Campion)
Sonchus arvensis (Perennial Sow Thistle)
Stellaria media (Common Chickweed)
Taraxacum sect. *Ruderalia* (Dandelion)
Urtica dioica (Common Nettle)
Veronica chamaedrys (Germander Speedwell)

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Vegetation management in forestry, amenity and conservation areas

The establishment of ground flora species in recently planted woodland

JOANNA L. FRANCIS, ALAN J. MORTON
Imperial College, Silwood Park, Ascot, Berks SL5 7PY, UK
LAURENCE A. BOORMAN
Institute of Terrestrial Ecology, Monks Wood Experimental Station, Abbots Ripton, Huntingdon, Cambs PE17 2LS, UK

SUMMARY

Results are given of the monitoring of a large scale field trial in Milton Keynes, where seeds and young plants of woodland herbaceous species have been introduced into young woodland sites. The results of the experiment demonstrate the feasibility and success of ground flora introductions into woodlands. They also indicate which species are more successfully introduced as seeds and which as young plants. Some recommendations concerning site pre-treatment, species choice and method of introduction are made.

INTRODUCTION

In recent years, large numbers of trees have been planted throughout Britain as a result of such incentives as the Farm Woodland Scheme, Community Forests and many urban woodland initiatives. Once established, the groups of young trees develop into plantations, which, whether or not they have previously received any weed-control treatment, are often characterised by a very rough, coarse field layer. This may consist of invasive ruderals, annual and perennial weeds, but will usually contain none of the more interesting and attractive ground flora components that are associated with mature woodlands. The isolation of new plantations from mature woodlands, and the poor colonising capacity of woodland species, such as *Primula vulgaris* (Primrose), *Hyacinthoides non-scripta* (Bluebell) and *Lamiastrum galeobdolon* (Yellow Archangel), results in only a very slow colonisation into new areas (Peterken & Game, 1984) or possibly none at all.

Introductions of woodland ground flora species therefore become necessary if the development of more attractive field layers is to be encouraged, and, by selecting a suitable range of species, ecosystems that are more similar to naturally existing ones can be created. The enhanced field layers have much public appeal and can be a useful educational resource, particularly in urban situations where access to mature woodlands is very limited. The behaviour and success of the introduced species can also be recorded and analysed to contribute to an understanding of their ecology.

The aim of the work reported here is to develop practical methods for introducing woodland ground flora species into new woodlands. The work encompasses a large-scale field trial in which the timing of such introductions, ground pre-treatments, species choice and introduction methods are all considered.

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SITES

Field trials for the large scale introduction of woodland herbaceous species into newly planted woodland have been established at Milton Keynes, Buckinghamshire. The woodland sites were formed during the building of the town and result from the creation of roads or housing estates. Various mixtures of mostly native tree and shrub species, were planted between 1976 and 1982. After planting, a bare-ground policy, achieved by repeated sprayings of herbicide, was practised for a few years to ensure rapid establishment of the trees (see Street & Mond, 1992). The sites are managed similarly to high forest and are thinned every five years. Of six original sites, four have been selected for detailed study.

MATERIALS AND METHODS

PLOT DESIGN

On each of four chosen sites, 40 experimental plots were positioned covering an area of 28m x 160m. Each plot, of 28m x 4m, was further split into three sections:

i) the first 3m for the introduction of pot-grown plants,
ii) the next 1m for a restricted seed mixture,
iii) the final 24m for the main seed mixture.

Each plot to be sown with the main ground flora mixture was therefore 24m x 4m. The planting areas of 3m x 4m were joined horizontally across the top of four of the sown plots, resulting in individual planting blocks of 16m x 3m.

SOWING

The two main seed mixtures, containing species selected to represent the ground flora of local woodlands, are listed in Table 1.

Five treatments were selected for the sown plots:

i) High Density Seed Mixture A: Total density 2300 seeds m^{-2}
ii) Low Density Seed Mixture A: Total density 230 seeds m^{-2}
iii) High Density Seed Mixture B: Total density 1700 seeds m^{-2}
iv) Low Density Seed Mixture B: Total density 170 seeds m^{-2}
v) Control with no seed sown.

The sowing densities were dependent on seed availability and weight. Low and high sowing densities were in the ratio 1:10. At high density, the Mixture A rate is equivalent to 20.9kg ha^{-1} (2.1g m^{-2}) and Mixture B 16.7kg ha^{-1} (1.7g m^{-2}). The mixtures, densities and controls were randomised among the forty plots at each site. Sowing took place in March 1987 with the seeds being broadcast by hand throughout each 24m x 4m plot. The sites had been out of the weed control programme for approximately six months and there was little existing vegetation.

A restricted seed mixture, made up of those species for which seed was in short supply, *e.g. Allium ursinum* (Ransoms) and *Stellaria holostea* (Greater Stitchwort), was also sown.

PLANTING

In addition to the direct sowing at Milton Keynes, seed was sown in trays at the Institute of Terrestrial Ecology, Monks Wood to raise material for planting during the following winter. This included another seven species for which the seed was in very short supply The four experimental sites were divided into two sub-groups, damp Sites 2 and 6 and dry Sites 4 and 5, and the plant species were selected for site suitability. The twenty chosen species were mostly those that were sown, but *Ajuga reptans* (Bugle), *Circaea lutetiana* (Enchanter's Nightshade), *L. galeobdolon* and *P vulgaris* were additionally included.

The original sowing plan, consisting of forty plots per site, allowed ten 3m x 16m plots to be positioned across the main plots. This gave five plots planted at high density and five at low density at each site. The high density was seven times the low density, with 7, 14 or 21 plants of each species per plot at high density and 1, 2 or 3 at low density. The two treatments were randomised and planting was completed in mid February 1988 There was little existing vegetation due to previous herbicide applications, so no further site pre-treatments were necessary.

MONITORING

Sown species.

In the summers of 1987 and 1988, the sown plots at each site were examined and some limited recordings of initial germination were made.

Between May and June 1990, four plots were chosen at random from each of the five sowing treatments at each site. The central strip of each plot was then divided into 24 units of $1m^2$. From these, five $1m^2$ quadrats were chosen at random and were subsequently monitored. All species growing within the quadrats, including sown species, colonisers from outside the plots, plants from the seed bank and regenerating tree seedlings, were listed. Individuals of each species present (including very small seedlings) were counted to give species density per square metre. In addition, the area covered by each species within the quadrat was estimated. Within the chosen plots, all plant species present throughout the whole of the 4m x 24m plot were also listed.

Planted species.

In the summer of 1988 the presence of all species at each site was recorded and site characteristics noted.

Between May and July during 1990 and 1991, the presence of all original plants and new seedlings was recorded at each site, and characteristics such as cover, flower and seed production were noted

RESULTS

SOWN SPECIES

The monitoring in 1987 indicated that *A. petiolata*, *G. urbanum* and *S. dioica* had germinated in the first season. By 1988, seedlings of fourteen sown species were found, with *G. mollugo*, *H hirsutum* and *T japonica* being particularly abundant, together with the three species found in 1987.

In the 1990 field season, seventeen species were recorded, with *C. latifolia* the only species not found at all From the field data, mean densities and percentage cover values were

calculated for each of the sown species at each site. The mean total density for all species in each seed mixture over all sites was 79.3 plants m^{-2} for Mixture A and 106.4 plants m^{-2} for Mixture B, both at high density. Table 1 gives the mean densities, with standard errors, and the mean % cover values for individual species in both species mixtures at Site 4. This has been selected as a representative site.

At Site 4, all sown species in Mixture A were recorded in 1990, with *A. petiolata*, *G. urbanum*, *H non scripta* and *T. japonica* having the highest densities. At high sowing density, *H. non-scripta* had a density of 37.4 plants m^{-2}, but a low corresponding mean percentage cover. *G urbanum* had the highest mean percentage cover. In Mixture B, eight of the sown species were recorded. *S. dioica* had the highest mean density and the highest mean percentage cover. At high density, it was present at a density of 264.7 plants m^{-2}, compared with an original sowing density of 215 seeds m^{-2}. Of the sown species recorded, the majority had flowered by 1990, but *C. majus*, *H. non-scripta* and *T. scorodonia* did not flower until 1991.

Table 1. *Density m^{-2} and mean % cover in 1990 of sown species at Site 4.*

		LOW SOWING DENSITY			HIGH SOWING DENSITY		
SPECIES MIXTURE A		MEAN	S.E.M.	%COVER	MEAN	S.E.M.	%COVER
Alliaria petiolata	Hedge Mustard	6 2	2.9	1.8	16.0	4.9	10.5
Campanula trachelium	Nettle-leaved Bellflower	+		+	+		+
Digitalis purpurea	Foxglove	+		+	+		+
Galium mollugo	Hedge Bedstraw	0 6	0.3	2.6	1.5	0.4	8.8
Geum urbanum	Wood Avens	5.0	1.2	6.7	8.5	2.0	17.0
Hyacinthoides non scripta	Bluebell	8.5	1.8	1.0	37.4	6.2	2.3
Stachys officinalis	Betony	+		+	+		+
Teucrium scorodonia	Wood Sage	+		+	+		+
Torilis japonica	Upright Hedge Parsley	9 8	2.0	10.8	15.2	3.7	13.5
SPECIES MIXTURE B							
Campanula lanfolia	Narrow-leaved Bellflower	0		0	0		0
Conopodium majus	Pignut	0 4	0.2	+	0.6	0.3	0.5
Galium odoratum	Sweet Woodruff	+		+	+		+
Hypericum hirsutum	Hairy St. John's Wort	+		+	+		+
Primula elatior	Oxlip	+		+	+		+
Silene dioica	Red Campion	80 0	21.1	34.7	264.7	72.3	45.0
Sison amomum	Stone Parsley	+		+	+		+
Stachys sylvatica	Hedge Woundwort	0.2	0.2	0.6	+		+
Viola odorata	Sweet Violet	0		0	+		+

+ . Present at very low density

PLANTED SPECIES

Figure 1 shows the recorded number of plants at Sites 4 and 5 resulting from the introduction of species as young plants in 1988. The bar chart of all planted species indicates that whilst plant density declined immediately after planting, this has substantially increased since. The other bar charts show the establishment of four species individually. At high planting density, *S. dioica* has increased from 140 original plants to 3161 in 1991, with a similar establishment pattern at low planting density. *H. non-scripta* and *P. vulgaris* have increased well at high planting density by 1991, but much less at low planting density. At both planting densities, the number of *T. scorodonia* plants initially declined and then stabilised for two years before increasing in 1991.

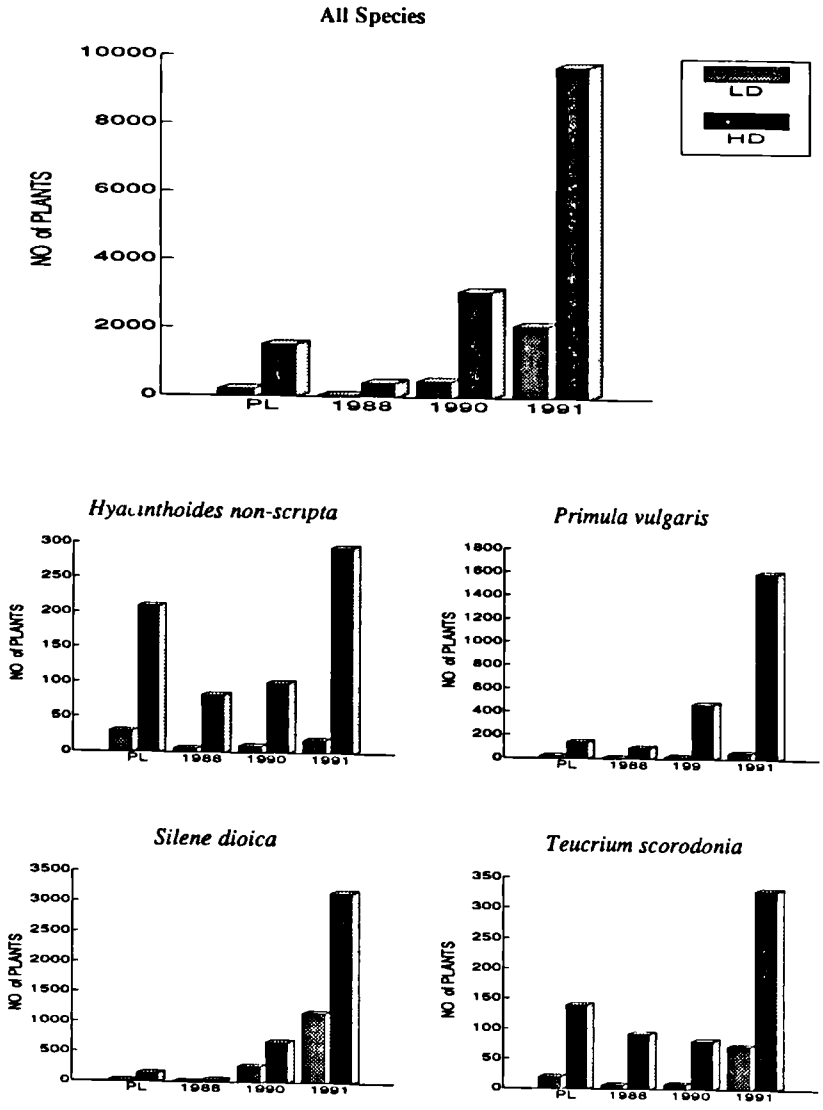


Fig 1 Recorded density of species introduced as plants at Sites 4 and 5, Milton Keynes (**LD**: Low density planting; **HD**: High density planting; **PL**: Number planted Feb 1988)

DISCUSSION

Experimental establishment of field layer species

Four years after sowing and planting, all but one of the species introduced as seeds and all of the species introduced as plants have been recorded. These figures clearly demonstrate the feasibility of introducing ground flora into new woodlands, by simple hand-sowing and planting methods.

Considering the established density and cover of the various sown species, however, differences are apparent in the success between species. *S. dioica* is the only species to be recorded at a density higher than its original sowing density. Factors which influence the seeds and developing seedlings from sowing time to the detailed monitoring in 1990 are unknown, but it is likely that some seeds fell "on stony ground", some were eaten, and others died after germination when the droughts of 1989 and 1990 were at their worst. The seed mixtures were sown at low and high densities in a ratio 1:10, yet none of the resulting species densities at any of the four sites are in this ratio. At Site 4, the recorded density ratios for *H. non-scripta* and *S. dioica* are 1:4 and 1:3 respectively, and, for these two species only, the number of plants at high and low densities are significantly different. The results are similar at other sites, with maximum ratios of 1:7 for *H. non-scripta* and 1:5 for *A. petiolata* at Site 6, but few are significantly different. It is clear from the results that the rate of establishment varies between the herbaceous species that were introduced. Of the sown species, some were quick to establish and soon flowered and set seed, whilst others have been much slower in their develop.nent from seed and are still very much in the establishment phase. Variation of success within individual species is also apparent, both at the same and different sites. The variation in performance is probably related to environmental factors, such as light, soil type and canopy species. The very urban nature of these sites may also explain some of the variability, since factors such as trampling, vandalism, dumping of refuse and chippings, and routine maintenance work to drains and pipelines all cause disturbance and thereby affect species' performance.

The species that were introduced as young plants into the new woodlands, have generally shown a large increase in plant densities over the four years, but success is variable. As with the sown species, similar categories of establishment are clear, with some of the species soon flowering and producing second and third generations from discrete individuals. Other planted species exhibit less flower production and seed set, but have spread well and have established vegetatively. These include *A. reptans*, *C. lutetiana* and *L. galeobdolon*. Individual plants of *A. reptans* have covered up to $1m^2$ during the four years since they were planted. Planting densities were in the ratio 1:7, and some species are still present in similar ratios, *e.g. H. hirsutum* and *P. elatior*. Others, *e.g. H. non-scripta* and *P vulgaris* have been recorded at much higher ratios of 1:15 and 1:30 respectively. This is a particularly interesting result for *P. vulgaris*, a species that is rather slow to mature from seed. Where it has been introduced as plants, the results at high planting density show that it has already been very successful in the production of large numbers of seedlings. It is considered that the introduction of this species as young plants clearly enhances its establishment ability.

Two distinct groups of species are recognisable: those that are characterised by quickly establishing and reaching maturity, and those that are still in the establishment phase and have yet to mature When grouped together, this variation in establishment success between the species can be explained in terms of different growth strategies. The first group are all light-demanding woodland edge, or marginal, species, whereas the latter are shade-tolerant, true

woodland species.

Field layer enhancement in practice

Foresters have long advocated the use of herbicides to ensure good tree establishment and policies such as the bare earth treatment at Milton Keynes are very effective in this context. Additionally, these repeated herbicide applications help to reduce the pool of potential weed competitors and therefore create ideal conditions for the introduction of ground flora species once the trees have established and the herbicide regime has ceased. This treatment also enables earlier introduction of species, when light levels are still relatively high and from which the ground flora species can benefit and establish well. Field observations made at Milton Keynes of the germination of species sown in spring 1991, have shown very reduced success where plantations have been out of herbicide treatment for a year or more. So, unless practitioners wishing to make introductions are prepared to wait many years until shade has increased sufficiently to reduce the growth of invasive weeds, an effective pre-treatment is extremely beneficial. Ground flora introductions are not only a logical step in creating a woodland ecosystem, but can also be an integral component of young woodland management, being complementary to the techniques used in tree establishment.

The choice of ground flora species for introduction into a particular site must be made carefully, and should be limited to those species commonly found in local woodlands, *i.e.* neither locally rare, nor from woodlands in other regions (see also Packham & Cohn, 1990). Species choice will undoubtedly be affected by availability, but any introductions made should always be documented and preferably monitored.

The results and observations from the experimental work reported here can be used in the development of an introduction plan, and knowledge of the varying growth strategies of the species can be utilised to aid decisions about sowing and planting. Those species which have been identified as quick to mature and establish, *i.e.* the light-demanding woodland edge species, can be introduced as seed and require only moderate sowing densities. The shade tolerant species will be slower to establish and reach maturity. Some of these, *e.g. G. odoratum*, *H. non-scripta* and *V. odorata* can be introduced as seed from which they will slowly, but successfully, develop. A sowing rate of about 10kg ha^{-1} (0.1g m^{-2}) is suggested, with a high proportion of the true woodland species and low proportion of woodland marginals. Species for which seed will never be available in quantity and which have poor germination rates are better introduced as planted units from which they vegetatively establish and spread (see also Buckley & Knight, 1989). Early results of current work in Berkshire to introduce ancient woodland ground flora species as plants into woodlands of different ages also indicate good survival and vegetative establishment. In some cases, (*e.g. P. vulgaris*), whilst a species can grow very slowly from seed, planting is worthwhile as it clearly enhances establishment. Plants should be introduced in single species groups, rather than individually, as this clearly helps establishment and more closely mimics the mosaics found in mature woodlands. Whilst sowing is considerably less expensive than planting in terms of both materials and labour, both techniques are probably necessary to introduce a full range of woodland ground flora. Regarding the specific timing of introductions, it is important that seed is sown in autumn or winter to ensure the vernalisation that so many woodland species require, and plants should be introduced in spring when the ground is warm, yet before dry conditions prevail.

The poor natural colonising ability of woodland ground flora species and the isolation of newly planted woodlands is likely to result in field layers that are low in species diversity. In

order to prevent this and enhance such field layers, the ground flora species may "have to be put there" (Buckley & Knight, 1989). The present work will lead to the production of simple plans for ground flora introduction into new woodlands, and, by doing so should aid habitat managers in devising re-creation schemes.

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