STUDIES ON GROWTH OF YOUNG OAK TREES AS AFFECTED BY THE ENVIRONMENT, IN PARTICULAR PHOTOPERIOD, TEMPERATURE AND ALSO GIBBERELLIC ACID APPLICATION.

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ABSTRACT

The effects of three environments (field, tube shelter, glasshouse), gibberellic acid application and continuous illumination on the growth of young oak trees were examined in a factorial experiment over two growing seasons. Both spot measurements and a computer based data-logging system were employed to monitor levels of environmental factors (light intensity, air temperature, CO_2 concentration, relative humidity) throughout to determine conditions within each environment, and relationships were derived to link with standard Meteorological data.

The tube environment was associated with reduced light intensity, increased temperature and very high humidities. All these factors combined to increase growth in length. Photosynthesis and respiration are affected by increased temperature and decreased light but there was no overall effect on dry matter production. High humidity must reduce transpiration in the tube conditions. CO_2 levels in the lower part of the tube were enhanced by CO_2 derived from the soil, but very low levels occurred higher up in the tube. The main effect of tube conditions appeared to be in a re-distribution of dry matter within the tree in favour of the shoot. The tube also physically restricts the tree and protects it from wind, these factors must affect growth but are difficult to quantify.

Glasshouse environment had higher day and night temperatures than in the field, humidity was similar, but light intensity was slightly reduced. With the easy application of extended daylength the glasshouse can be used to produce larger container-grown seedlings all year round. GA_3 application increased height growth in both the tube and glasshouse. In the latter environment GA_3 application in combination with 24 hour light did not increase height above the maximum attained in 24 hour light alone.

In field conditions the plants remained small with the highest proportion of dry matter in the form of roots.

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INTRODUCTION

During the 1970's broadleaved species accounted for only 1% of the annual Forestry Commission's planting, their major interest was in conifers, governed mainly by financial considerations since conifer plantations start to produce usuable harvest from thinning after 20-25 years (CAS Report 1980). In recent years, however, there has been an increase in interest in broadleaved trees, both for their timber and amenity value. Encouragement is given to the use of broadleaved species where sites are suitable and the existing landscape is essentially broadleaved in character.

One of the main problems with hardwood woodlands is the low proportion of high quality timber that is produced. Economics of production of timber depends upon many factors, including establishment and maintenance costs, rotation length and yields obtained, and also important is the successful marketing of the timber (Brazier 1985). Two aspects can be considered as particularly important, the choice of broadleaved species, and the growing of the trees to produce high quality timber (Brazier 1985).

Oak, a broadleaved species, produces an excellent timber which has many uses, for example prime clean timber is used for veneer and furniture (Blatchford 1978). However oak is a relatively slow growing species and it takes approximately 120 years to produce timber of marketable quality. It would therefore be an advantage to reduce this time by accelerating the growth of oak.

The Forestry Commission started an investigation into the use of plastic tree shelters (tubes) in 1979 when it was noted that tree guards enhanced the growth of trees, particularly oak (Tuley 1980, 1981, 1982a). Plastic mesh treeguard had first been used to protect trees planted at wider spacing. It was hoped that such tree shelters would overcome some of the problems associated with the establishment of broadleaved trees on woodland and amenity sites (Tuley 1985), i.e. by protecting trees from damage by rabbits, deer and small mammals, as well as enhancing early growth and aiding chemical weed control. Moreover in the field they identify the position of the tree. Also with plantings up to about 15ha, taking grants into account, it is thought to be both cheaper and more effective to use shelters instead of a fence to protect newly planted trees (Lang-Brown 1985). Tuley (1982b, 1983, 1985) only recorded the effect of tree shelters on height and diameter growth. Clearly other growth parameters such as dry weight, leaf area, number of growth flushes,

degree of branching must also be affected.

Tuley thought tree shelters acted as a "miniature greenhouse" around each individual tree (Tuley 1982b, 1984), and he suggested that the effect on growth was primarily through increasing temperature. But other environmental factors must also be altered within the tube shelters, i.e. one would expect increased humidity, decreased light intensity, reduced ventilation (gas exchange); also there would be physical restriction on growth by the tube itself.

The major part of this study was to characterise the environment within the tube shelter in terms of light intensity, temperature, CO_2 content of the air and relative humidity with a view to comparing this with conditions in the field and glasshouse environments.

Other methods are known to have been used to increase the growth of oak. For example height growth may be increased by the application of gibberellin together with increasing temperature and extending day-length to continuous illumination (Schwabe and Sultan 1982). Furthermore one would expect to find interactions of these factors; thus how would the growth of oak in tube shelters compare with that in the glasshouse and field environments with different photoperiodic regimes? Also how would the effects of gibberellic acid and continuous illumination be affected when applied in the field, tube and glasshouse environments?

In order to examine further the growth of oak within tree shelters and to answer some of the questions raised above an experiment, which combined factorially the field, tube and glasshouse environments, in natural day or continuous illumination, with and without gibberellic acid treatment was carried out over a two year period.

LITERATURE REVIEW

1.1 Pattern of Growth in Oak

In the oak shoot growth is not continuous but takes place in flushes, it results from the expansion of preformed primordia in terminal buds on the main axis and branches. Once the terminal shoots have expanded there appears to be a period of inactivity until new terminal buds are formed and subsequently expand provided they do not become dormant, which is the more usual (Kramer and Kozlowski 1979). Thus only one bud may expand on a shoot each year or two or more may form sequentially and expand in the same year. Most north temperate trees either make a simple short flush in spring e.g. Aesculus or have a prolonged period of shoot extension e.g. Betula. Quercus and sometimes Fagus can have recurrent flushes of terminal growth interspersed with rest periods. This habit is common in the subtropics and tropics e.g. Hevea, Thea, Mangifera where the genus Quercus may have evolved (Longman and Coutts 1974).

The total amount of growth made by any oak tree varies according to (i) the number of growth flushes undergone in a growing season, (ii) the length of "rest" periods between flushes, (iii) the amount of growth during any one flush and (iv) the relationship between root and shoot growth (Reich, Teskey, Johnson and Hinckley 1980). The period of shoot elongation may be short perhaps only 2-3 weeks followed by a "resting" period of 4-6 weeks (Longman and Coutts 1974). Multiple flushes in seedlings are common in spring when environmental conditions are not limiting. In the greenhouse under continuous light Q.robur seedlings can be induced to make as many as 14 flushes of shoot growth in a 12 month period, resulting in straight stemmed seedlings 2.15m tall with few side branches (Smith 1977).

Longman and Coutts (1974) state that the roots of oak do not exhibit any clear cut intermittent growth habit seasonally. The rate of root elongation fluctuates considerably and is not always related to the periodicity of shoot growth. Under continuous light root and shoot growth periods do not appear to be correlated (Smith 1977). However in seedling white oak grown under near optimum conditions in the glasshouse flushes of shoot growth alternated with periods of root growth (Reich et.al. 1980). The peak of root growth occurred only during periods of shoot and leaf 'rest' and immediately preceded or followed each of the flushes of shoot and leaf growth.

Borchert (1973) produced a simulation for tree growth under

constant conditions. The model implied that (i) growth rhythms observed under constant conditions are endogenous, (ii)there are only gradual and no basic differences between rhythmic and continuous growth, (iii) the period length of the rhythm depends on the genetic factors determining rates of shoot, leaf and root growth as well as on the set of environmental conditions under which a plant is growing and (iv) if there are fluctuations in environmental factors, as in virtually all natural habits, a secondary exogenous rhythm may be superimposed over the basic rhythm.

Borchert (1975) showed that shoot growth patterns in oak agree well with those predicted by this model. The growth of seedlings of the blackjack oak (Q.marilandica) after germination in the glasshouse coincided in both the duration and timing of the second flush, though the amount of growth varied greatly (Reich et.al. 1980). In mature trees and seedlings grown in the field synchronous flushing is regularly observed since the time of bud burst and leaf emergence is closely associated with heat sums and the onset of activity of apical buds or root tips. Longman and Coutts (1974) suggest that the start of a flush of shoot growth in oak seems to be under photoperiodic control but the cessation of growth under internal control.

1.2 Source-Sink Relationships

The final size of oak seedlings after the first year's growth is strongly related to initial leaf area (Farmer 1980), while the initial leaf area is itself positively correlated with acorn size. Farmer (1980) concluded that in attempts to improve growth attention must first be given to increasing leaf area investment by environmental manipulation and genetic selection. A study by Foster and Farmer (1970) showed that fertilisation,use of large planting stock and weed control by mowing will promote good juvenille growth of red oak (Q.rubra) on an old field site suitable for hardwoods. Soil factors are thought to be relatively insignificant in the early stages of growth of oak because of the large reserves of nutrient contained within the acorn (Brooks, Wigston and Bourne 1980).

In a simple analysis, growth could be considered in terms of the relationships between 'sources' where metabolites are synthesised and nutrients absorbed, and 'sinks' where they are utilised to create new tissues (Scott-Russell 1977).Thus root growth depends to a large extent on the shoot for a supply of photosynthetic products and also growth regulating substances, and the shoot depends on the root for its supply of water, mineral salts, vitamins and various growth regulators as well as the roots

providing anchorage for the plant.

Wareing and Patrick (1975) discuss the partitioning of assimilate i.e. total dry matter production and utilisation within the whole plant, between the whole shoot and whole root, and also within the individual parts of the shoot e.g. leaves, stems, fruit, in terms of source-sink relations. Thornley (1977) too discusses with appropriate mathematical models, the physiological concepts of priorities, sources and sinks, including also the involvement of hormones, growth factors and active and passive models of transport in relation to the distribution of growth within a plant. One model, developed by Reynolds and Thornley (1982) partitions growth between shoot and root by balancing carbohydrate synthesis by the shoot and nitrogen uptake by the root in terms of transport and utilisation in the shoot and root compartments of these two substrates.

It is obviously highly important that a proper balance is maintained between shoot and root. A tree with a poor root system is likely to be at a disadvantage in the exploitation of the soil for water and nutrients, apart from the mechanical problem of anchorage and at the same time the shoot may be deprived of essential cytokinins. The root system of a forest tree is not normally of direct economic value with present methods of exploitation, and dry matter present as roots represents an undesirable, though unavoidable loss, which should be kept to a minimum with regard to the requirements of the tree (Wareing 1970).

Borchert (1975) considered shoot growth to be determined by a functional relation between root and shoot. Thus the maximum shoot size (leaf area) attained in a season is dependent upon its relation to the root system. Borchert (1975) considered internal water deficits resulting from an unbalanced root/shoot ratio to be the most likely physiological basis for the cessation of shoot growth during flushing. Maggs (1964) suggested that neither leaf nor root are continuously limiting growth, but that both are usually operating below their maximum efficiency, thus buffering against accidents and short term fluctuations in the environment.

The shoot/root ratio tends to show considerable genetic variability and it is markedly affected by environmental conditions. When there are limitations in the supply of carbohydrates e.g. at low light intensity, or by reduced leaf area through grazing or cutting, or by reduced CO_2 concentration or through prolonged periods of dark, roots are much less efficient than shoots in attracting carbohydrates from

the general pool, even when other conditions are near optimum (Brouwer 1977). Maximum shoot growth occurs under long day conditions with root growth correspondingly reduced when compared to the growth of roots under short day conditions when shoot growth is inhibited (Smith 1977). The root/shoot ratio of oak decreases with increasing photoperiod (Immel, Rumsey and Carpenter 1978) but increases with increasing light intensity (Jarvis 1964).

When growth essentials provided by root activity e.g. absorption of water and minerals, kinetin production are limited root systems are more successful in acquiring carbohydrates from the common pool (Brouwer 1977). Both availability of water and the transpirational conditions in the shoot environment interact to determine the water potential gradient between root and shoot. Thus lowered water potentials in the soil which alter growth in favour of the roots at high transpirational demand such as sunny weather, may not do so under conditions of low transpiration e.g. cloudy weather (Brouwer 1977). Under conditions of poor aeration of the root environment whether shoot or root growth will be more depressed will depend upon the extent of retardation of root growth compared with root function (Brouwer 1962).

1.3 Effects of Temperature

The actual temperature of different plant tissues varies with changes in the external temperature. Most of the energy exchanged between a plant and its environment occurs through the leaves and, depending on conditions, a balance is established between heat gain or loss such that plant temperature may be above or below the ambient (Sutcliffe 1977). Different parts of a plant are usually at different temperatures as they are exposed to different environmental conditions. For example leaves may experience a larger range in temperature than roots which are buffered by the soil (Berry and Raison 1981).

Mechanisms which are involved in translocation and partitioning of materials within the plant may respond to temperature. Studies of kinetics and partitioning of growth as a function of temperature show that there are differences between species in the amount of new growth made at different temperatures and its distribution between leaves, stem, flowers, roots, and these in turn can account for some of the differences in growth rates (Berry and Raison 1981). Where growth of roots occurs as an alternative to the growth of new photosynthetic capacity this may have a feedback effect on the rate of exponential growth leading to accumulative differences in growth.

The relation between growth and temperature shows an optimum at a lower temperature for root growth than for shoot growth, thus shoot/root ratio increases with increasing temperature. When root temperature is varied whilst shoot temperature is held constant or near optimal, there is an "optimal" root temperature where shoot growth is maximal and root/shoot ratio is minimal (Berry and Raison 1981). For example in Quercus robur a high shoot/root ratio is obtained when both roots and shoots are subjected to a low temperature (15°C) or when the roots are at a high temperature (25°C) and the shoots at a low temperature. At higher shoot temperatures with roots at either a high or low temperature, a greater proportion of the dry matter is found in the shoot (Smith 1977).

Care must be taken when assessing the physiological basis of the effect of temperature on shoot/root ratio since temperature affects development and therefore shoot/root ratio (Brouwer 1962); it also influences the ratio of photosynthesis and respiration and thus the amounts of carbohydrate available. The overall pattern of the response to temperature is generally dominated by the response of photosynthesis to temperature (Berry and Raison 1981).

Chabot and Lewis (1976) showed that photosynthesis of northern red oak (Quercus rubra var. borealis) adapts to average temperature conditions rather than to extremes. Acclimation of net photosynthesis was relatively insensitive to the amplitude of temperature variation. However when day/night temperatures were asymmetrically distributed around the daily mean photosynthesis acclimates to those temperatures experienced for the major portion of the 24hour period, such that net gas exchange is most favourable at the predominant temperature.

Temperature can affect growth in a number of different ways: the effect of day versus night temperature; the requirement for a day/night temperature differential (thermoperiod) and the effect of temperature in terms of a total daily heat supply. Thermoperiod can operate over different time scales, not only a day/night differential but also seasonally as seen in the requirement for a cold period to break dormancy (Lavender 1980). Thermoperiodism in plants can affect their distribution (Went 1957). Some of the possible effects of temperature on trees are given in table 1.1.

Brix (1971) studied the response of douglas fir and western hemlock seedlings to the different aspects of temperature regulation of growth. Although the total daily heat sum received by plants was important for growth the specific temperature during part of the 24hour cycle also

TEMPERATURE	POSSIBLE EFFECTS	REFERENCE
Below freezing	Killing of late season shoots Damage to opening vegetative or floral buds	Kozlowski (1979)
Alternate freezing/ thawing	Stem lesions and cankers	Kozlowski (1979)
45°C - 60°C	Stem lesions, sun scald and bark scorch, particularly from large diurnal fluctuations in temperature. Indirect injury - loss of carbohydrate, formation of toxic products, breakdown of protoplasmic proteins, increased transpiration leading to desiccation.	Kozlowski (1979)
Chronic exposure (days/weeks) to high temperature	Decreased availability of gases, accelerated breakdown of metabolites, metabolic rate inbalance.	Steponkus (1981)
Acute exposure (minutes/hours) to high temperature	Coagulation of protoplasm, cytolysis, nuclear changes, altered mitosis, inhibition of protoplasmic streaming, increased protoplasmic viscosity, loss of membrane semi-permeability.	Steponkus (1981)

Table 1.1 Possible temperature effects on trees.

had some influence. Thus increasing the day temperature had a greater effect on dry matter production than increasing night temperature. Extreme high temperature had an adverse effect even when it occurred during the day only, whereas a similar heat sum attained from more moderate day/night temperatures was favourable for growth. A differential day/night temperature regime was not required for optimum growth of either species. At given levels of daily heat sum dry matter production was as good or better at a constant temperature than under a regime of alternating temperature.

Within a plant different growth parameters may have different temperature optima. For fraser fir seedlings (Abies fraseri) each growth parameter has not only an optimum differential between day and night temperature but also a specific range of optimum day/night temperatures (Hinesley 1981). Therefore to optimise the growth of containerised fraser fir seedlings a compromise must be reached.

Studies on the effect of temperature on plant growth are complicated by changes in other environmental factors which vary with temperature. For example in temperate latitudes seasonal changes in air temperature are linked with changes in daylength, solar elevation, precipitation patterns (Berry and Raison 1981). The effects of temperature may vary according to the stage of growth e.g. following seed germination soil temperature may influence development of leaf area index of the young seedling. Gradually however air temperature and other climatic factors e.g. light, become of greater importance during the vegetative and generative phases (Bierhuizen 1973).

1.4 Effects of Tree Shelters

One of the major problems of growing oak as a forest tree is the length of time taken for trees to grow to a size of marketable value. The rotation time for oak is about 120 years and it would be an advantage to reduce this time. It is possible to force the growth of oak in the glasshouse to produce taller trees; for example the height growth of young oak may be increased by the application of gibberellin together with increasing temperature and extending daylength to continuous illumination (Schwabe and Sultan 1982).

However when such 'forced' trees are planted in the forest they may require a period of several years to adjust during which time growth may be reduced, though evidence for such 'transplant shock' is unclear. In order to protect newly planted trees shelters could be used. These are plastic tubes 1.2m tall and between 8-10cm in diameter, which would

act as an individual 'miniature greenhouse' around each tree. For trees like oak, in which apical dominance is less pronounced, tall shelters may also be a way of obtaining long lengths of straight timber from trees planted at wide spacing (10m apart) instead of the traditional close spacing of less than 1.0m (Tuley 1984).

Early experiments at Alice Holt Forest showed that several designs of plastic shelter based on polypropylene mesh tree guards covered with polythene improved not only the survival, but also the growth of oak (Q.petraea) transplants (Tuley 1980). After two years height growth of oak in such shelters was four times that of control trees. The mean stem diameter was also increased (Tuley 1981). Comparisons between shelters of different diameter (8cm, 16cm) and shape (cylindrical, conical) with open or closed tops showed little difference in growth after two seasons, though better growth was obtained in the shelters with open tops and the smallest volume (Tuley 1982b).

When shelters were removed after 3years the height growth of previously sheltered trees was small in the following two years but there was a considerable increase in stem diameter and hence volume (Tuley 1985). Indeed once the trees had grown to about 0.3m above the height of the shelter height growth declined, stem diameter increased and a crown started to develop (Tuley 1983). Comparisons of dry weight of stem, branches,leaves and roots of sheltered trees with mesh-guarded trees showed the shelter to have increased the growth of all these components (Tuley 1985). No comparison is given for sheltered trees and those grown without any form of protection i.e. without shelter or mesh-guard.

Differences in bud break and retention of leaves of oak have been noted in tube shelters. In spring once the buds have developed to a stage where some green is visible they appear to open earlier in the shelter conditions than outside. Also in the autumn leaves within a shelter remain green longer but there was no observable damage by early autumn frosts (Tuley 1985). Any side branches produced inside shelters tend to be thin and most die to produce a straight, branch-free stem.

Other broadleaf and conifer species have been grown in tube shelters with the growth of alder and Japanese larch proving the most promising. Beech, sycamore, birch, common alder, field maple and hawthorne had all grown twice as much in height after two years in shelters than in tree guards (Tuley 1982a).

1.5 Light Intensity Effects

Experiments on the effect of reduced light conditions on trees have often involved the use of screens or mesh-covered boxes (Ovington and MacRae 1960, Jarvis 1964, Phares 1971). Grime and Jeffrey (1965) created a gradient of light intensity around a single shoot using vertical transparent tubes which had a layer of black paint on the inner surface. The intensity and vertical extent of shading depending on the diameter of the tube and the height of the painted layer.

Methods such as these, which are intended to reduce light intensity also alter other environmental factors: reduced ventilation, increased humidity, mechenical restriction and possible overheating (Grime and Jeffrey 1965). Nylon-covered cages were noted to reduce the amount of precipitation reaching ground level and to decrease annual and diurnal temperature fluntuations (Ovington and MacRae 1960).

Grime and Jeffrey (1965) noted that the growth of Quercus rubra was greater in an unshaded tube than where there was no tube though the differences were small and not thought to be signigicant. Similarly McClenaham and Dochinger (1981) in a study to assess mineral element accumulation by Pinus strobus, Fraxinus americana and Quercus robur in round, transparent open top chambers (3m in diameter) near an industrial site, noted a consistent trend of slightly better growth in chamber-grown seedlings than those without chambers. Specific factors within the chambers causing the effect were unclear though air temperature was slightly (1-2°C) higher in the chambers.

Plants exhibit two basic reactions to shade from other vegetation. Many competitive and ruderal herbs and pioneer tree species can be considered as 'shade avoiders'. In shade internode extension is favoured at the expense of leaf development, thus the young leaves are brought nearer to the light source. Alternatively plants may be 'shade tolerators'. Their response to shade involves a transition to a conservative utilization of resources, as reflected in a low growth rate, structural and biochemical changes enhancing the efficiency of photosynthesis and reducing respiratory losses (Smith 1982).

Oak trees share a number of physiological features with shade plants i.e. high photosynthesis at low light intensities, low respiration rate at all light intensities and a low compensation point (Longman and Coutts 1974). Maximum growth of oak seedlings occurs in 20-40% of full daylight (Shaw 1974), conditions which are found in open canopied woodland or in small clearings. Full daylight of high light intensity reduces the amount of chlorophyll in oak (Q.petraea), the

capacity of the photochemical process, the rate of photosynthesis at light saturation and net assimilation rate (all per unit leaf area) are also reduced (Jarvis 1964). Shading during growth reduced net assimilation rate, the rate of photosynthesis per unit chlorophyll and the stability of the photosynthetic mechanism on exposure to high light intensities, and increases the capacity of the photochemical process and rate of photosynthesis at light saturation.

Other responses to increasing shade include an increase in leaf area, specific leaf area i.e. the leaves become thinner, and in leaf area ratio and leaf weight ratio, decreases occur in relative growth rate, root weight and root/shoot ratio (Jarvis 1964). Dry weight is greater under conditions of full daylight (Ovington and MacRae 1960, Phares 1971). Seedling oak, and several other tree species, utilise a large amount of assimilate in the formation of massive root systems, at higher light intensities in fact a greater proportion of assimilate is utilised in roots than in shoots. Since stem weight is independent of light intensity the increase in stem height with shading must be considered as partial etiolation (Jarvis 1964).

Grime and Jeffrey (1965) noted that the greatest elongation response to shade occurred in species with larger seeds. However in several species e.g. Quercus rubra, the height attained in shade was considerably lower than that expected if quantity of seed reserve was the only factor limiting height growth. They considered that the number and properties of extension sites in the shoot were also related to the facility with which a seedling escaped low shade.

1.6 Spectral Composition of Light

The spectral quality of light can have a profound effect on the growth of plants. Axelsson, Klockare and Sunqvist (1979) studied the effect of light of different spectral quality on the growth of oak (Q.robur). Seeds were germinated and plants grown in the dark for 3weeks before being transferred to continuous long far-red (LFR), far-red (FR), red, blue or white light. Stem growth was enhanced by LFR, this increase was due to an increase in both the number of nodes and length of internodes. After 15days plants in white light terminated their first flush with one whorl of leaves clustered more or less together. In LFR light the leaves were scattered along the stem, the apical bud continued to grow forming the 'second' flush and lateral bud development was inhibited. No dormant bud was formed in blue light.

The effect of light quality may vary according to daylength and

temperature, though this depends upon species (Asakawa, Sasaki & Morikawa 1974). The growth response of pine (Pinus thunbergii) seedlings to light quality was nearly the same under different temperature and daylength conditions whereas that of birch (Betula ermani var. communis) varied.

1.7 Effects of Photoperiod

The duration of the light period, or photoperiod, may affect the vegetative growth of a plant to a large extent. Typically stems are longer under long days producing taller plants with less dense foliage (Salisbury 1981). Stem elongation depends on the number of internodes that are formed as well as their length, and both may be influenced by daylength. In general the rate and duration of elongation growth in woody plants is increased by long days while in short days the rate of growth is decreased and the onset of dormancy hastened (Vince-Prue 1975).

Apart from the duration of extension growth and internode extension other vegetative processes affected by photoperiod in woody species include leaf (needle) growth in conifers, time of leaf abscission, duration of cambial activity, time of bud break and seed germination (Wareing 1956), flowering may also be dependent upon photoperiod as in herbaceous species (Nitsch 1957a).

The effect of photoperiod is difficult to study in isolation since plant growth is also sensitive to other environmental factors e.g. temperature, humidity, soil moisture, mechanical stresses. The quantity of light is especially important and difficult to control, plants under different photoperiods should be given comparable amounts of photosynthetically active radiation (Salisbury 1981). Increasing light intensity during extended photoperiods had a significant effect on seedling shoot length and weight and delayed the incidence of terminal bud set in amabilis fir, mountain hemlock and white and Engelmann spruce (Arnott 1979).

Four responses to photoperiod can be recognised (Vince-Prue 1975). Plants of some species e.g. Robinia pseudacacia, Betula pubescens, Acer rubrum continue to grow in longdays more or less indefinitely provided temperature is favourable. In short days growth usually ceases within about 2-4weeks. In the second group the onset of dormancy can be delayed but not prevented entirely by long days e.g. Acer pseudoplatanus, Paulownia tomentosa. In some species e.g. Pinus sylvestris, Quercus robur extension growth proceeds in a series of flushes the duration of the dormant period between successive flushes is shortened

by long days, and in some cases this happens to such a degree that growth appears to be continuous. The fourth group includes plants which are insensitive to daylength, these include a number of common fruit plants such as apple and pear.

Although growth may be increased with increased photoperiod greater height may not always be obtained under continuous illumination. First year seedlings of Pinus sylvestris made more growth in 20hour days than in 24hour photoperiods. This effect in pines being largely one on juvenile growth, with adult plants responding differently (Vince-Prue 1975). It is likely that the onset of dormancy under natural conditions is controlled by photoperiod in species such as Larix, Populus, Betula which continue growth well into the autumn. Where dormancy is delayed by long days there may be a critical daylength beyond which growth can be maintained. For example in daylengths of 12hours or below plants of Weigela florida, Acer rubrum cease to grow while growth is continuous in photoperiods of 14hours or more (Vince-Prue 1975). In other species there appears to be no critical daylength above which growth can be maintained indefinitely, in such species the response to daylength is essentially a quantitative rather than qualitative one (Wareing 1956). Under natural conditions in some species extension growth ceases in midsummer, i.e. well before the days shorten, here endogenous conditions appear to over-ride photoperiodic effects (Vince-Prue 1975).

In temperate regions the duration of the period of active growth is limited to the frost free period when dormant trees are more resistant to frost damage, and this plays a vital role in determining whether a species will survive under certain conditions. This type of dormancy is distinct from temporary summer dormancy which occurs between flushes in growth and lasts for only a few days to a few weeks (Kramer and Kozlowski 1960). Where the time of onset of dormancy is controlled by shortening daylength the induction of frost resistance is also affected e.g. Pueraria hirsutus. In Russia Robinia pseudacacia, a species of southern origin, is regularly killed by early frosts in Northern Russia, but as little as 20days of short day treatment, applied at the correct time, increases hardiness (Nitsch 1957a).

1.8 Interaction of Temperature and Photoperiod

Photoperiod and temperature may interact to affect bud dormancy. In sweetgum (Liquidambar styraciflua) the number of short days required to cause irreversible bud set is not a precise number, under warmer conditions more short days are required (Hellmers and Hesketh 1974).

Leaf abscission may also be regulated by daylength though temperature is also an important factor. In the greenhouse seedlings of Rhus glabra and Liriodendren tuliperifera dropped their leaves at the normal time under natural autumn daylength but retained them throughout the winter under long days. However seedlings of Quercus alba retained their leaves in the greenhouse even under natural short day conditions (Wareing 1956).

1.9 Bud Dormancy Breaking

Many trees once they have become dormant will not resume growth until dormancy had been broken by exposure to a sufficiently long period of low temperature. In Quercus robur the quiescent period between successive flushes can be broken by long day treatment but once winter resting buds have been formed further growth cannot be induced by continuous illumination, defoliation or disbudding (Longman and Coutts 1974). Catalpa bignonioides plants will resume growth if returned to long days immediately after the terminal bud had abscissed, however after several more weeks in short days growth will only resume following 2-3weeks of temperatures below 10°C (Vince-Prue 1975). Fagus sylvatica shows no response to chilling, seedlings can be induced to resume growth at any time by exposure to continuous illuminatiin. Betula pubescens however responds to chilling, e.g. after 6weeks at 5°C they will break dormancy under short days or even in continuous darkness (Wareing 1956). Thus when dormancy is fully broken by low temperature the resumption of bud growth is usually independent of daylength.

1.10 Flowering

When flower buds are both initiated and open during the same growing season, trees and shrubs may behave like herbaceous plants with regard to their response to photoperiod. There can be long day plants such as Weigela florida, Abelia grandiflora which initiate flower primordia under long days, and short day plants e.g. Bougainvillea glabra, also day neutral types e.g. Malvaviscus conzattii (Nitsch 1957a). Often, however, flower primordia are laid down during one season and the flowers open the following season, but even in these species photoperiodic treatments may still have an influence upon flowering. Thus flower primordia are only formed under long days in Ulmus glabra, but daylength has little effect upon flower initiation in apple or Cornus florida.

1.11 Cambial Activity

In many species cambial activity is dependent on the supply of growth substances e.g.auxin from the actively growing shoot. In such species any direct effect of daylength on extension growth may have an indirect effect on cambial activity (Wareing 1956). However in some species e.g. Pinus sylvestris, Quercus robur cambial activity continues several months longer than extension growth and phtotperiod may have a direct effect on cambial activity independent of any effect on extension growth. In second year seedlings of Pinus sylvestris extension of natural day with low intensity supplementary illumination prolonged the duration of cambial activity, and shortened days hastened the cessation of cambial activity (Wareing 1956).

1.12 Humidity Effects

High humidity often increases plant growth though almost saturated air can have delerterious effects, it may favour pests and diseases and reduce growth, also plants may be morphologically unusual suggesting that their hormonal balance had been disturbed (Ford and Thorne 1974). Experiments with sugar beet, kale and wheat showed that changes in humidity had a greater effect on top growth than root growth. Leaf expansion was affected more than growth in dry weight, thus net assimilation rate decreased with increasing humidity. Specific leaf area was increased at higher humidities, and in sugar beet and kale total leaf area was also increased due to increased area of individual leaves (Ford and Thorne 1974).

Changes in relative humidity also affected the growth of red oak seedlings. Low relative humidity decreased top and root growth and increased the time to bud break by 6-12days at various levels of soil moisture stress (Larson 1980). High moisture stress and low relative humidity resulted in significant die-back of stems of freshly planted trees. Low daytime humidity combined with a dry surface soil could significantly delay seedling establishment. High humidity (greater than 61%) at the time of flowering reduced fruit set in bear oak (Quercus ilicifolia) (Wolgast and Stout 1977).

The effects of humidity on growth appear to be mediated via transpiration rates (Ford and Thorne 1974). Very dry air caused excessive transpiration which must if the root system or water supply are inadequate, induce a water deficit in the plant that restricts growth. Important environmental factors affecting transpiration are light intensity, temperature, relative humidity, wind and water supply to the roots.

Plant factors affecting transpiration include leaf area, leaf exposure and structure, stomatal behaviour and the effectiveness of the roots as an absorbing surface (Kramer and Kozlowski 1979).

Potential water loss from a plant is determined by vapour pressure deficit i.e. the difference in vapour pressure between the water in the cells of the leaf, in the intracellular spaces and in the atmosphere (Downs and Hellmers 1975). Transpiration rate increases with increasing temperature because of a direct effect on the diffusion coefficient of water, and also because there is an increase in the vapour pressure gradient between the plant and surrounding air (Sutcliffe 1977). Trees therefore tend to become dehydrated during the day as absorption lags behind transpiration. Such recurrent temporary midday water deficits in leaves, because of excess transpiration, are not serious when the soil is well watered as the leaves usually rehydrate and regain turgor during the night when stomata are closed (Kozlowski 1976). Thus water deficits are often recurrent and inevitable but nevertheless they are probably more important than any other factor in growth loss, injury and killing of trees.

Transpiration is partly controlled by plant structure and stomatal behaviour, however transpiration rate is not consistently related to stomatal frequency, pore size or relative pore area. For example Quercus macrocarpa has a high transpiration rate but low stomatal frequency, large stomatal pores and low relative pore area (Davies and Kozlowski 1974). In different Populus clones transpiration rates were more closely related to stomatal size, frequency and control than to internal leaf anatomy (Kozlowski 1976).

Water loss from the shoot is largely confined to stomata, however appreciable amounts evaporate directly from epidermal cells passing through the cuticle. Such loss can be half the total water loss in young leaves with incompletely developed cuticle or in leaves developed in shade (Simon, Dormer and Hartshorne 1968).

1.13 Effects of Wind

Strong winds affect the biomass of plants as reflected in reduced dry weight, leaf area and height growth. Wind reduces relative growth rate and leaf area ratio of herbaceous plants (Grace 1977). Evidence suggests that the effect of wind on whole plants has often been the result of an impaired water status of leaves. There may however be other possible influences. Wind has an effect on surface temperatures which influence phtotsynthetic rate, wind also affects vapour pressure

deficit and this in turn may have an effect on stomatal aperture. Another possibility is that plants respond directly to the effects of shaking.

Dixon and Grace (1984) showed the transpiration rate of Pinus sylvestris, Quercus robur, Fagus sylvatica and Sorbus aucuparia to decline with increasing wind speed as predicted by the Penman-Monteith equation. It was thought that wind would increase transpiration by removing layers of humid air which accumulate adjacent to plant surfaces. However wind also affects heat transfer, by increasing the latent heat loss by evaporating water, which under high radiation causes a reduction in leaf temperature and hence in water vapour pressure at the site of evaporation. Transpiration rate depends upon the difference between water vapour pressure in the substomatal cavities and the ambient water vapour pressure, and is inversely proportional to resistances in the diffusion pathway. Thus the effect of wind on transpiration is complex since it affects vapour pressure deficit, and is affected by leaf surface and aerodynamic resistances.

The effect of wind on transpiration also varies with species. Transpiration is increased with increasing wind speed in Fraxinus but decreased in Acer. This reflects differences in stomatal size, structure and control of stomatal opening (Davies, Kozlowski and Pereira 1974).

1.14 Effects of Stem Movement

If trees are supported over a period of several years so that they cannot sway they grow taller and thinner than trees which are subjected to wind. Natural swaying causes eccentric trunk development in the line of the prevailing wind (Grace 1977). Extension rates of leader and lateral shoots of Pinus contorta were reduced by about 20% by high wind speed. Water potentials were slightly higher in plants subject to high wind, thus wind appears to affect growth of P.contorta without causing water stress (Rees and Grace 1980a). Continuous shaking also caused a 20% reduction in extension growth of leading and lateral shoots of P.contorta. Radial growth was unaffected. The stems of shaken trees however contained fewer cells than controls, though cell size was little affected (Rees and Grace 1980b).

The response to sway may not be a direct response to movement but simply to displacement from the vertical position (Grace 1977). When trunks of certain tree species are displaced from the vertical position reaction wood is formed. The mechanism of sway-stimulated cambial division is unclear, it has been shown experimentally that supra-optimal

auxin concentration will induce reaction wood formation in conifer species. A similar phenomenon is the formation of buttress roots which appear in response to uneven loading caused by an unbalanced crown or to more or less unidirectional force of prevailing wind. Buttress roots form on the windward side and therefore benefit the tree as tension members.

1.15 Photosynthesis

For the production of wood maximum stem growth rather than total growth is required. The bulk of tree growth is an accumulation of carbon compounds which are ultimately derived from fixation of CO_2 through photosynthesis. In Populus tremuloides carbon accumulation over a 56day period was within 7-14% of that estimated by continuously recording CO_2 exchange (Ledig 1976). However, frequently the rate of CO_2 uptake bears no relation to, or is negatively correlated with seedling growth as measured by dry or fresh weight of top growth. Positive relationships between rate of CO_2 uptake and growth are most commonly observed in controlled environments. Maximal net CO_2 exchange rate, under saturating photosynthetic photon flux density, was positively correlated with first year's shoot length of poplar clones (Ceulemans and Impens 1983).

Field studies of photosynthesis are particularly susceptible to changes in ambient CO_2. Photosynthesis under field conditions is commonly limited by CO_2 availability. In dense canopies and within the tree crown CO_2 deficiencies can occur under conditions which are otherwise conducive to active photosynthesis. However in most weather conditions there is vigorous mixing of air in the canopy and the atmosphere above it (Helms 1976). Such vigorous mixing is unlikely to occur within tube shelters.

Enhancing atmospheric CO_2 levels can lead to an increase in growth of trees as well as herbaceous plants. Elevated CO_2 concentration significantly increased height, leaf area, basal stem diameter and total dry weight of sweetgum (Liquidambar styraciflua) seedlings grown under high irradiance and to a lesser extent under low irradiance (Tolley and Strain 1984). Increases in dry matter accumulation were associated with early enhancement of net assimilation rate, but increases in leaf surface area contributed towards the maintenance of larger size as the seedlings aged.

Increasing CO_2 increased height growth, stem diameter and shoot dry weight of sitka spruce and lodgepole pine seedlings in the green-

house. Height and shoot dry weight of lodgepole pine could also be increased with increased frequency of liquid feeding, however the beneficial effect of increased nutrient level only occurred at higher CO_2 concentration (Canham and McCavish 1981). The growth of oak (Quercus pedunculata, Q.rubra) with increased CO_2 concentration was also affected by type of nitrogen fertiliser used. Nitrate-grown oak made better use of CO_2 enrichment than ammonium-nitrate grown plants (Milhet and Costes 1984).

CO_2 enrichment, resulting in increased growth rates, may provide a suitable method to reduce the time required to produce a containerised seedling in the glasshouse suitable for planting out. The length of time needed to produce a seedling the same average height as one produced under normal conditions in 16weeks was reduced by 1-2weeks for sitka spruce, 1½-2weeks for lodgepole pine and by about 2weeks for corsican pine by a four-fold increase in CO_2 (Canham and McCavish 1981). CO_2 enrichmant of greenhouse atmosphere enhanced the propagation of ornamental conifers by cuttings (Milhet and Costes 1984).

1.16 Stomatal Conductance

CO_2 has an effect on stomatal conductance, which decreased with increasing CO_2 in Pinus taeda and Liquidambar styraciflua. The rate of decrease declining as concentration of CO_2 increased (Rogers, Thomas and Bingham 1983). Water use efficiency, defined as milligrams of CO_2 fixed per gram water transpired, increased dramatically with increasing CO_2. So although the plants grown at high CO_2 levels were larger, they used available soil water at a lower rate because of stomatal closure. Stomatal conductance to diffusion of water vapour and CO_2 is a compromise between promotion of carbon assimilation and minimisation of water loss (Farquhar, Schulze and Küppers 1980). This compromise is effective if stomata tend to open in response to conditions that favour rapid assimilation of carbon and close in response to conditions that favour rapid transpiration. Thus the ratio of sensitivities of transpiration rate and assimilation rate to changes in stomatal conductance remains relatively constant over a range of humidities. Results consistent with this were found in Nicotiana glauca and Corylus avellana (Farquhar et.al. 1980) and in tropical species Podocarpus oleifolius and P.rospigliosii (Meinzer, Goldstein and Jaimes 1984).

Stomata of most plants appear to be insensitive to a reduction in CO_2 concentration below about 0.01%. In the leaves of most species the CO_2 concentration in the intercellular atmosphere does not fall

below about 0.01% when the surrounding air contains the normal 0.03% (Meidner and Mansfield 1968). Other environmental factors interact with CO_2 concentration to affect stomatal opening. Higher temperature and removal of CO_2 can together lead to wide opening of stomata. Also, the higher the light intensity the higher the concentration of CO_2 required to produce a given degree of stomatal closure.

Significant changes in leaf conductance which occurred within seconds of changing humidity in apple were attributed to alteration in stomatal aperture (Fanjul and Jones 1983). An increase in humidity causes stomatal opening and a decrease in humidity stomatal closure. A humidity change at high light intensity having less effect on stomatal resistance than a similar change in humidity at low light intensity (Davies and Kozlowski 1974). In Populus low light intensity and high vapour pressure deficit interact to give greater stomatal closure than is obtained under low light or high pressure deficit alone (Pallardy and Kozlowski 1979).

In woody species stomatal resistance generally increases as light intensity is decreased and temperature increased. Temperature dependent stomatal closure is greater at low than at higher light intensities (Pereira and Kozlowski 1977). For sitka spruce temperature in winter ($\leq$5°C) is the dominant environmental factor affecting stomatal conductance, but has little direct effect on diurnal trends of stomatal opening during the remainder of the year (temperatures between 5-20°C).

1.17 Growth Regulators

All five known plant growth regulators i.e. auxins; cytokinins; gibberellins; ethylene;and abscisic acid have large effects on developmental processes and growth; some examples are given in table 1.2. Their activity varies throughout the year when they are believed to bring about seasonal changes in growth activity.

The cytokinin activity in the sap of Quercus robur has been shown to vary throughout the year (Smith and Schwabe 1980). Activity was low in January, increasing in February-March to reach a peak just before bud break. Activity then decreased in April and May during leaf expansion, but increased again in June prior to the second growth flush. Cytokinin then steadily decreased until a minimum was reached in November and December. In willow growth in spring is proceded by a decrease in abscisic acid and increase in cytokinin activity (Alvim, Hewett and Saunders 1976). The onset of dormancy in willow is associated with low levels of cytokinins and high content of abscisic acid.

Table 1.2

Effect of growth substances on developmental processes (Hill 1973).

GROWTH/DEVELOPMENTAL PROCESS	SUBSTANCE	EFFECT OF GROWTH SUBSTANCE
STEM GROWTH	GIBBERELLINS	INCREASE
	INHIBITORS	DECREASE
LEAF EXPANSION	GIBBERELLINS	INCREASE
APICAL DOMINANCE	GIBBERELLINS	ENHANCED
	CYTOKININS	REDUCED
	INHIBITORS	REDUCED
SENESCENCE	CYTOKININS	RETARDED
	ETHYLENE	ACCELERATED
ABSCISSION	SOME AUXINS	RETARDED
	ETHYLENE	ACCELERATED
	ABSCISIC ACID	ACCELERATED
DORMANCY	SOME INHIBITORS	ENHANCED
	GIBBERELLINS	BROKEN
FLOWERING	GIBBERELLINS	ACCELERATED
ROOTING OF CUTTINGS	SOME AUXINS	IMPROVED

Juntilla (1982) recorded GA-like activity in the shoots of Salix pentandra. This activity decreased before cessation of growth and shoot tip abscision, indeed low GA-like activity in the shoots may be a pre-requisite for apical growth cessation and for the development of lateral flower buds. Application of gibberellic acid to the apex of the shoot in spring greatly enhances shoot elongation and prevents both tip abscission and initiation of flower buds. The mechanism triggering these seasonal changes in GA-like substances under natural conditions is not known since hormonal changes occurred at a time (June-July) when changes in the main environmental factors, such as radiation, temperature, are very small.

Daylength is one environmental factor which may have an effect on hormone acticity, e.g. cambial activity in Betula pubescens ceases within 2-3weeks of the beginning of short photoperiods; this is preceeded

by a marked reduction in the level of GA-like substances (Jones 1973).

In Pinus elliottii bud dormancy induced by short day treatment can be broken by application of exogenous gibberellic acid (Bourdeau 1958). The growth of elongating shoots exposed to short days is also stimulated by gibberellic acid. There is, however, no response to GA_3 under long days, suggesting that natural gibberellins become deficient only under short days (Bourdeau 1958). Dormancy in red oak can also be broken by gibberellic acid in the glasshouse without receiving any cold pretreatment. Gibberellic acid treatment however does not maintain growth in winter, even in the glasshouse (Schoeneweiss 1963). Of course, GA_3 is not effective in breaking dormancy in all species e.g. in conifers Pinus coulteri, Pseudotsuga macrocarpa (Lockhart and Bonner 1957).

Cold hardiness is often associated with dormancy which is induced by short days in Acer negundo. However, gibberellic acid given after the induction period under short days lowers hardiness again but does not completely eliminate the effect of short days (Irving and Lanphear 1968). Leaves exposed to short days had relatively low levels of gibberellin-like compounds and higher levels of inhibitor than those exposed to long days. This supports the idea that long days inhibit hardiness as a result of high gibberellin activity, while short days promote hardiness by building up an inhibitor able to counteract gibberellin (Irving and Lanphear 1968).

The exogenous application of hormones to plants has yielded much information on how the different hormones affect plant growth and development. Initial root elongation, stem height growth and number of leaves per seedling of northern red oak are promoted by the application of gibberellic acid or by stratification of seed (Vogt 1970). Gibberellic acid may perform an initial role in promoting hydrolysis of polysaccharide food reserves; if it is applied to acorns prior to stratification their respiration is increased and their germination time decreased. Gibberellic acid, applied to fully chilled seeds, produces seedlings with greater stem growth and reduced root growth.

Application of hormones (IAA and GA) by spraying onto the shoots of common oak produces growth effects after the first year of growth (Michniewicz and Samek 1968). IAA promoted growth of roots and GA the shoots. However the greatest stimulation of growth occurs when both hormones are supplied at the same time. The balance between GA and IAA, and not the absolute quantity of either, that appears to be the primary factor involved in their action on leaf abscision, which is delayed by IAA and accelerated by GA (Lewis and Bakhshi 1968). Smith and Schwabe

(1980) applied hormones to Quercus robur at the time of transplanting. Again gibberellin was found to increase shoot growth at the expense of the root, and auxin promoted root growth. Cytokinin increased branching and leaf number, however the greatest increase in growth was obtained with a combination of all three growth regulators.

The timing, method and duration of exogenous gibberellin treatment are important for growth acceleration. Primary shoot height of Populus euramericana was promoted through foliar spray or soil drench, but direct micropipette application to the node immediately below the shoot meristem was the most effective (Rood, Daicos and Blake 1984). Injection of gibberellic acid into Pinus contorta in April increased internode length, whereas injection in June increased mean stem growth and node number (Longman 1982).

For the most part gibberellin requires either an intact plant,or the presence of an active, or potentially active , meristematic centre e.g. stem apex for full expression of its growth promoting effects (Paleg 1965). Gibberellin can affect cell division in the stem apex. The increase in cell number, supplying potentially expansible cells, accounts for a portion of the tremendous growth response frequently recorded with gibberellin treatment. But the daughter cells are also stimulated to elongate by such treatment (Paleg 1965).

The response of trees to gibberellin may depend upon their inherent growth characteristics. In Populus, Platanus, Liriodendron gibberellin promoted extension by increasing the internode rather than increasing the rate at which nodes were formed (Stuart and Cathey 1961). Other factors involved in the response of a plant tissue to a growth regulator include the age and type of tissue; the kind and concentration of growth substance; environmental factors such as light and temperature; and the level of other endogenous hormones in the tissue (Low 1975).

Stuart and Cathey (1961) state that gibberellin often induces its maximum response when growth conditions are adversely influenced by temperature, nutrition or other environmental factors. Possibly under these conditions synthesis of both native gibberellin and inhibitors is retarded permitting a greater response from exogenous gibberellin. For the most part applied gibberellin does not establish new growth patterns but accelerates those in progress.

The addition of sucrose (as a foliar spray) to Quercus robur substantially enhanced the effect of gibberellic acid suggesting that carbohydrate was a limiting factor in the response of shoots to GA_3 treatment (Smith and Schwabe 1984). The application of sucrose alone

had no effect thus under normal growing conditions carbohydrate was not limiting extension growth. Treatment of teak with urea and trace elements as well as gibberellic acid gave greater overall growth (Mebrotra and Dadwal 1978).

Another environmental factor affecting the response of plants to gibberellin is soil water stress. GA-stimulated stem growth of red and white oak was only observed at low soil water stress (Larson and Palashev 1973). Moderate and high stress conditions completely suppressed the stimulation of growth by gibberellin. GA-treated white oak appeared less tolerant of soil stress than untreated seedlings, it is therefore doubtful whether gibberellin treatment would help seedlings to compete more effectively (Larson and Palashev 1973).

MICROMETEOROLOGICAL METHODS

1.18 Radiation

Instruments to measure radiation can be classified according to the type of measurement required, for example into those to measure shortwave, photosynthetically active and net radiation (Burrage and Varley 1984). Shortwave radiation consists of wavelengths <3000nm, and can be divided into a direct component from the sun and a diffuse component which has been scattered by particles e.g. water, dirt, in the atmosphere. Radiation can be considered as energy travelling in the form of electromagnetic waves (van Wijk 1966) as such it has the dimensions of energy e.g. joule $m^{-2}s^{-1} = Wm^{-2}$. Photosynthetically active radiation (PAR) lies in the visible range of the spectrum with a waveband ranging from 400 to 700nm. However more closely related to plant physiological processes is the number of photons received rather than their energy (Ludlow 1982). A photon is a quantum of visible radiation and has the units $molm^{-2}s^{-1}$, where 1mol = Avogadro's number (6.023×10^{23}) of photons of a particular wavelength or waveband. Quantum flux meters are used to measure the wavebands of PAR as their sensitivity is proportional to the number of quanta per unit wavelength (Szeicz 1975). Net radiation is the energy available for evaporation of water and to heat soil and air and represents the difference between long and shortwave radiation gained by the surface and that lost by reflection and longwave emission (Painter 1976). Longwave or thermal radiation consists of wavelengths >3000nm.

Solarimeters are a commonly used instrument to measure total solar radiation, both direct and diffuse, received by a horizontal surface. In practice this is covered with a hemispherical glass dome (Unwin 1980). Most solarimeters employ as sensor a thermopile which consists of a series of very closely spaced differential thermocouples. One set of thermocouple junctions is connected to a black surface, the other to a white surface, either both are exposed to radiation or the white surface is connected to an unexposed heat sink. Radiation energy absorbed by the black surface is transformed to heat, less energy is absorbed by the white surface and the difference in temperature is proportional to the incidental radiation (Sheehy 1985). The thermopile is constructed so that the ambient temperature affects both sets of junctions equally. The glassdome protects the sensor from wind, rain and dirt, also it transmits only wavelengths of 300-3000nm, the blackened surface being uniformly sensitive to all wavelengths in this range (Szeicz 1975).

Internal reflection within the dome can lead to errors in measurement, though these are usually confined to periods when the sun is near the horizon. The Kipp solarimeter, using a Moll thermopile of constantan and manganum with a double glass dome to minimise internal reflection, is the standard instrument used in many countries.

Net radiometers consist of two thermopiles, one responding to incident radiation received by the instrument the other to radiation coming away from the surface being studied. Their outputs are subtracted electrically to give the 'net radiation'. The two thermopiles of a net radiometer, like that used at the Meteorological Station, Wye, are covered with hemispherical polythene domes kept inflated by nitrogen gas. Polythene is transparent to all wavelengths, except a few narrow bands between 3-14μm (Szeicz 1975). The polythene domes protect the sensors from wind to which they are sensitive, alternatively the sensors may be ventilated at a constant flow rate.

Photosynthetically active radiation can be measured using solarimeters with associated filters. Selenium cells have a spectral response similar to the human eye but do not respond linearly. They also have low sensitivity at the blue and red ends of the spectrum though there is a fairly sharp cut off at 700nm. The silicone cell has a response which approaches the ideal quantum response but has no cut off at 700nm (Ludlow 1982).

Ideally PAR should be measured using a quantum flux sensor which is equally sensitive to photons between 400-700nm. Photoelectric cells used in quantum flux meters measure energy rather than quanta and the energy per quantum decreases with increasing wavelength. To measure the quantum content of radiation, silicone cells are used which are placed under special filters to give a response which is proportional to wavelength and hence to the number of quanta per unit energy at a specific wavelength.

Instruments must be calibrated against a standard e.g. a Kipp solarimeter. Imperfections in moulded glassdomes may give misleading results under a focussed beam of light so it is preferable to calibrate the instrument out of doors. A number of spot readings over a wide range of irradiances may be adequate, but comparison over a few days using a recorder or data logger is more satisfactory. The calibration factor then being determined from hourly means. An important source of error in radiation measurement is concerned with the spectral sensitivity of sensors (Unwin 1980). If light of different or altered spectral distribution is being measured systematic errors will occur. For

example silicone cells absorb approximately 90% of the sun's radiation with a peak at about 0.9μm. Provided the spectral distribution of the light to be measured is similar to that emitted by the sun this instrument is satisfactory, errors can occur if the distribution is altered e.g. by passing through a leaf. Thus comparisons, including calibration, should always be made using an appropriate radiation source thus minimising errors due to uneven spectral response.

1.19 Temperature

The method used to determine temperature is determined by a number of factors including the sensitivity and response time required, the temperature range to be measured, the conditions of use i.e. field or laboratory and the method of recording to be used. Temperature detecting systems operate through a measurable change in the condition of the sensor, such as a change in volume of a liquid, differential expansion of metals or change in electrical resistance (Downs and Hellmers 1975).

The temperature of the sensor depends upon several factors: the convective heat exchange between sensor and the air, or other medium being measured; radiative heat exchange between the sensor and its surrounds; and heat conduction to the sensor along the thermometer support. To measure temperature accurately heat exchange other than convection must be minimised (Szeicz 1975). Thermometers must also be in thermal equilibrium with their surrounds and all parts of the thermometer at the same temperature. Ideally thermometers should be used in the same conditions as those prevailing during calibration (Bell and Rose 1985). Described below are the principles of some of the types of devices used to measure temperature.

The differential volume change of a liquid e.g. mercury, alcohol contained in a solid e.g. glass has provided the most common instrument for temperature measurement. They are relatively cheap, robust and accurate, though disadvantages include their large volume and slow response time (Bell and Rose 1985). Mercury-in-glass thermometers are used in standard meteorological stations for measuring maximum and minimum temperature and for humidity determination (Painter 1976). The thermometers are placed in a louvred screen to prevent direct radiation, which could be a source of substantial errors, and to allow for natural ventilation, but under very calm condition considerable errors can occur even so (Unwin 1980).

Thermographs use a bimetallic strip as sensor, changes in temper-

ature cause differential expansion of the two narrow sheets of different metals joined along their flat faces causing bending. This is magnified and recorded by a pointer attached to the bimetallic strip (Painter 1976). Thermographs are generally unsuitable for microclimate measurements due to their size, the radiative exchange between the large case and its surroundings, slow response time and in humid conditions they may stick.

The change in electrical resistance of pure metals with temperature can also be utilised to measure temperature e.g. for platinum there is a change in resistance of 0.4%/°C over the temperature range -20°C - +50°C (Szeicz 1975). The change in resistance is usually assumed to be linear; although this is incorrect, the errors arising from this assumption are very small over the temperature range -20°C - +50°C (Burrage and Varley 1984). The main source of error in metal resistance thermometers is corrosion of the element and for this reason platinum is preferred.

The resistance of the element is determined by passing a small, known current through the sensor and measuring the voltage across the resistance. Depending upon size, resistance thermometers have a response time of 0.5 - 5 seconds and are suitable for measuring air and liquid temperatures. Platinum resistance thermometers are very stable and accurate and because of this they are often used as standards against which other sensors are calibrated (Burrage and Varley 1984). As with other sensors which depend upon the measurement of electrical properties platinum resistance thermometers are suitable for use with computer data logging systems in the field and laboratory.

Two other methods for measuring temperature based on the electrical properties of the sensor are the use of thermistors and thermocouples. Thermistors are semiconductors consisting of semi-conducting metal oxide mixtures whose resistance decreases with temperature. They can be made in many forms, the most useful being glass or epoxy-coated beads ranging in diameter from 0.2-3mm, small beads having a response time of 1 second. The response to temperature is non-linear however microcomputers can easily be programmed to take account of this non-linearity, the accuracy and stability of thermistors being dependent upon the circuitry used to measure the resistance of the sensor (Bell and Rose 1985). Their large temperature coefficient and small current consumption make thermistors particularly suitable for use with portable, battery-powered meters.

The flow of electrons between two dissimilar metals in a thermo-

couple changes with temperature. When two thermocouple junctions are joined the voltage (V) is proportional to the difference in temperature (t_1-t_2), thus $V=k(t_1-t_2)$ where k is the temperature coefficient depending on the nature of the two metals. If the temperature of one junction is known the temperature of the other can be calculated $t_1=V/k+t_2$ (Ludlow 1982). A large range of metals can be used for the thermocouples but copper and constantan are widely used because they are cheap and they do not rust or corrode. They are available in a wide range of sizes and coverings and are easily soft soldered.

The voltage produced by thermocouples is quite small and slightly dependent upon the temperature at which the temperature difference is being measured. For example a difference of 1°C between junctions of copper and constantan will result in an output of 30μV at 0°C, 42μV at 40°C and 46μC at 100°C, though a constant of $40\mu V°C^{-1}$ is most commonly used in microclimatological work (Unwin 1980).

When correctly used thermocouples are highly accurate. Errors usually arise from electrolytic effects at the junction, from spurious thermal potentials caused by thermal gradients in the wires and in the microvoltmeter, from electrical interference and from mechanical stress in wires and switches (Bell and Rose 1985). The traditional technique for using thermocouples involves keeping the reference junction in a thermos flask of ice, assumed to be at 0°C. This is not the ideal arrangement since the greater the difference in temperature between the junctions the more important the characteristics of the thermocouple become (Unwin 1980). In addition the ice bath has to be frequently checked, also temperature differences can occur within the flask giving errors of 1-2°C (Burrage and Varley 1984). It is better to use a reference at ambient with its temperature independently monitored e.g. an aluminium block with its temperature recorded using a platinum resistance thermometer.

Thermocouples can be combined in series to increase output per unit temperature difference or in parallel to provide a better spatial average (Szeicz 1975). If a number of thermocouples are connected in parallel and when the resistances are equal, the output will be proportional to the mean temperature of all the junctions. If thermocouples are in series each one needs an individual but thermally common reference junction, wheras for a parallel arrangement a single common reference can be used.

A thermocouple junction is very small and hence has low thermal capacity and relatively rapid response time which can be less than

1 second in still air (Bell and Rose 1985). When measuring leaf temperatures with thermocouples it is essential to use fine wires, this is particularly important for small leaves. Thermocouples need to be insulated with a neutral agent since metals left in contact with leaf tissue for several days may cause localised damage. When leaf thermocouples are installed for continuous recording allowance must be made for movement of the leaves, they must also be placed on the under surface of the leaves to minimise error caused by direct radiation and conduction.

1.20 Humidity

Relative humidity is a measure of the amount of water in the air relative to the amount that could be present if the air was saturated at the same temperature. Provided no water is added to or removed from the atmosphere the relative humidity will decrease approximately 4% for each 1°C increase in temperature (Downs and Hellmers 1975).

Many different devices can be used to measure humidity of air, but few are suitable for use in the field (Szeicz 1975). The absolute standard for humidity measurement is the gravimetric hygrometer which involves the precise weighing of increase in mass and the precise determination of the volume of the associated gas of known density upon absorption of water vapour by a solid desiccant. However this instrument is not suitable as a working laboratory or field instrument (Day 1985).

Wet and dry bulb psychrometers are the most commonly used device for measuring humidity. Two thermometers, identical in size and shape are used, one measures the temperature of the air, the other is covered with a sleeve of wet muslin and measures a low temperature as a result of evaporative cooling (Szeicz 1975). The difference is known as the wet bulb depression and is related to the degree of saturation of the air.

Psychrometers are subject to a number of errors which tend to overestimate humidity: heat conduction down the stems of the thermometers must be minimised; there must be efficient radiation shielding; the muslin sleeve must be kept clean and also provided with an adequate reservoir of water. A true wet bulb depression cannot be obtained unless the wet bulb is adequately ventilated (Painter 1976). In non-aspirated psychrometers, such as those used on meteorological stations inside a Stevenson screen which rely on natural ventilation, it is assumed that the rate of air movement is $1ms^{-1}$ and at this rate the wet bulb depression reaches 83% of the value it would reach at a higher

rate of ventilation i.e. >3ms^{-1}. In still air the relative humidity is therefore overestimated.

The dew point method for determining humidity determines the temperature at which condensation occurs. It is usually measured by cooling a surface below the point of saturation, allowing water to condense onto it, then gradually raising the temperature until the film of condensation starts to evaporate. The presence of the film of condensation can be measured optically, electrically or simply observed. Methods of cooling the surface include electrical techniques or evaporation of a volatile fluid such as ether or a refrigerant gas from an aerosol (Unwin 1980). This method is slow but can be used for reasonably small scale measurement. Calibration stability makes them suitable for a calibration standard, but they do not operate over the whole range of environmental humidities to be measured (Day 1985). Principle sources of error are temperature gradients between the water surface and the thermometer, effects of droplet size and the uncertain condition of the condensed layer, and temperature measurement.

Other methods to determine the water content of the air include spectroscopic methods in which an infra-red gas analyser is used to give a very precise record of water vapour concentration in the field (Szeicz 1975), and hygroscopic sensors which measure humidity through changes in resistance or capacitance (Day 1985). For example the sulphonate polystyrene layer type sensor which changes its resistance in response to humidity. It has a reasonably slow response, 2-3 minutes, and usually suffers from a certain amount of hysteresis ($\pm$3%) (Unwin 1980).

Capacitance hygrometers measure change in capacitance caused by the absorption of water into a dielectric usually aluminium oxide. They have a quick response and can be reasonably accurate. Sensors used in this study consisted of a perforated plastic case containing a membrane of non-conducting foil coated on both sides with gold. The membrane and coating form the dielectric and electrodes respectively of a parallel plate conductor whose capacitance depends upon the ambient relative humidity. It is of low cost and has a high level of stability in the range 10-90%. The response is non-linear but this was corrected with electronic circuitry (Burrage and Varley 1984).

Mechanical hygrometers are based on the changes in length of human hair with humidity. Although cheap and simple the response to humidity is non-linear and shows cramping at the top end of the scale (Painter 1976). Hair hygrometers are also affected by temperature and response

time is slow. If adjusted to read correctly at 15°C it will read 1% low at 38°C and 10% high at -6°C (Unwin 1980). Calibration must be checked regularly as it can be permanently affected by humidities less than 15% or greater than 90% (Day 1985).

Equilibrium humidities above salt solutions are particularly useful for calibration of instruments not dependent upon temperature measurement. For best results the salt and water must be pure, the solution must be uniform temperature throughout the system as salt solubility varies greatly with temperature (Day 1985). Some solutions have equilibrium humidities that are significantly affected by temperature and should only be relied on to give the correct humidity at temperatures for which calibration is known (Unwin 1980). Also containers must be properly sealed, since, if opened, it may take some time before the equilibrium humidity is re-established.

MATERIALS AND METHODS

2.1 Plant Material

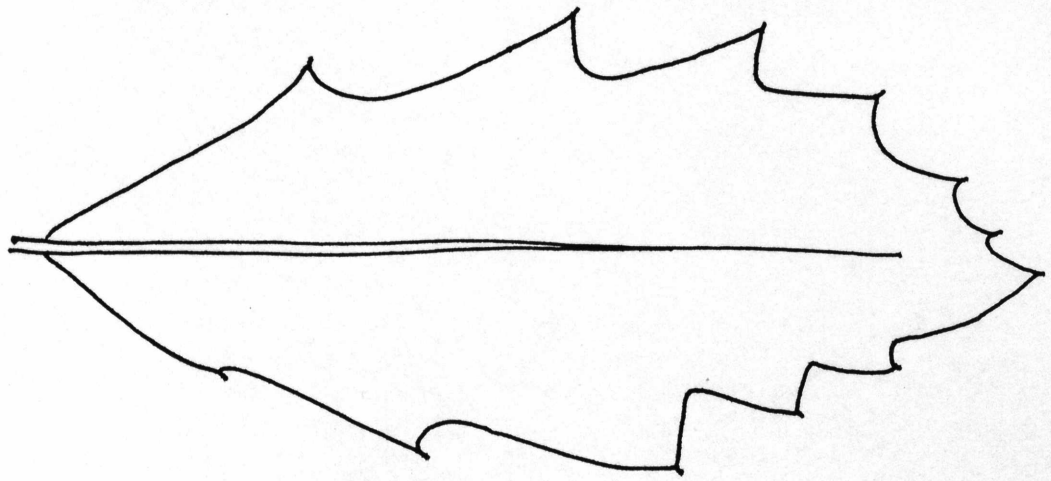
Seedlings of oak (Quercus robur) were raised in the glasshouse. For experiments beginning in 1983 acorns were collected from the ground beneath mature oak trees at Silks on the Wye College Farm Estate (NGR:TR064454) at the beginning of November 1982. The majority of acorns had already germinated and care was taken not to damage the radicles which had been produced. The acorns were washed and surface dried then weighed, and those with a fresh weight in the range 4.0-6.9g were used as experimental material i.e. eliminating both the very large and very small seed. The acorns were kept cold and moist before planting individually into 12.5cm square pots. A standard compost mixture was used throughout, 3 parts peat: 1 part grit + base fertiliser and water.

For experiments beginning in 1984 seedlings were raised from oak (Q.robur) seed provided by the Forestry Commission, from a Dutch source, as no acorns had been produced in the autumn of 1983, a poor seed year combined with the occurrence of a parasitic wasp (Jukes 1985). Some of the seedlings produced from this seed had leaf characteristics which seemed abnormal for Q.robur (fig. 2.1) suggesting that the material may have been of a hybrid nature. Seedlings with the most distinctive non-Q.robur-like characteristics were discarded, otherwise all the seedlings used for experiments in 1984 were taken from the same imported seed source.

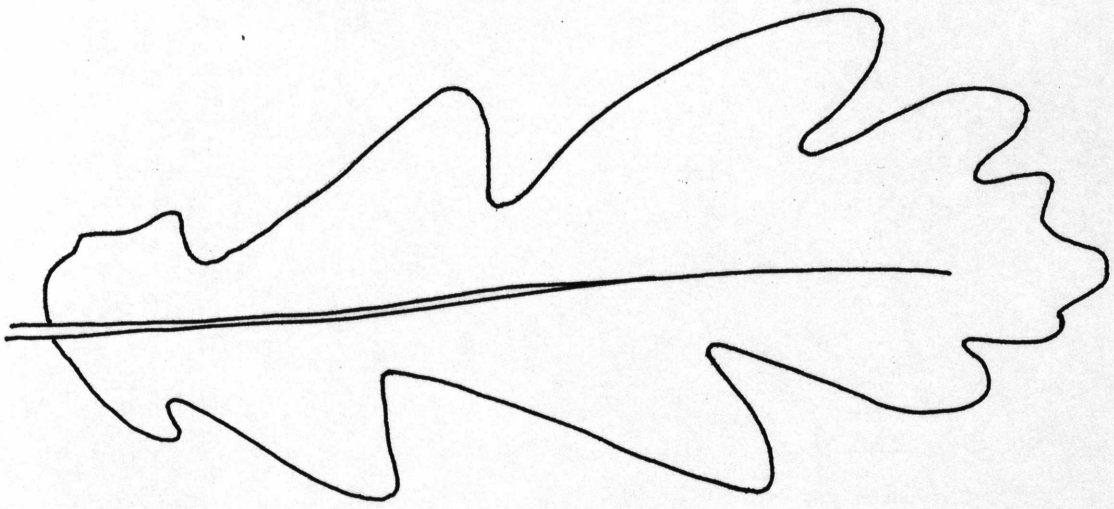
Beech seedlings (Fagus sylvatica) were also raised in the glasshouse from mast kindly supplied by the Forestry Commission, again originating from a Dutch source. Beech seed requires both soaking and chilling pretreatments before it will germinate. A sample of seed was taken to determine the moisture content of the seeds before (24%) and after soaking for 24 hours (35%), an adequate uptake. All the seeds were then soaked for 24 hours before being chilled at 3°C for a period of 10 weeks before planting.

Oak seedlings used in experiments in 1985 were raised from seed collected from beneath a number of mature oak (Q.robur) in the New Forest, Hampshire. Acorns were kept in a cold room between collection and planting into 12.5cm pots in the glasshouse.

All seedling oak and beech were raised in the glasshouse under continuous illumination i.e. natural daylight plus light throughout the night supplied by 60W bulbs at 1m spacing,giving a light intensity



(A)



(B)

Figure 2.1 Leaf shape of seedlings grown from seed provided by the Forestry Commission, (A) suspected hybrid (B) Quercus robur.

(400-700nm) of 0.8-1.0Wm^{-2}. Before planting out the seedlings were "hardened-off". In the first year, 1983, the seedlings were transferred to a polythene tunnel at the end of March. For the first two weeks a heater was used at night to prevent frost damage, then the seedlings were placed outside during the day but brought back into the tunnel at night or during bad weather conditions such as thunderstorms. Illumination at night was continued whilst the plants were in the tunnel. For the succeeding two years the seedlings were first taken outside the glasshouse during the day only, then finally left outside in a sheltered area between two glasshouses.

An experiment was also carried out using older oak and beech trees. 1+0 oak (Q.robur, Q.petraea) and beech (F.sylvatica) were supplied by the Forestry Commission in March 1983. These were kept outside in their pots until being used for experimental material in 1984.

2.2 Experimental Site

Two adjacent experimental plots were used for the field experiments. Each measured approximately 3 x 32m and ran in a north-south direction with a Cupressus leylandii hedge along the southern edge and glasshouses on the northern side. Both had been cultivated, they were manured (50 tonnes/acre) in 1981 and rotavated in early 1982 and 1983. The soil is high in potassium and phosphorus and relatively high in nitrogen (P.Buckley pers.comm.). The plots were well watered, particularly through the dry summer months, and weeds controlled by hoeing. In the glasshouse the seedlings were potted-on into bigger pots as required. They were watered as necessary and fed with a liquid N:P:K (summer 3:1:1, winter 2:1:4) fertiliser at regular intervals.

The glasshouse used was adjacent to the field plot. Seedlings were raised and experiments carried out within one cubicle, 14.7 x 12.8m, on the north side of the glasshouse. The benches used (1m wide, 80cm high and 50cm apart) were covered with capillary matting underlaid with polythene. When the trees became too tall to stand upon the benches they were stood on capillary matting on the floor of the glasshouse. Cubicle day temperature was set at 18°C and night temperature at 14°C, though these did vary according to external weather conditions. Roof vents were controlled automatically, they were closed at night and opened during the day when the temperature rose above 22°C.

2.3 Pest Control

A number of insecticides and fungicides, listed in table 2.1, were used against insect pests and fungal infections affecting the young trees in the glasshouse and field.

2.4 Experimental Design

Cox (1958) lists the advantages of the factorial design as follows: greater economy, greater precision for estimating overall factor effects and the possibility of investigating interaction between different factors. The majority of experiments carried out in this study followed a factorial design and were complete, i.e. all combinations of factor levels were used.

Factors can be divided into qualitative factors,for which there is no natural order to the different levels and for which each level is of intrinsic interest e.g. environments, and quantitative factors for which the different levels correspond to well defined values of some numerical quantity e.g. concentration of hormone, duration of day-length. If only two levels of a quantitative factor are used, for analysis qualitative and quantitative factors can be considered equivalent.

Over the basic factorial design experimental units were either arranged in a completely randomised or a randomised block design. When a given set of experimental units is simply allocated to treatments randomly subject only to the restriction that each treatment is applied to a fixed number of units then this is a completely randomised design (Mead and Curnow 1983). However with this design there is always the chance of all the 'better' units being allocated to one treatment, this would give misleading estimates of the true differences between the effects of treatments.

It is not possible to know the exact variation between units but if differences can be recognised between them it is possible to group them so as to distribute the variability fairly. Consequently variation between units within a group should be small relative to variation between the means of different groups. Thus the observed differences between two treatments should yield much more accurate estimates of the true difference. The treatments are then assigned so that each occurs once in each group or block giving a randomised block design. Alternatively blocks can be used where there may be variation due to site factors e.g. slope, change in soil type.

An extension of the randomised block design is represented by

CHEMICAL	ACTIVE INGREDIENT	APPLICATION	DOSE	PEST/INFECTION	SITE
AATERRA	35% ETRIDIAZOLE	ROOT DRENCH	0.5g/l	ROOT ROT	GLASSHOUSE
AGROTHION	51b FENITROTHION/gallon	FOLIAR SPRAY	0.6ml/l	GENERAL	GLASSHOUSE
ALIETTE	80% w/w FOSELYL AL	ROOT DRENCH	10g/10l/ m^2	PHYTOPHTHORA	GLASSHOUSE
BASUDIN	40% DIAZINON	ROOT DRENCH	1g/l	ROOTFLY LARVAE	GLASSHOUSE
BASUDIN	40% DIAZINON	FOLIAR SPRAY	1g/l	ROOTFLY ADULTS	GLASSHOUSE
DIAZITOL	10% DIAZINON	FOLIAR SPRAY	1ml/l	THRIPS	GLASSHOUSE
DIMILIN	25% DIFLUBENZURON	ROOT DRENCH	0.5g/l	ROOTFLY LARVAE	GLASSHOUSE
PIRIMOR	500g PIRIMICARB/Kg	FOLIAR SPRAY	0.5g/l	WOOLLEY APHID	GLASSHOUSE
PIRIMOR	500g PIRIMICARB/Kg	FOLIAR SPRAY	0.5g/l	GREENFLY	FIELD
PLICTRAN	250g CYHEXATIN/Kg	FOLIAR SPRAY	0.5g/l	REDSPIDER MITE	GLASSHOUSE
SULPHUR	POWERED SULPHUR	DUSTING		OAK MILDEW	FIELD
TEMIK	10% ALDICARB w/w	GRANULES		REDSPIDER MITE	GLASSHOUSE

Table 2.1 Insecticide and fungicide chemicals used throughout the 3 year study period.

the Latin square design which is used where it is required to control more than one source of variation. For example Latin square designs can be used, as in this study, when the rate in which experimental material can be dealt with is limited, and in which it is worth balancing out certain time variations (Cox 1958).

2.5 Treatments

2.5a Light

The effect of light duration (photoperiod) was examined under two light regimes, natural daylength and 24 hour light. Both in the field and glasshouse, continuous illumination consisted of a combination of natural daylength plus light throughout the night supplied by ordinary 60W incandescent bulbs. In the glasshouse the bulbs were at 1m spacing in a single line 1m above the level of the bench, giving a light intensity (400-700nm) of 0.8-1.0Wm^{-2} at bench level beneath each light bulb. In the field a line of lights, 60W bulbs at 1m spacing, was suspended 1m above the ground and the trees planted at a distance of 0.5m either side of a light bulb. The operation of the lights, as in the glasshouse, was controlled by a time switch which was automatically adjusted to the length of day and night according to the time of year. In practice the lights came on ½hour before sunset and switched off ½hour after sunrise. Regular checks were made on the lights and any broken bulbs replaced.

2.5b Hormone

The plant growth regulator gibberellic acid (GA_3) at 50ppm was applied to the seedling trees as a foliar spray at the beginning of the experiment. The trees were individually sprayed using a hand-held sprayer, both surfaces of the leaves being wetted until run-off occurred. To prepare the solution the required amount of gibberellic acid (mol. wt. 346.4g) was weighed and dissolved in ethanol, final concentration 10%. Distilled water was then added slowly to the ethanol whilst stirring to prevent the hormone from precipitating out of solution. Tween 20, final concentration 0.05%, was added as a wetting agent, and the solution made up to final volume with distilled water. The solution of GA_3 was kept in the dark in the cold room before use, and was used within 24 hours of preparation.

2.5c Tube Shelters

Tube treatment consisted of placing around the seedling tree an individual square plastic shelter. For all experiments the tubes used were made from translucent corrugated polypropylene, supplied by the Forestry Commission either as ready formed tubes or in flat sheets of the correct size which had to be folded and fastened into the tube shape. Tubes were approximately 120cm tall and 10 x 10cm in cross-section, they were supported in an open and upright position around the tree by an internal 2.5cm batten stake. The stake was driven into the ground to a depth of about 30cm and then the tree planted at the base of the stake. It was decided to plant the tree after positioning the stake to prevent possible damage to the tree roots whilst pushing the stake into the ground. The tube was then carefully placed over the stake and tree and secured to the stake using wire. The tube itself was also slightly pushed into the ground for further support. To secure the tube firstly two lengths of wire were pushed through one edge of the tube, one at the base the other about 2/3 along its length. The wires were opened up into loops inside the tubes which were slipped over the stake. The tube was then securely fastened by twisting the wire (fig. 2.2) taking care not to trap any part of the tree between the wire and the stake.

Preformed tubes could not be opened, so in order to measure the tree the tube was slipped up the stake, having loosened the wire fastenings, thus exposing the tree. After completion of the measurements the tube was carefully replaced around the tree. Tubes formed from flat sheets were held together by simple wire fasteners and could be opened easily to examine the tree inside, without having to move the tube on its stake. In order to study the environment within the tube three holes (diameter approximately 2.5cm) at 30cm, 60cm and 90cm were cut in the side of the tube through which sensors for temperature, humidity and light could be pushed. Whilst not in use the holes were sealed.

2.6 Plant Measurements

2.6a Height

Height was measured from the point of attachment of the acorn to the tip of the tallest shoot, measured to the nearest 5mm. The length of each flush of growth was also recorded, to the nearest 5mm.

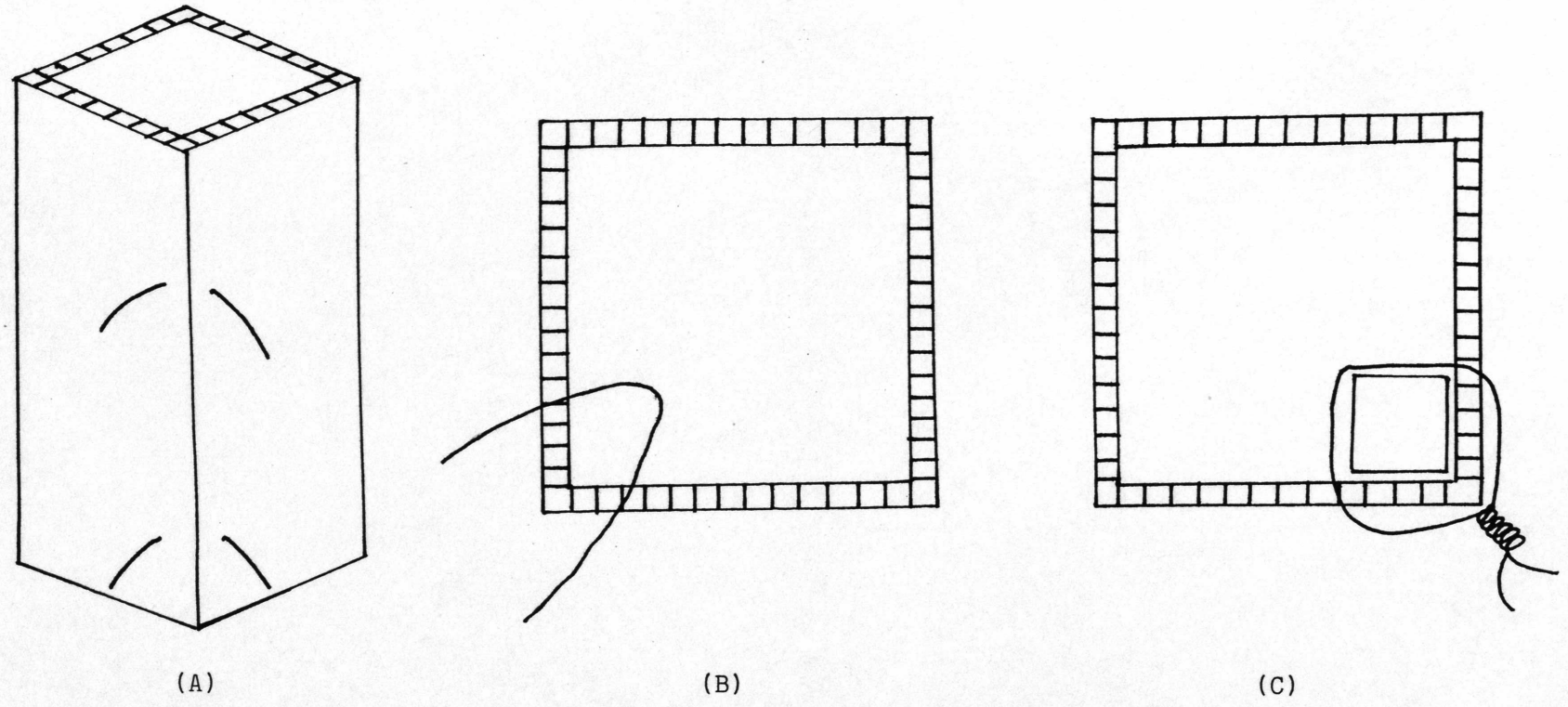


Figure 2.2 Fastening of the tube to the stake, (A) wire pushed through the edge of the tube, (B) wire formed into a loop inside the tube, (C) wire tightened around stake and tube and fastened by twisting.

2.6b Number of Flushes

The number of growth flushes of each tree was recorded before and after treatment as well as the total at the termination of the experiment.

2.6c Branching

The number of primary branches was counted and the length of each measured to the nearest 5mm. The number of secondary branches was also noted, if present.

2.6d Number of Nodes and Internode Length

The number of nodes present and mean internode lengths were determined. The total number of nodes in each flush was counted and since the length of each flush was known the mean internode length per flush could be calculated. A node represents one axillary bud, and internode lengths were taken from the base of one bud to the base of the next (fig. 2.3A).

2.6e Stem Diameter

Stem diameter was measured to the nearest mm using callipers graduated in 1mm divisions. Diameters were measured at 5cm intervals from the base of the stem (0cm).

2.6f Leaf Area

Several methods were used to assess leaf area.

(i) A relationship between leaf length (mm) and leaf area (mm^2) was derived from simultaneous measurements (n=224) on leaves from seedling trees raised in the glasshouse. Leaf length was taken from the base of the leaf blade to its apex (fig. 2.3B). To obtain the area of each leaf the outline of the leaf (held flat on the paper) was first traced onto $1mm^2$ squared graph paper, then the number of 1mm squares covered by each leaf shape counted. Logarithmic transformation was carried out on the data and the coefficients for the linear regression determined:
$\log_e$ Area = -1.5149 + 2.0859 $\log_e$ Length r=0.987 with 97.5% of variation accounted for by the regression. The exponential relationship between leaf length (mm) and leaf area (mm^2) in the form:
Area = 0.2198 $Length^{2.0859}$ (fig. 2.4) gave a good fit for the data. This relationship provided a non-destructive method for determining leaf area from leaf length measurements made on the attached leaves. The main disadvantage of this method is that it is very time-consuming, if a large number of leaves are involved.

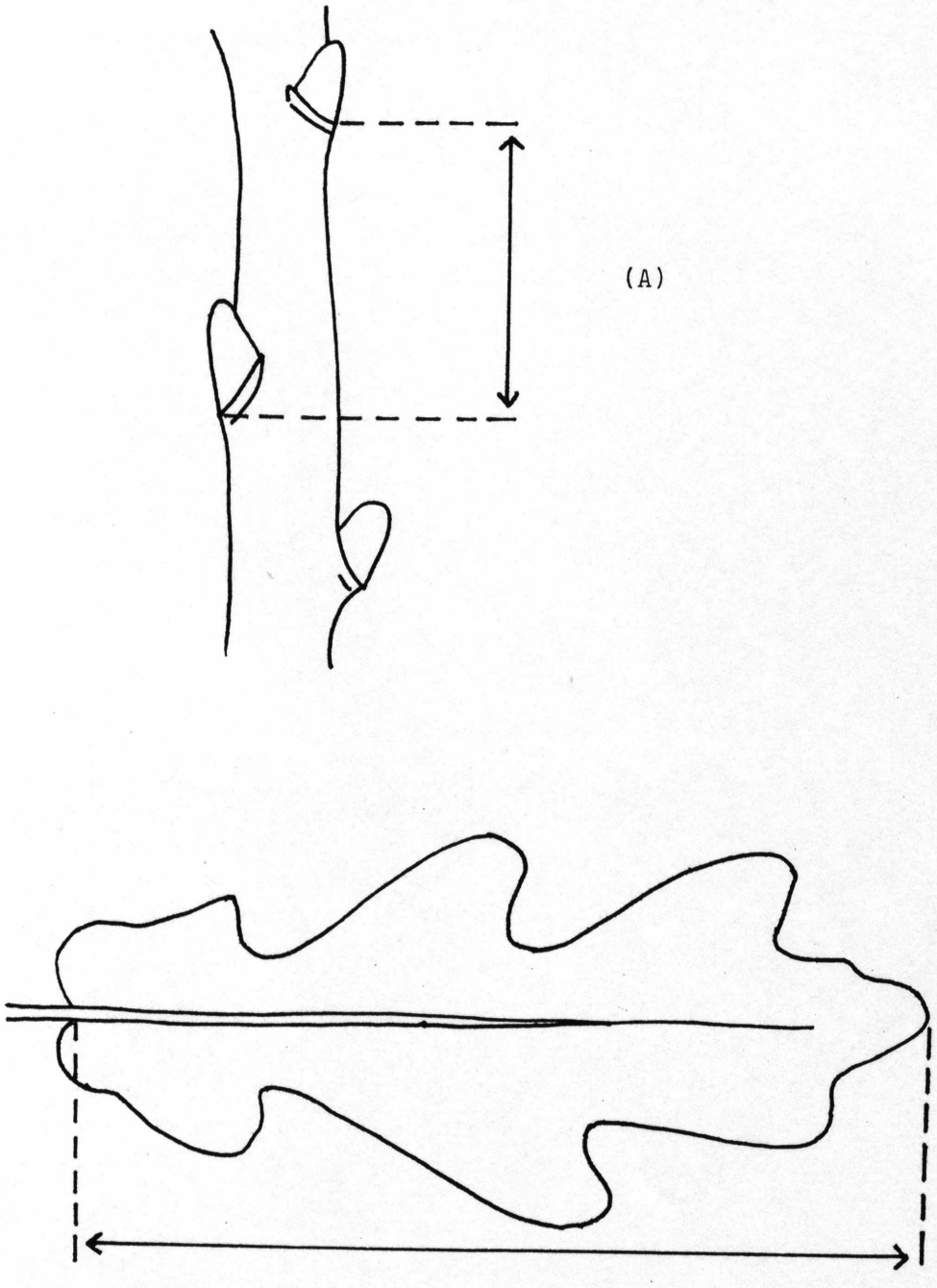


Figure 2.3 Measurements of internode length (A) and leaf length (B).

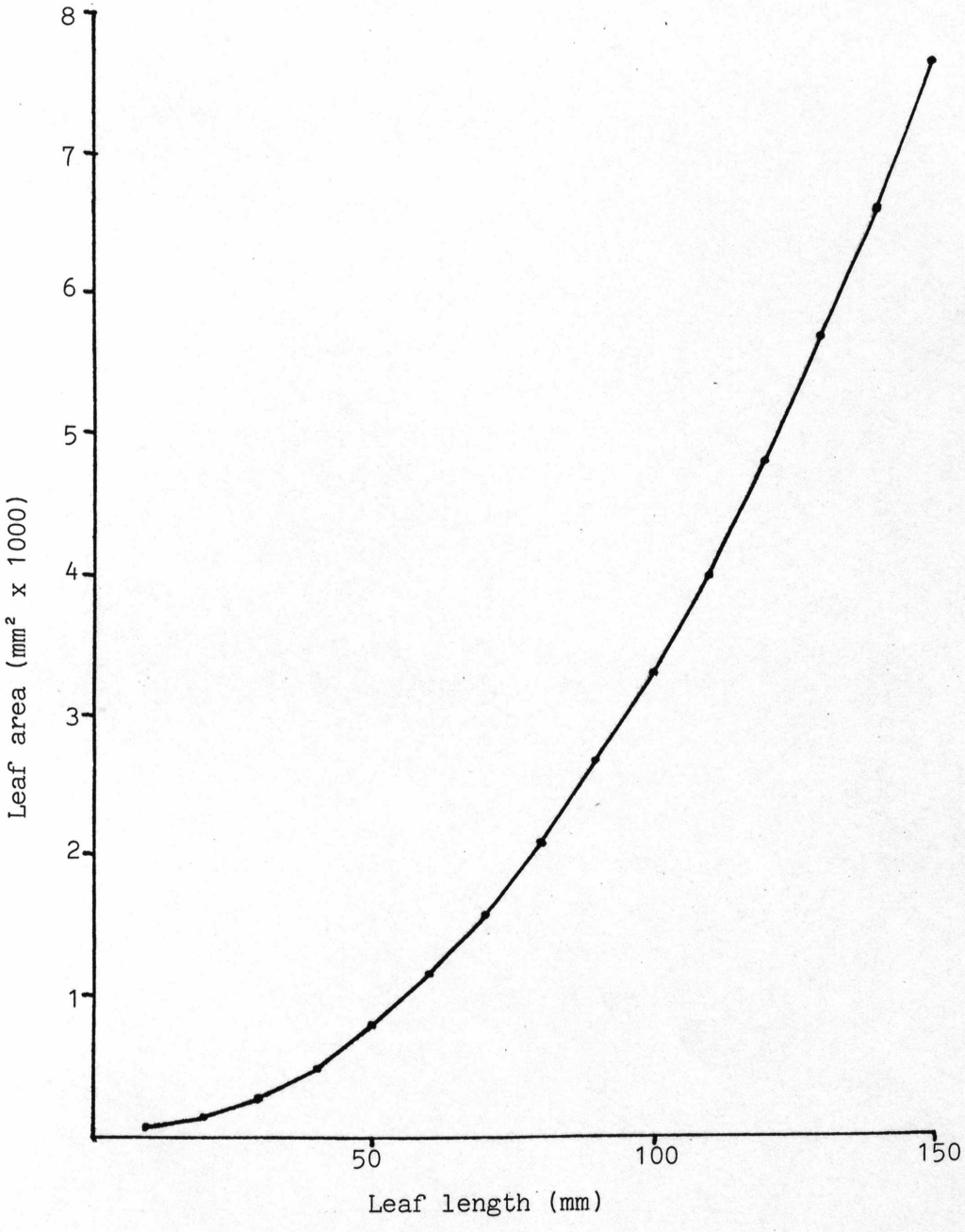


Figure 2.4 Exponential relationship Area = 0.2198 . Length $^{2.0859}$ between leaf length (mm) and leaf area (mm²).

(ii) A second non-destructive method to measure leaf area was tried. A set of leaf shapes of known and increasing area was prepared from tracings of oak leaves. Starting with a leaf area of 137mm^2 it was aimed to have an approximate increase of 20% in area between successive leaf areas (table 2.2), the leaf shapes most closely corresponding to the predicted areas, numbered 1-22 for reference, were mounted on stiff card. To assess leaf area the shapes were compared with each attached leaf on the tree until two successive shapes were found which most nearly matched the leaf to be measured, and their numbers were then noted. To convert the numbers of the leaf shapes into area the mid-point between the pair of successive leaf shapes was used, leaves with an area corresponding to shape 1 or less were given a value of 137mm^2.

This is a very subjective method for assessing leaf area and problems were encountered due to differences in leaf shape and the position in which the shape was held in relation to the leaf being assessed. Similar to measuring leaf lengths this too proved to be a very time-consuming method.

(iii) Once the outline of the leaves have been drawn onto 1mm^2 graph paper there are several ways of assessing the area of the leaf. (a) Counting the number of 1mm squares as already mentioned. (b) The paper areas can be cut out and weighed after calibrating area against weight provided the paper is of uniform thickness. This is still a rather laborious method, depending on leaf shape. (c) The area of the 'paper leaves' can also be measured using an automatic area measurement system, detailed below. Once the paper replicas of the leaves have been obtained, which is time-consuming, then determining the area by weight or with the automatic system is relatively quickly and easily achieved.

(iv) The automatic area measurement system uses a video camera held above a box containing a light source to detect the area of an object placed over the light box. The opaque area produced when a leaf sample is positioned over the light box is detected by the camera which must first be calibrated using samples of known area. When the total area of a large number of leaf samples is to be determined they can be individually fed onto a conveyor belt which is placed over the light box. The area of each leaf is measured and added to the total, which is itself displayed on a video screen. The conveyor system consists of twin belts of clear plastic between which the leaf is sandwiched and thus flattened as it is carried beneath the camera. If the conveyor belt is to be used the calibration must be carried out with a moving object. Several errors

can arise when using this system, on the conveyor belt the leaves must not follow each other too closely i.e. the previous object must be clear of the camera's view before putting the next object through the conveyor. The leaves must be completely within the area detected by the camera, any part of the object outside the field of view of the camera will not be measured. This system can be used to measure the area of leaves directly without first having to trace the leaves onto paper.

Due to the large numbers of leaves involved in this study during destructive sampling the conveyor belt was used to carry the leaves across the light box, the area of each leaf being added to the previous total and displayed on the video screen and the final total area recorded.

2.6g Dry Matter Production

In order to assess the dry weight of the trees in the field and tubes they were carefully dug out to recover as much of the root system as possible. Glasshouse trees were removed from their pots. For all the trees the roots were separated from the stem, the cut being made at the point where the acorn had been attached, and washed thoroughly. The remainder of the tree was divided into leaves, stem and branches, the leaves were usually picked off the tree before cutting the remainder into its component parts. The separate parts of each tree were then placed into individual paper bags for drying at 80°C. Larger stems and roots were cut lengthwise to aid more rapid drying. Sections of stem, approximately 2cm in length, were removed from the trees for anatomical study. These sections were weighed and preserved in Formol-acetic-alcohol (FAA): 5% formalin, 5% glacial acetic acid, 60% ethanol, 30% distilled water. Once the water content of the stem was known the dry weight of the stem was adjusted to take account of the material removed for anatomical study.

2.7 Examination of Stomata

Examination of stomata was carried out using impressions taken with nail varnish which were mounted onto a slide and examined under the microscope (Davies and Kozlowski 1974, Turner and Heichel 1977). To obtain the leaf impressions, which gave a negative image of the leaf surface, a layer of nail varnish was painted onto the abaxial leaf surface whilst the leaf was still attached to the tree. Nail varnish contains acetone as the solvent which is toxic to plant material, and 4-5 hours after the nail varnish had been applied the leaf was seen to brown. Despite this effect it was decided to use this method as the nail

varnish dries quickly enough to give an accurate picture of the stomata before they are adversely affected. This enabled the degree of opening of the stomata to be observed. Once the nail varnish had completely dried the leaf was removed from the tree and the nail varnish carefully peeled from the leaf surface. Care was taken not to stretch the nail varnish strip as this would distort the impression and lead to erroneous measurements of the size of the guard cells and degree of opening of the stomatal aperture.

An alternative non-toxic method to obtain impressions of the leaf surface (Sampson 1961) was also tried however this proved unsuccessful. It involved the use of silicone rubber to obtain the initial (negative) impression of the leaf surface, then once this had set a positive image was obtained from the silicone rubber using nail varnish. The main problem encountered was that the silicone rubber did not set quickly enough to obtain an accurate picture of the stomata. Problems also occurred with obtaining the positive impression in nail varnish.

The stomatal index $\frac{\text{no: stomata}}{\text{no: stomata + no: epidermal cells}} \times 100$ was determined from random counts taken from the nail varnish impressions under the microscope (x400). The number of stomata and epidermal cells were counted within an area 0.01755mm ^{2}. The area (0.13 x 0.135mm) was formed by a home-made graticle using hair attached to a metal ring placed inside the eye-piece of the microscope. To measure the size (length and width) of the guard cells photographs (x128) were taken of the nail varnish impressions, and also of a scale with divisions of 0.001mm. All the photographs were enlarged to the same extent giving final magnification of x555.5 or 1mm = 1.8 x 10^{-3}mm (fig. 2.5).

2.8 Wood Anatomy

The sections of stem taken for anatomical study and preserved in FAA were washed in water before sectioning using a sledge microtome. Many transverse sections were cut and the best were mounted on microscope slides in glycerol jelly. Sections of stem were taken from one tree for each treatment, in October 1983 base- and mid- sections of stems were taken from a third and half way along the length of the stem from its base. In October 1984 sections were taken from 5-10cm from the base of the stem and a second section taken from the top of the stem, for tube trees this was above the top edge of the tube.

Two measurements were made, the number of vessels was counted and vessel size (diameter including the vessel wall) determined. For the larger sections the number of vessels was counted within successive

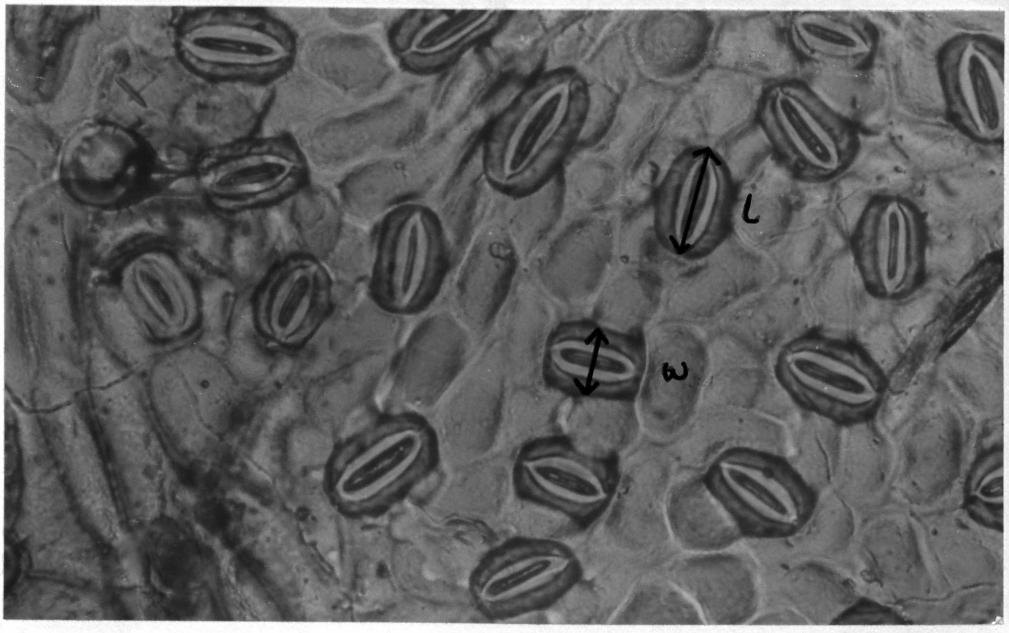


Figure 2.5 Guard cells; measurements of length (l) and width (w).
1mm = 1.8 x 10^{-3}mm

areas, each 0.57 x 0.57 = 0.325mm ^{2}, from the edge of the pith to the inner edge of the bark (fig. 2.6). Four lines were taken on each section and three sections were used for each treatment. On the smaller sections e.g. top sections 1984, the number of vessels in four squares (0.12 x 0.12 = 0.014mm ^{2}) was counted. For base sections taken in October 1984 results, where possible, were divided into 1st and 2nd year's growth. From these data the mean number vessels/mm^2 was obtained for each section and also the change in density of vessels across the section from the centre.

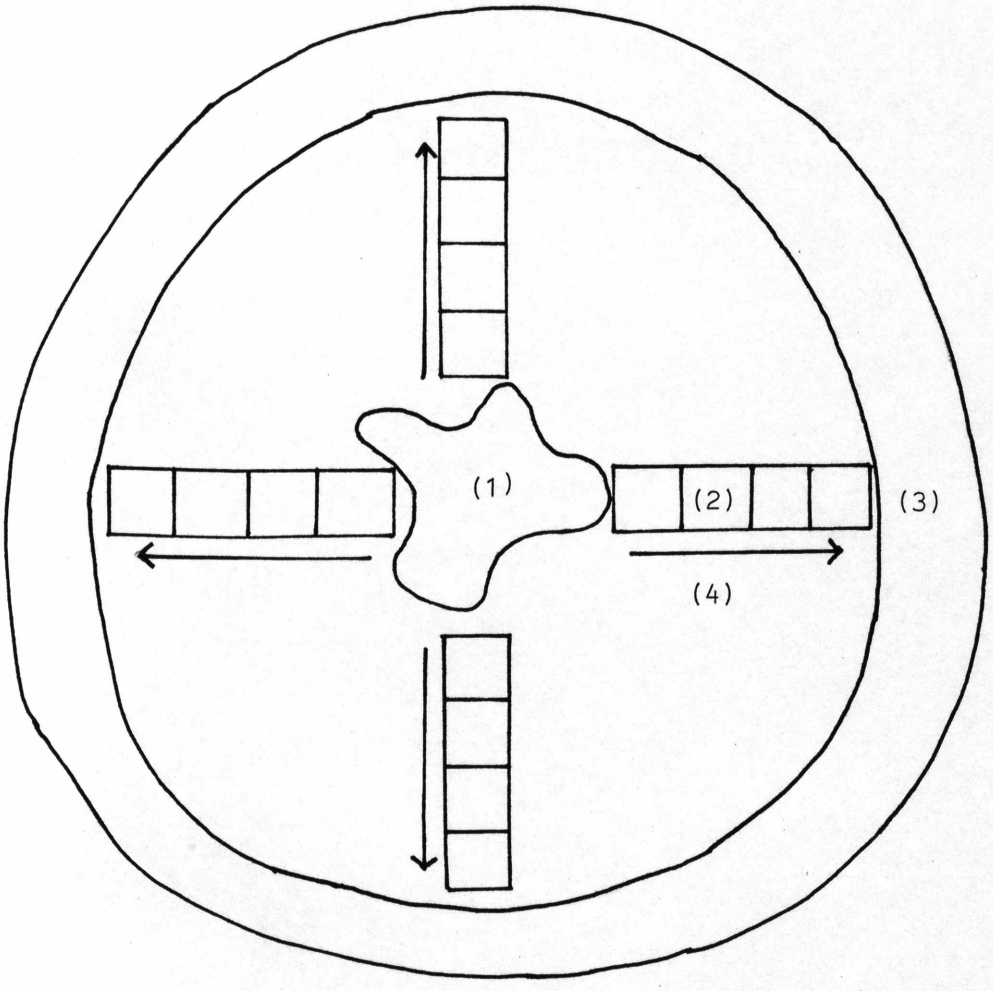
Size of vessels was measured using a calibrated graticle in the eye-piece of the microscope, 1 unit = 0.01mm. Vessels were either measured, as with number of vessels in successive squares, 0.57 x 0.57mm, along two lines from the centre (the results for the squares being combined), or approximately 200 vessels were measured for each section. Where the latter measurement was taken vessel diameters were taken for all the vessels as they occurred from the centre to the edge of the bark, or to the end of the year's growth, so all sizes of vessel were encountered. Results present the mean vessel size and the frequency of vessel size across the whole section.

2.9 Environmental Monitoring

2.9a Radiation

Total shortwave radiation, in the range 300-3000nm, was measured using a solarimeter. The sensor consisted of a thermopile, a circular network of thermocouples beneath alternate black and white areas, mounted on a flat board. The thermopile was covered by a glass dome which protected it from dirt and water, the glass also excluded thermal radiation (>3000nm). Attached beneath the board was a box containing an amplifier to convert the signal from the solarimeter into a suitable form for the computer to register (fig. 2.7). The black areas absorb radiation and this increased their temperature in relation to the white areas, the temperature difference created between the two areas creates a voltage which is linearly related to the level of radiation.

The solarimeters were calibrated against a Kipp solarimeter which is accurate to $\pm 5 Wm^{-2}$. To calibrate, the solarimeters and Kipp were placed on the roof of the Horticulture building at Wye College in an exposed, unshaded position and simultaneous readings were taken from the Kipp (Wm^{-2}) and the solarimeters (V). From these constants for the solarimeters were calculated: $\frac{\text{solarimeter reading (V)}}{\text{constant}} = Wm^{-2}$.



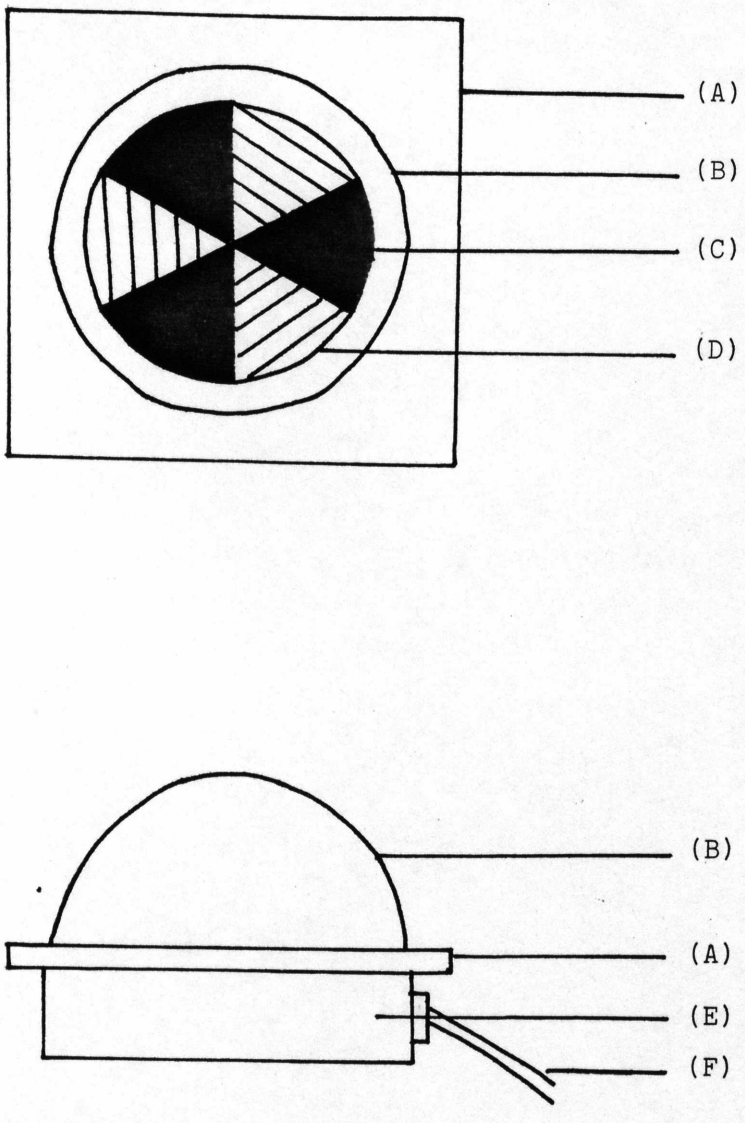
(1) Pith

(2) Area 0.57 x 0.57 = 0.325mm²

(3) Bark

(4) Direction in which measurements were taken

Figure 2.6 Method used to assess the number of vessels present in a transverse section of wood.



(A) Board
(B) Glassdome
(C) Black area of Thermopile
(D) White area of Thermopile
(E) Amplifier box
(F) Cable

Figure 2.7 Solarimeter.

Readings, which were taken on a clear sunny day were as follows: Kipp 532Wm^{-2}; solarimeter(1) 0.861V; solarimeter(2) 0.643V. These gave constants 0.00162 and 0.00121 for solarimeters (1) and (2) respectively for use in the computer data-logging system to convert the voltage reading from the sensor into Wm^{-2}. A linear relationship exists between radiation and the voltage output of both solarimeters (fig. 2.8).

For measurement of radiation in the field the solarimeters were held at 60cm above soil level on a small platform attached to a stake driven into the ground. To measure radiation within the tube the solarimeter was again held 60cm above soil level on a small platform, a length of tube was then placed over the solarimeter so that there was 60cm of tube material above the level of the sensor.

2.9b Temperature

Temperature and humidity measurements were carried out using one instrument containing both temperature and humidity sensors. Three such instruments could be used with a portable, battery-operated meter, others were used in combination with the computer data-logging system, all had the same basic design (fig. 2.9). Two sorts of temperature sensor were used. The first, used in the portable battery-operated system, were constant current source sensors (334Z) which have a linear relationship between change in temperature and change in current. The current from the sensor is passed through a resistor converting it to a voltage, this voltage is then amplified to give $0.05V°C^{-1}$ and measured. The second type of sensor, a platinum resistance thermometer, is a resistor (100ohms). The voltage across the resistor changes with temperature, and this change is detected, again with a constant of $0.05V°C^{-1}$.

Calibration of the zero setting was carried out in a refrigerated cabinet containing a fan to circulate the air within the cabinet to eliminate any temperature gradients which may exist. Temperature within the cabinet was monitored by a calibrated platinum resistance thermometer. The temperature sensors, mounted in their boxes, were placed into the cabinet and allowed to equilibriate in temperature with the cabinet, the offset was then adjusted to give the same reading as the cabinet temperature. This required opening the cabinet, thus disturbing the environment within, therefore the process had to be repeated until a steady reading was obtained. The gain was then adjusted whilst the sensors and reference platinum resistance

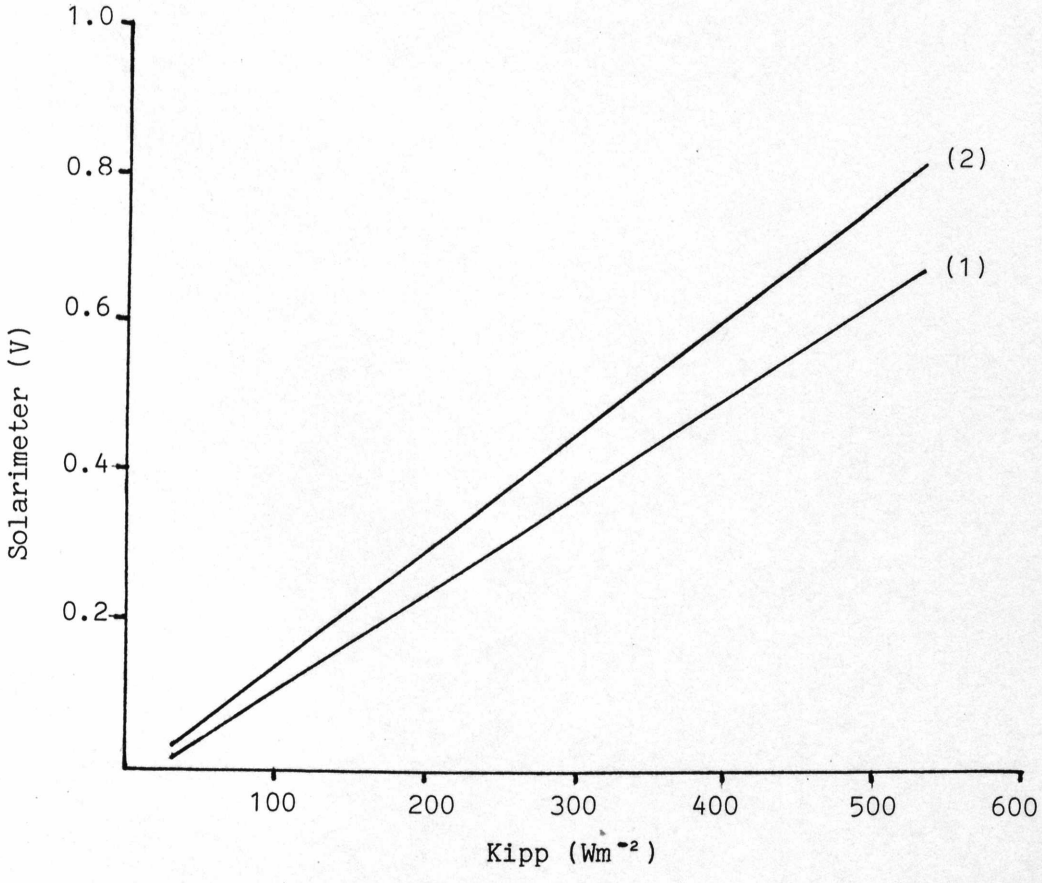
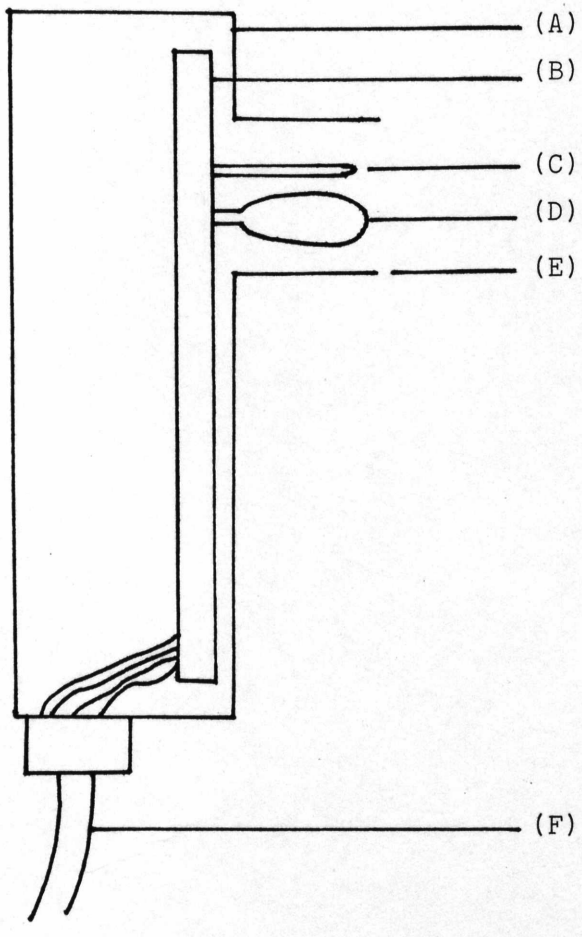


Figure 2.8 Relationship between shortwave radiation (x) and voltage output (y) of the solarimiters (1) and (2).

Solarimeter (1) $y = -0.00342 + 0.00157x$

Solarimeter (2) $y = -0.01527 + 0.00132x$



(A) Box
(B) Circuitry
(C) Temperature sensor
(D) Humidity sensor
(E) Shield to protect the sensors
(F) Cable

Figure 2.9 Instrument to measure temperature and humidity.

thermometer were placed on a shaded laboratory bench. A fan was used to disturb the air around the sensors to ensure an even temperature. Once the gain had been set the sensors were checked at several temperatures to ensure they were reading correctly.

2.9c Humidity

The humidity sensor (Philips "valvo") is a variable capacitance 110-180pF measuring humidity 33%-92% with an accuracy to within 5%. Capacitance can be related to oscillation of known frequency, and as the capacitance of the sensor varies with humidity this alters the frequency of oscillations. It is the difference between this and a fixed frequency from a known capacitance which is detected, and this is linearly related to humidity over the range indicated.

Humidity sensors were calibrated using saturated salt solutions above which the air is of a known relative humidity after equilibriation. Two solutions were used:

%RH at 25°C	Temp. Coeff. %RH/°C	Operating Temp. °C	Salt
32.7	0.06	15	Magnesium chloride hexahydrate $Mg\ Cl_2 . 6H_2O$
92.7	0.12	20	Ammonium dihydrogen phosphate $NH_4\ H_2\ PO_4$

The humidity of the saturated solutions had to be corrected for temperature e.g. for calibrations at 20°C %RH of magnesium chloride = 32.7 - 0.06(20 - 25) = 33% and ammonium dihydrogen phosphate = 92.7 - 0.12(20 - 25) = 93.3%. To calibrate the humidity sensors they were held above the saturated solution in a sealed container (fig. 2.10), and left to equilibriate i.e. until no further change in reading from the sensor occurred. The offset was adjusted to the lower humidity (33%RH) and the gain adjusted using the higher humidity (93%RH). The sensor was transferred from the lower to the higher humidity several times until no further adjustments were required.

In the field and glasshouse the boxes containing the temperature and humidity sensors were held at the correct height above soil level on a stake or retort stand. They were positioned so that the actual sensors were shaded from direct sunlight. For measuring temperature and humidity in the tube the shield surrounding the sensors was pushed through a hole in the side of the tube at the required height, the holes were such that there was no gap left between the instrument

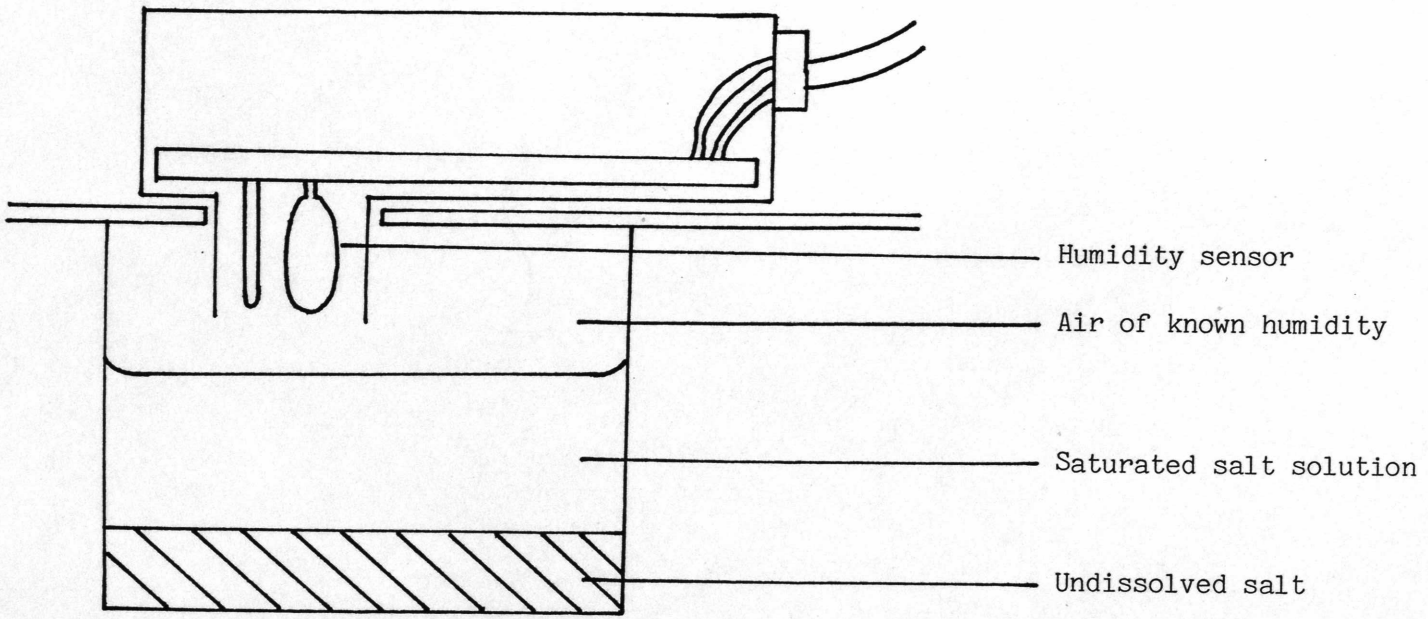


Figure 2.10 Calibration of humidity sensor using saturated salt solution of known relative humidity.

and the tube. Originally the shield surrounding the sensors had holes cut in it to allow free circulation of air around the sensors. However it was found that rain or run-off from leaf surfaces tended to saturate the humidity sensor making it unreliable, so the holes in the shield were covered with waterproof tape.

2.9d Leaf Temperature

Leaf temperature was measured using copper-constantan thermocouples. When two thermocouple junctions are joined the voltage between them is proportional to the difference in temperature between the two junctions,one of which is usually kept at a constant temperature and is referred to as the reference junction. Typically the reference thermocouple is held at 0°C using melting ice in water. However for measurements carried out during this study a variable reference was used e.g. soil temperature which was recorded separately using a platinum resistance thermometer. The voltage signal from the thermocouples is too small for a microcomputer to register, therefore it had to be amplified from 39.5$\mu V°C^{-1}$, the constant for copper-constantan thermocouples to 0.05$V°C^{-1}$ which can be detected. The amplifier for the thermocouples was set-up with a 1V offset so that when the thermocouple was at the same temperature as the reference there was a signal of 1V instead of 0V. This allowed the temperature of the thermocouple to fall below that of the reference junction and still give a positive voltage. The amplifier itself is affected by temperature, with a change in temperature of 50°C there is an error of 1-1.5°C. For this reason the amplifier was enclosed in a white box to reduce the heating effect of radiation.

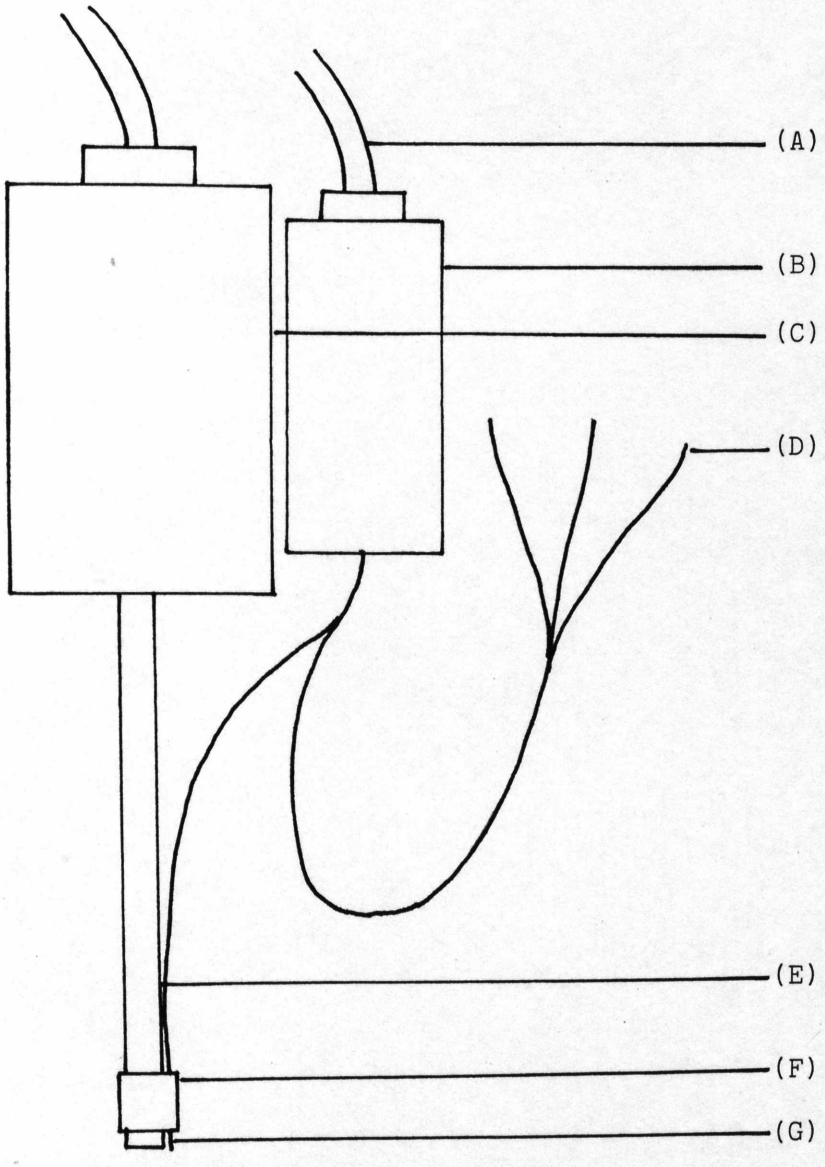
The amplifier for the thermocouples was set up using a known voltage source. Firstly with 0V input the offset was set to zero, then 3.95mV was supplied (equivalent to a difference in temperature between the thermocouple and the reference of 100°C) and the gain adjusted to give 5V. The offset was then adjusted to 1V, as the thermocouples themselves give a 0.5°C error when connected into the circuit this was adjusted for in the offset of the amplifier. To check the offset the reference junction, which was held in close contact with a platinum resistance thermometer (using shrink-fit tubing) and the thermocouples were placed into ice and water at 0°C, giving a reading of 1V. Then the thermocouples were placed in water of known temperature and the gain checked to be reading the equivalent of 0.05$V°C^{-1}$.

2.9e Soil Temperature

Platinum resistance thermometers were used to measure soil temperature as a reference for the thermocouples (fig. 2.11). The resistance of a platinum resistance thermometer changes with temperature, this is detected as a change in voltage which through amplification is adjusted to give $0.05V°C^{-1}$.

Calibration of the platinum resistance thermometers was carried out using water, contained in vacuum flasks, at different temperatures. Zero was set using ice and water and the gain adjusted with the thermometer in warm water of known temperature, measured by a calibrated platinum resistance thermometer. This process was repeated until steady readings were obtained, then the thermometers were checked in water at a range of different temperatures.

In the field and tube the thermocouples (6 connected in parallel) were held in close contact with the lower surface of the leaves using white hairgrips. Before use the thermocouples were protected with a coating of epoxyresin. The reference thermocouple and platinum resistance thermometer, to which it was attached, were pushed into the soil. Figures for leaf temperature represent the mean value for 6 leaves, corresponding to the 6 thermocouple junctions used. At first the platinum resistance thermometers were placed in an open position, however on sunny days unusually high soil temperatures were recorded. This was thought to be due to heat being absorbed by the box of the thermometer (containing the circuit board), which was above the soil, being transmitted down the metal rod of the thermometer itself. Although this meant that the soil temperatures were unreliable it should not have affected the leaf temperature readings as the thermocouple temperature was related to the reference junction which was in close contact and therefore assumed to be at the same temperature as the platinum resistance thermometer. During subsequent recordings the thermometers were still pushed into the soil, however to prevent heating from the surface the tops of the thermometers were covered by a polystyrene box held down onto the soil surface. When the thermometers were thus protected from radiation the mean difference between the measured soil temperature and that recorded at the Meteorological Station was reduced from +2.3°C to +0.7°C.



(A) Cable

(B) Amplifier box for Thermocouples

(C) Box containing circuitry for thermometer

(D) Thermocouple junction

(E) Platinum resistance thermometer

(F) Shrink fit tubing

(G) Reference thermocouple junction

Figure 2.11 Platinum resistance thermometer and thermocouples to measure soil and leaf temperature.

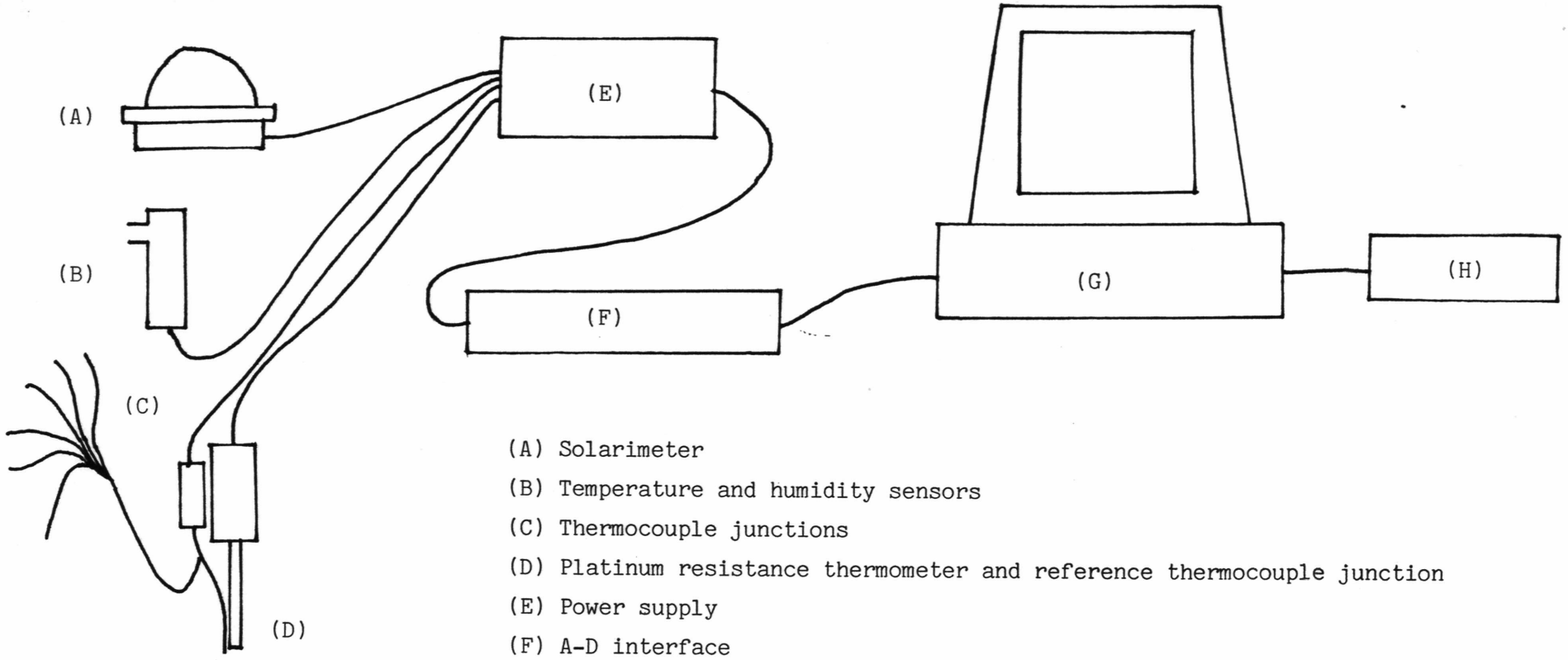
2.9f Measuring Sub-Zero Air Temperatures

The A-D interface used with the computer data-logging system could only read positive voltages. Temperatures below 0°C were detected by the temperature sensors however the resulting voltage was negative and therefore not recorded by the computer system. To overcome this problem the thermocouples and platinum resistance thermometers were used. These had been set up so that the thermocouples could read a temperature which was up to 20°C lower than that of the reference junction (using a 1V offset) and still give a positive voltage. It was important to prevent the temperature of the platinum resistance thermometers from falling below zero which would result in negative voltage. For this purpose the thermometers were placed in a polystyrene box containing a 15W light bulb controlled by a thermostatic switch to keep the temperature at approximately 10°C, using the heating effect of the light bulb. This allowed the air temperature to fall to -10°C and still result in a positive output from the thermocouples. Although the temperature within the box, as recorded by the platinum resistance thermometers, did vary between 7-19°C depending on weather conditions, this did not affect the recording of subzero air temperatures.

In the field the thermocouples were placed at approximately 60cm above ground level in a shaded position. For measurement of the tube temperature the thermocouples were pushed through the wall of the tube into the interior, also at a height of 60cm. White card was placed around the tube to shade an area approximately 10cm in height about the position of the thermocouples to prevent direct heating by the sun.

2.9g Data-Logging System

Measurements of radiation, temperature and humidity in the field, tube and glasshouse were taken and recorded by a microcomputer based data-logging system. This consisted of the sensors: solarimeters, temperature and humidity sensors, thermocouples and platinum resistance thermometers which were connected via a DC power supply to an A-D interface (16 channel Analog to Digital converter). Signals from the A-D interface were then read by the microcomputer (Commodore 4000 series) and recorded onto tape (fig. 2.12). The computer programme used to collect and record the data was developed by M.J.Varley at Wye College for specific use with such a system. The programme was altered to accommodate the use of the platinum resistance thermometers as the reference for the thermocouples, the sensor code for the thermocouples becoming TX. The constants used to convert the voltage



(A) Solarimeter
(B) Temperature and humidity sensors
(C) Thermocouple junctions
(D) Platinum resistance thermometer and reference thermocouple junction
(E) Power supply
(F) A-D interface
(G) Microcomputer
(H) Tape recorder

Figure 2.12 Microcomputer-based data-logging system.

signal from the sensors into the appropriate units were as follows:

solarimeter(1)	0.00162
solarimeter(2)	0.00121
temperature sensor	0.05
humidity sensor	0.01
thermocouple	0.05
platinum resistance thermometer	0.05

The computer was set to scan the sensors at 30s intervals and to calculate, and record onto tape the mean value for each sensor every 60mins. Thus over a 24hour period hourly means were obtained for each sensor used, each mean the result of 120 scans at 30s intervals.

The microcomputer, A-D interface, taperecorder and power supplies were all housed in a wooden hut at the end of the field plot. The sensors were then connected to the power supply and interface using cables which ran out along the ground. All the sensors were sealed with silicone rubber to make them waterproof. The plugs and sockets connecting the cables to the sensors were also watertight. The computer was checked regularly to ensure it was running correctly.

2.10 Carbon Dioxide Studies

The absolute concentration of CO_2 was determined using infra-red gas analysis. Two methods of sampling the air were employed, the first method, described below, was used for CO_2 studies carried out in 1983 and 1984. This method involved taking samples of air using air-tight 50ml syringes. A hypodermic needle was attached to each syringe allowing samples to be taken from within the tube shelter at different heights by passing the needle through the side of the tube. To take a sample of air (50ml) the plunger of the syringe was withdrawn slowly, care was also taken not to breathe near the syringe as this would have raised the level of CO_2 in the sample. Once a series of samples had been collected, each retained within an individual syringe, they were returned to the laboratory where an infra-red gas analyser (IRGA) (URAS2) was used to measure the absolute concentration of CO_2 within each sample.

Prior to analysis of each series of samples the IRGA was calibrated using a known CO_2 concentration. This was achieved using a standard of 495ppm CO_2 which was passed via a diluter, to obtain different concentrations of CO_2, to the IRGA (Fig.2.13). The diluter contained a filter of magnesium perchlorate to remove all traces of moisture from the standard and a filter of soda lime to remove CO_2, which in combination

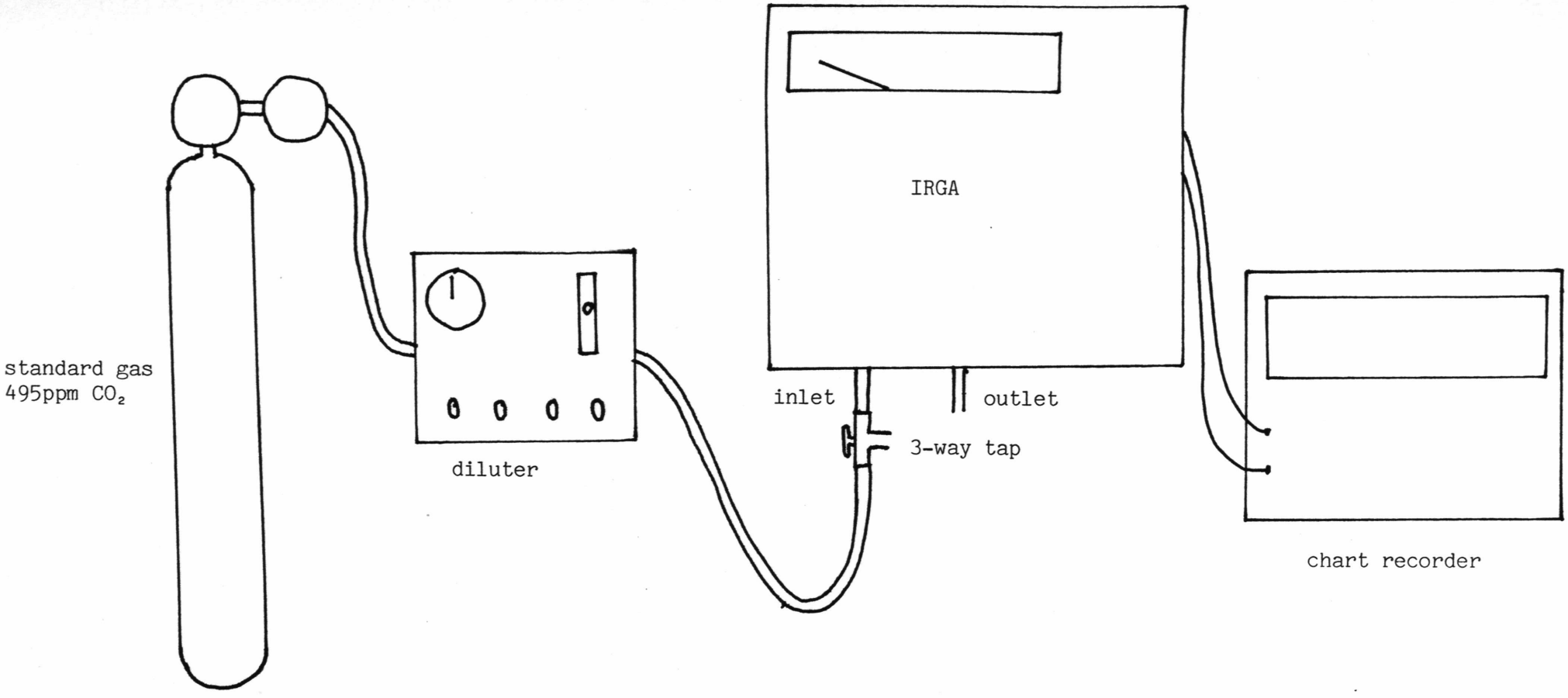


Figure 2.13 System for calibration of the infra-red gas analyser (not to scale).

with a system of valves and bypass pipes resulted in a series of concentrations of CO_2 from 0-100% of the standard. Concentrations of CO_2 used for calibration of the IRGA ranged from 34.0%-78.6% of 495ppm CO_2 i.e. 168-389ppm CO_2. The IRGA was connected to a chart recorder which recorded the results in arbitary units, these were later converted into ppm CO_2 using calibration curves (straight lines) determined using linear regression analysis. Once the IRGA had been calibrated the air samples collected in the syringes were injected into the inlet via the 3-way tap.

To assess whether this sampling technique could be accurately replicated 15 samples were taken from the same position 1m above ground level in the field. The mean concentration recorded was 285.4 $\pm$1.8ppm CO_2, thus replicate samples were accurate to within $\pm$0.6%.

The accuracy of the syringe technique was assessed using the apparatus shown in figure 2.14. The standard was passed from the cylinder through the diluter, to obtain the required concentration, into the jar and from there to the IRGA. The standard was passed through this system until all the original gas within the apparatus had been replaced by the desired gas and a steady reading was obtained from the IRGA. When this equilibrium had been reached a sample of gas was taken from the jar using one of the 50ml syringes and this sample injected directly into the IRGA. This procedure was repeated five times for each concentration of CO_2. The mean difference between the CO_2 concentration of the sample taken using the syringe and the actual concentration was -18.9 $\pm$1.8ppm CO_2. Thus the lower the concentration of CO_2 in the air the greater the percentage error due to this sampling technique i.e. at 400ppm CO_2 there is a 4.7% reduction in the reading, but at 200ppm the error is 9.4%.

The second method used for CO_2 studies in 1985 involved the use of a battery-operated portable IRGA (LCA-2) (fig. 2.15). This enabled direct readings of CO_2 concentration to be taken in the field, tube and glasshouse environments without the need to take air samples with syringes. The analyser pumps air at a rate of 150mlmin^{-1} through the system. After a trial run it was found that the readings stabilised after the pump had been running for 20-30s. If the analyser was left to pump air from a tube shelter for longer than 30s the reading dropped and then started to fluctuate as the analyser began to suck air from a larger area within the tube. So for each sample the analyser was switched on and the reading taken after 30s, after which time a 75ml sample of air had been taken. For all sampling a 3m length of 3mm bore butyl

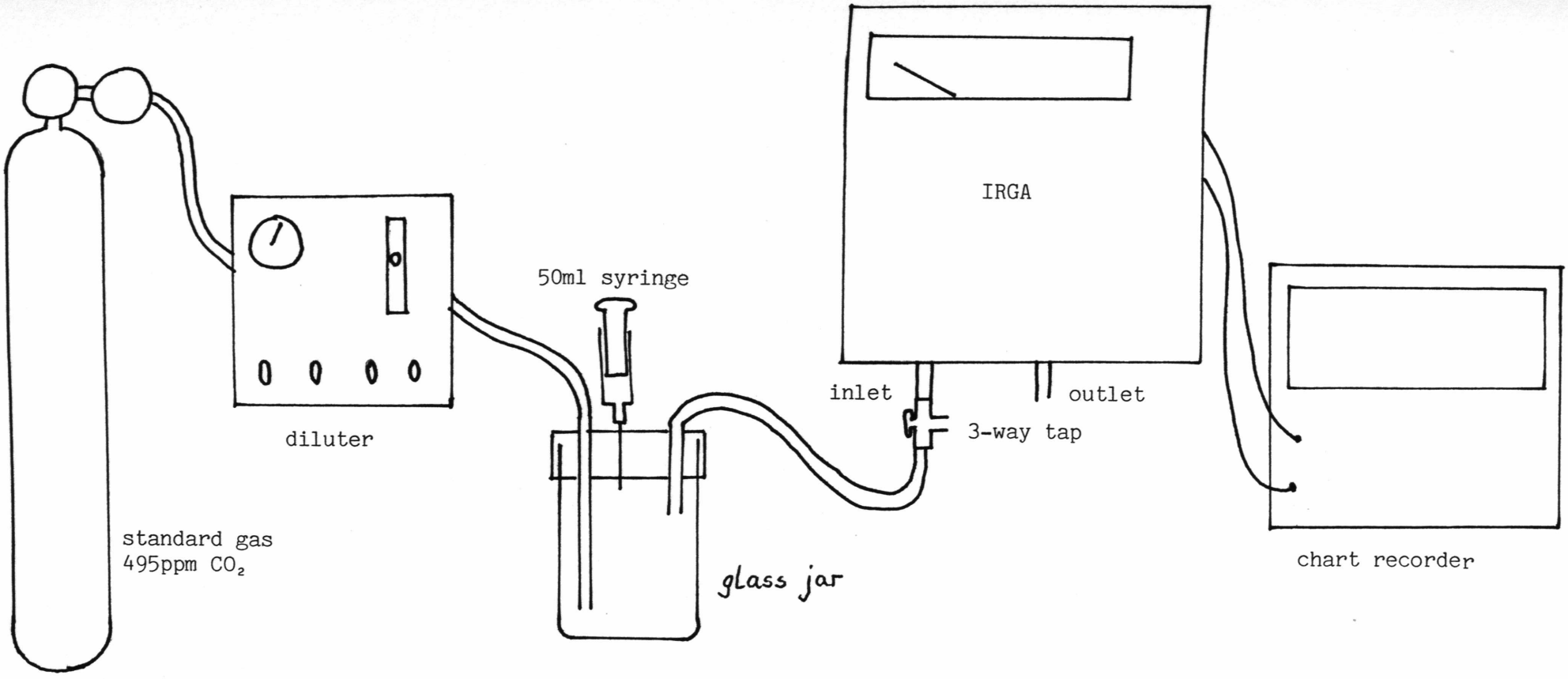


Figure 2.14 Apparatus used to assess the accuracy of the syringe sampling technique(not to scale).

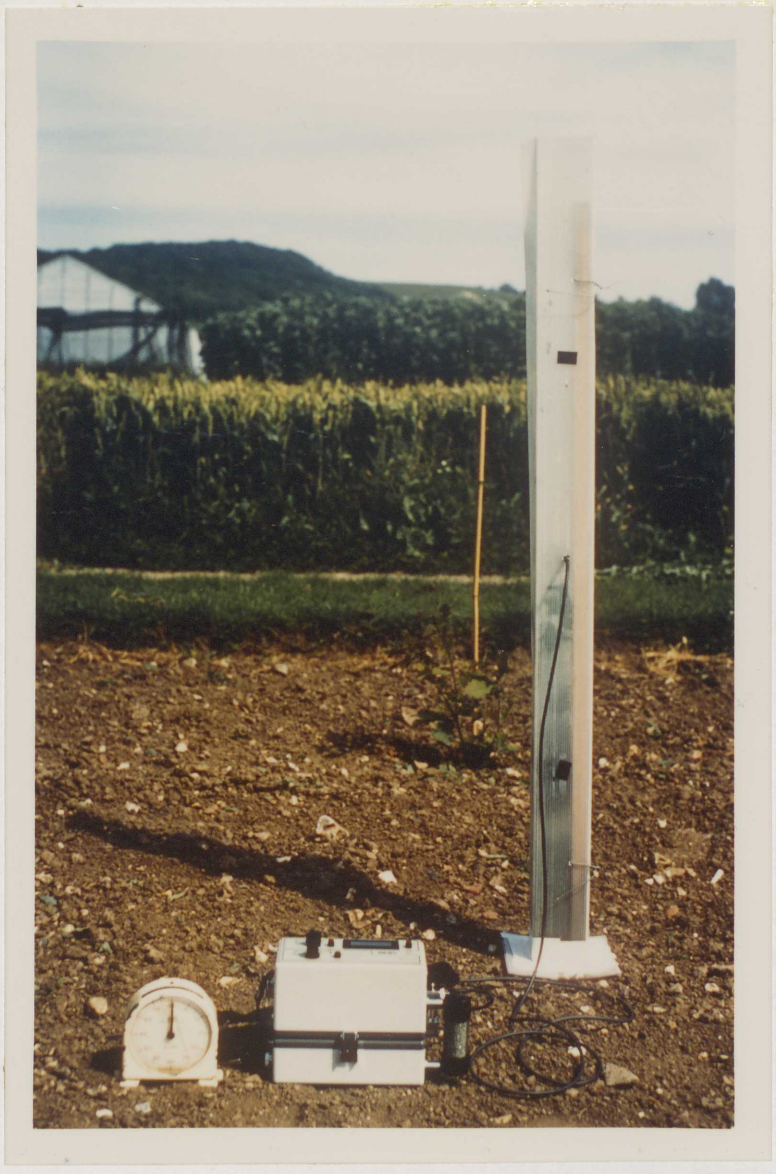


Figure 2.15 CO_2 measurement using a battery operated portable infra-red gas analyser.

tubing (volume 21.2ml) was used to connect the analyser to the tube shelter or position in the field or glasshouse to be sampled.

To determine the effect of the soil on the level of CO_2 in the tube environment the soil surface was covered using a mat of polypropylene, similar to the tube material itself. The mat, which was 5cm greater in diameter than the tube shelter was placed over the soil surface within the tube, with a suitable hole cut for the tree stem, then completely sealed with tape around the tree stem and the exterior of the tube shelter.

2.11 Relationship Between Relative Humidity and Vapour Pressure Deficit.

When considering certain plant physiological processes e.g. stomatal opening, transpiration, perhaps a more relevant measure of the water content of air than relative humidity (%RH) is the vapour pressure deficit i.e. the difference between the actual vapour pressure of water in the air and the saturated vapour pressure at a particular temperature, as this, among other factors, determines rate of evaporation (Downs and Hellmers 1975).

Vapour pressure is usually determined from wet and dry bulb temperatures which are substituted into the equation (Meteorological Office Hygrometric Tables Part III 2nd Edition 1978):

$$e = e'w - Ap\,(T - T')$$

where e = vapour pressure

e'w = saturated vapour pressure at T' of wet bulb

p = atmospheric pressure taken as 1000millibars, suitable for all conditions below 3000ft.

T = temperature of dry bulb (°C)

T' = temperature of wet bulb (°C)

A = constant which depends on rate of ventilation of psychrometer, latent heat of evaporation of water and the temperature scale in which the thermometers are graduated.

Figures for saturated vapour pressure correspond to those where there is no depression in temperature of the wet bulb i.e. where T = T' and thus e = e'w. Linear regression analysis was used to determine the relationship between temperature (t°C) and saturated vapour pressure (svp millibars) taking data from the Meteorological Office Hygrometric Tables Part III 2nd Edition (1978). The relationship (significant at $P<0.01$) is represented by the equation:

$$svp = 4.79 + 0.219t + 0.037\,t^2 \qquad r = 0.997$$

The relationship between relative humidity (%RH), vapour pressure (vp), saturated vapour pressure (svp) and vapour pressure deficit (vpd) at a given temperature (t°C) is then derived as follows (Downs and Hellmers 1975):

$$\frac{vp}{svp} \times 100 = \%RH$$

$$vp = \frac{\%RH}{100} \times svp$$

$$vpd = svp - vp = svp - \left(\frac{\%RH}{100} \times svp\right)$$

2.12 Relation Between Two Measures of Photosynthetically Active Radiation, Wavelengths 400-700nm.

Simultaneous readings (n=143) of shortwave radiation 400-700nm (Wm^{-2}) and photosynthetically active radiation (PAR $\mu molm^{-2}s^{-1}$) were taken throughout several days to establish a relationship between these two measures of radiation. Both were measured with silicone cells filtered to give the required response, shortwave radiation measured by a flat response sensor and PAR by a quantum sensor. A strong linear relationship (r=0.997) was found, represented by the equation: $y = -2.580 + 2.153x$ where x = shortwave radiation 400-700nm (Wm^{-2}) and y = PAR ($\mu molm^{-2}s^{-1}$).

Coombs and Hall (1982) state that of full sun daylight at $950Wm^{-2}$, approximately $1800\mu molm^{-2}s^{-1}$ or $399Wm^{-2}$ is photosynthetically active radiation (400-700nm). For total radiation they give $1Wm^{-2}$ as approximately equivalent to $1.895\mu molm^{-2}s^{-1}$. To convert Wm^{-2} (PAR) to $\mu molm^{-2}s^{-1}$ (PAR) for most daylight-type light sources McCree (1981) multiply by 4.6.

2.13 Statistical Analysis of Data

Results were analysed using analysis of variance, this estimates the residual standard deviation, in effect it calculates the variation between observations on units receiving the same treatment making systematic allowance for any systematic deviation between blocks, as in a randomised blocks design, or row and columns, as in Latin square designs (Cox 1958). To give a good estimate of the residual standard deviation the different units should respond independently of one another and any source of uncontrolled variation balanced out in the design of the experiment e.g. sums of squares for blocks should be removed before calculating the standard deviation. The result of

analysis of variance, F-test, is an overall test of the significance of the differences that have been observed between the means of all the treatments in the experiment (Mead and Curnow 1983). With a factorial design the analysis is divided into components for the main effects and the interactions between factors. Where there are missing values an estimate of the value is made such as to reduce the error sum of squares to the minimum. The degrees of freedom are, of course, reduced according to the number of missing values.

Certain assumptions underlie an analysis of variance (i) normality- in the population from which the sample is taken the observations should be normally distributed (ii) homogeneity of variance- variance must be the same for each population in order to pool the variance estimates (iii) additivity- the difference expected between the effects of treatments is the same for all units irrespective of the block in which they occur (Mead and Curnow 1983). When these assumptions breakdown it may be necessary to transform the data to a different scale thus giving an anlysis for which these assumptions are valid. For analysis of results in this study various transformations were tried as follows:-

height, stem diameter, dry weight, branch length: log (x)

number flushes, number branches: $\sqrt{x}$

% dry weight: arcsin $\sqrt{x/100}$

stem:root ratio: arcsin $\sqrt{x}$

However transformation of the data in most cases led to an increase in residual sum of squares and did not alter the significances of results compared with analyses on untransformed data. For this reason and also because transformed data are more difficult to present and interpret, analyses of variance were carried out on the untransformed values.

Where least significant differences (LSD) are given for non-significant differences, these are the LSD's that would be required to give a significant difference, however they should not be used for comparison between treatments.

Linear regression analysis (Mead and Curnow 1983) was used to examine the quantitative relationship between two or more variables, to derive predictive equations and as covariance analysis to reduce random variation of observations by using preliminary information on the experimental units. The regression slope, b, is an estimate of the rate at which y changes for a unit increase in value of x.

The simplest possible relationship between two variables is a straight line. Plotting of results, y on x, gave some idea of the

possible relation between variables, log transformation was carried out on exponential relationships, $y = ax^b$, to give the linear relation $\log y = \log a + b \log x$.

2.14 Use of Richards' Diagrams

Richards (1941) devised an interaction diagram for the results of factorial experiments. Thus for a hypothetical 3x2x2 experiment the three levels of one factor may be represented by O P_1 P_2 and the higher levels of the other two factors by Q and R. In order to draw the diagram it is necessary to treat P_1 as factorially equivalint to the higher level of either Q or R and to treat P_2 as equivalent to combination in pairs of higher levels of Q and R and P_1. Thus $P \equiv Q \equiv R$ and $P_2 \equiv P_1 Q \equiv P_1 R \equiv QR$.

Taking the 3x2x2 design used in the main experiment of this study:
Factor 1: FTG-environment: field (F); tube (T); glasshouse (G)
Factor 2: Light: natural daylength (ND); 24 hour light (24hr)
Factor 3: Hormone: - gibberellic acid ($-GA_3$); + gibberellic acid ($+GA_3$)
Applying the terms used by Richards field = O, tube = P_1, glasshouse = P_2, 24 hour light = Q and + gibberellic acid = R. Thus in order to draw the diagram it is necessary to assume that tube is factorially equivalent to 24 hour light and + gibberellic acid treatments, and that the glasshouse environment is factorially equivalent to combinations of tube and 24 hour light, tube and gibberellic acid and 24 hour light and gibberellic acid.

Therefore the FTG-environments have in effect been ranked field-tube - glasshouse. The tube environment being considered as 'halfway' between the field and glasshouse environments. Trees can thus be grown in the field, the control environment, or in tubes, thinking of a tube shelter as an addition to the field treatment, a "miniature greenhouse" around each tree, or finally in the glasshouse, which may be considered to provide "the best conditions for growth". These "assumptions" apply, of course, in the construction of an interaction diagram and do not imply any physiological or other conclusions. For this purpose then, for each Richards' diagram the treatments have been numbered as follows:

1	Field	ND	$-GA_3$
2	Field	ND	$+GA_3$
3	Field	24HR	$-GA_3$
4	Field	24HR	$+GA_3$
5	Tube	ND	$-GA_3$
6	Tube	ND	$+GA_3$

7	Tube	24HR	$-GA_3$
8	Tube	24HR	$+GA_3$
9	Glasshouse	ND	$-GA_3$
10	Glasshouse	ND	$+GA_3$
11	Glasshouse	24HR	$-GA_3$
12	Glasshouse	24HR	$+GA_3$

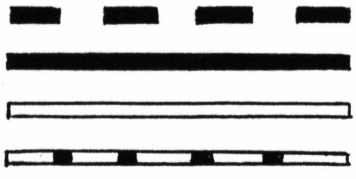
Also the same symbols have been used throughout; the difference between field and tube is represented by a broken black line, that between tube and glasshouse by a solid black line. Differences between natural day-length and 24hour light, and between $-GA_3$ and $+GA_3$ are indicated by white and pied lines respectively. Thus

Field - Tube

Tube - Glasshouse

ND - 24HR

$-GA_3$ - $+GA_3$



The Richards' diagram consists of a series of quadrilaterals each of which represents an interaction such that the interaction is represented by the degree by which any one quadilateral deviates from a parallelogram, if the interaction approaches zero the appropriate quadrilateral becomes a parallelogram. Table 2.3 gives details of each quadrilateral formed and the interaction it represents.

Table 2.3

Details of the interactions represented on a Richards' diagram of the FTG-environment x light x hormone (3x2x2) factorial experiment.

INTERACTION BETWEEN:	LEVEL OF OTHER FACTOR:	QUADRILATERAL FORMED BETWEEN POINTS:
Tube x gibberellic acid	ND	1 2 5 6
	24HR light	3 4 7 8
Glasshouse x gibberellic acid	ND	5 6 9 10
	24HR light	7 8 11 12
Tube x 24HR light	$-GA_3$	1 3 5 7
	$+GA_3$	2 4 6 8
Glasshouse x 24HR light	$-GA_3$	5 7 9 11
	$+GA_3$	6 8 10 12
Gibberellic acid x 24HR light	Field	1 2 3 4
	Tube	5 6 7 8
	Glasshouse	9 10 11 12

RESULTS I

PART A - ENVIRONMENT

3A.1 Radiation 1983

A quantum sensor was used to take spot readings of photosynthetically active radiation (400-700nm) in the three environments of field, tube and glasshouse on one day each in June, July, August and September 1983. Readings were taken at heights of 30cm, 60cm and 90cm above ground level at five different locations within each environment, each location corresponding to a particular tree. The sensor was always held in a vertical position and was placed amongst the leaves of the tree at the appropriate height. Measurements were taken during three periods of the day, 0900-1000hr,1230-1330hr, 1600-1700hr, the order in which the readings were taken was determined using random numbers.

Table 3A.1

Mean photosynthetically active radiation ($\mu molm^{-2}s^{-1}$) in field, tube and glasshouse, and at three heights above ground level during four days in the summer of 1983.

	JUNE 9/6/83	JULY 19/7/83	AUGUST 26/8/83	SEPTEMBER 29/9/83
FIELD	737	635	1079	227
TUBE	384	443	298	36
GLASSHOUSE	325	235	309	73
SIGNIFICANCE	***	***	***	***
LSD (P0.05)	110	61	112	16
30CM	391	356	479	88
60CM	503	469	562	114
90CM	552	507	643	134
SIGNIFICANCE	*	***	*	***
LSD (P0.05)	110	61	112	16

Comparison between the light intensity in the three environments on the four occasions studied allowed the three environments to be placed in order of magnitude as follows: for June field > tube =

glasshouse; July field > tube > glasshouse; August field > tube = glasshouse; and for September field > glasshouse > tube, where = shows no significant difference (table 3A.1). For all environments there was an increase in intensity with height, though the precise relationship between light intensity and height varied as follows: for June and July 30cm < 60cm = 90cm; August 30cm = 60cm < 90cm; and September 30cm < 60cm < 90cm (fig. 3A.1), this must reflect changes in leaf distribution and density and/or angle of incidence of light.

3A.2 Temperature and Humidity 1983

Spot measurements of temperature and humidity were taken during July, August and September 1983. Once placed in position at 30cm, 60cm and 90cm above ground level the sensors were left to equilibriate for 5 minutes before 10 replicate readings were taken at 30s intervals to give average temperature and humidity readings. Five positions in each environment were used, each corresponding to an individual tree and the sensors were placed amongst the leaves of the tree. Due to the length of time taken to record the measurements for one environment, approximately 1 hour, each environment was sampled at a different time of day. Over a period of three days, using a Latin square design, the field, tube and glasshouse environments were infact sampled at three times of day: 0900-1000hr(1), 1200-1300hr(2) and 1600-1700hr(3) as follows:

JULY	DAY 1	DAY 2	DAY 3
FIELD	3	2	1
TUBE	2	1	3
GLASSHOUSE	1	3	2

AUGUST	DAY 1	DAY 2	DAY 3
FIELD	3	2	1
TUBE	1	3	2
GLASSHOSE	2	1	3

SEPTEMBER	DAY 1	DAY 2	DAY 3
FIELD	1	2	3
TUBE	2	3	1
GLASSHOUSE	3	1	2

This design allowed day and time to be removed as sources of variation in the analysis of variance so that any differences between environment and height could be investigated.

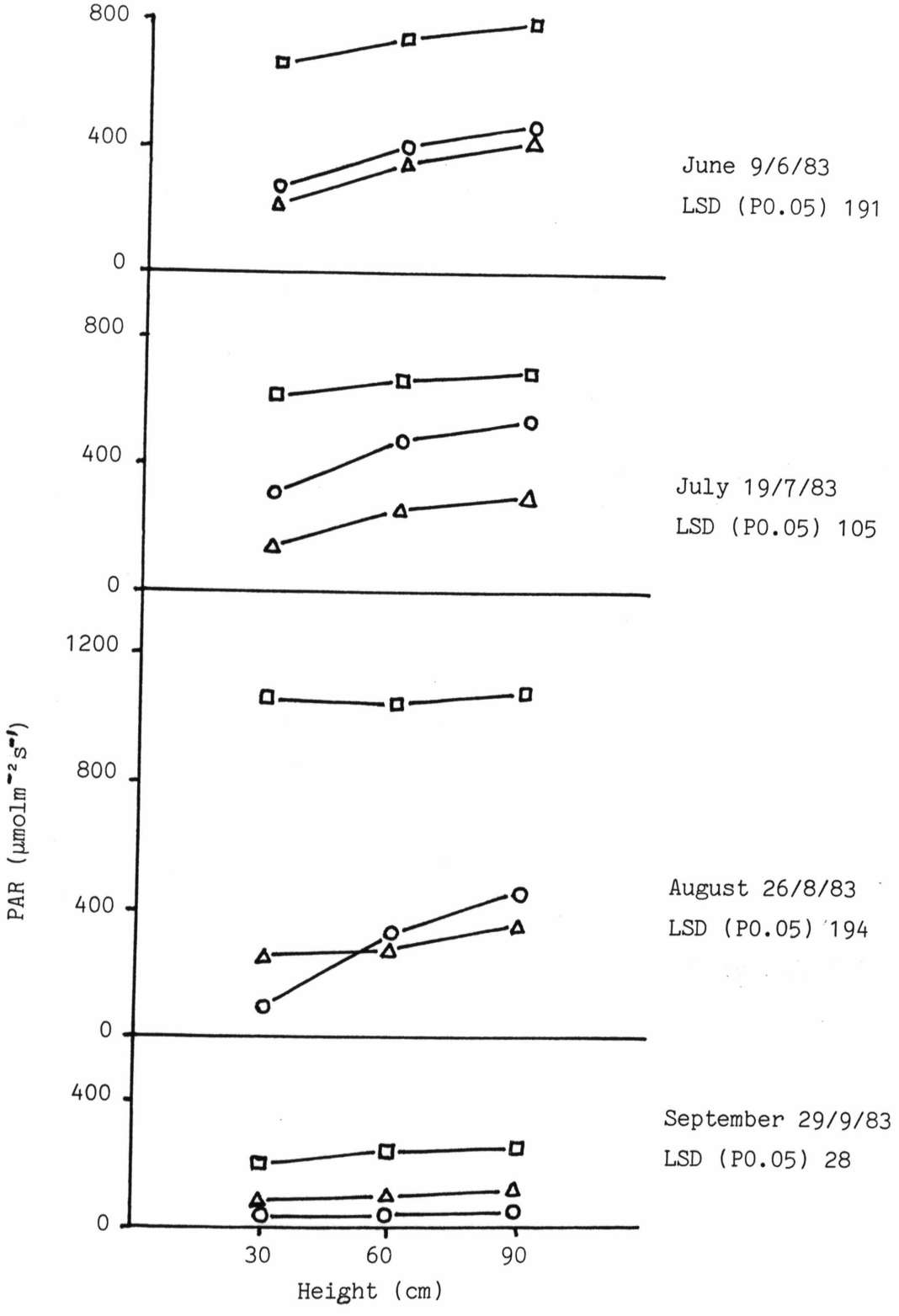


Figure 3A.1 Photosynthetically active radiation (PAR) in field (□), tube (○) and glasshouse (△) at 30cm, 60cm and 90cm on four days during the summer of 1983.

Significant differences in temperature and humidity were shown between field, tube and glasshouse (fig. 3A.2). For temperature the three environments can be ordered: for July tube > glasshouse > field; August tube > glasshouse = field; and September glasshouse > tube > field where = shows no significant difference (table 3A.2). In July there was a difference in mean temperature of 8.6°C between the tube and field environments. Significant differences in temperature were also detected between the three heights above the soil however the actual difference was only 1-2°C.

Table 3A.2

Spot readings of mean temperature (°C) in field, tube and glasshouse and at three heights above ground level for July, August and September 1983, sampled over a 3 day period at 3 different times of day using a Latin square design.

	JULY	AUGUST	SEPTEMBER
FIELD	28.0	21.9	16.6
TUBE	36.6	27.2	20.2
GLASSHOUSE	32.8	22.9	21.7
SIGNIFICANCE	***	***	***
LSD (P0.05)	0.6	0.6	0.4
30CM	32.6	23.7	19.5
60CM	33.4	24.6	19.9
90CM	31.5	23.5	19.0
SIGNIFICANCE	***	**	**
LSD (P0.05)	0.6	0.6	0.4
DAY	***	***	***
TIME	***	***	***

Humidity in the tube was greater than that in the glasshouse and field on all three occasions (table 3A.3). The relationship between the environments can be described as follows: in July tube > field > glasshouse; in August tube > glasshouse = field; and in September tube > field > glasshouse. The relation between humidity and height varied between the sampling periods. For July there was a decrease in humidity with height in the three environments. In August

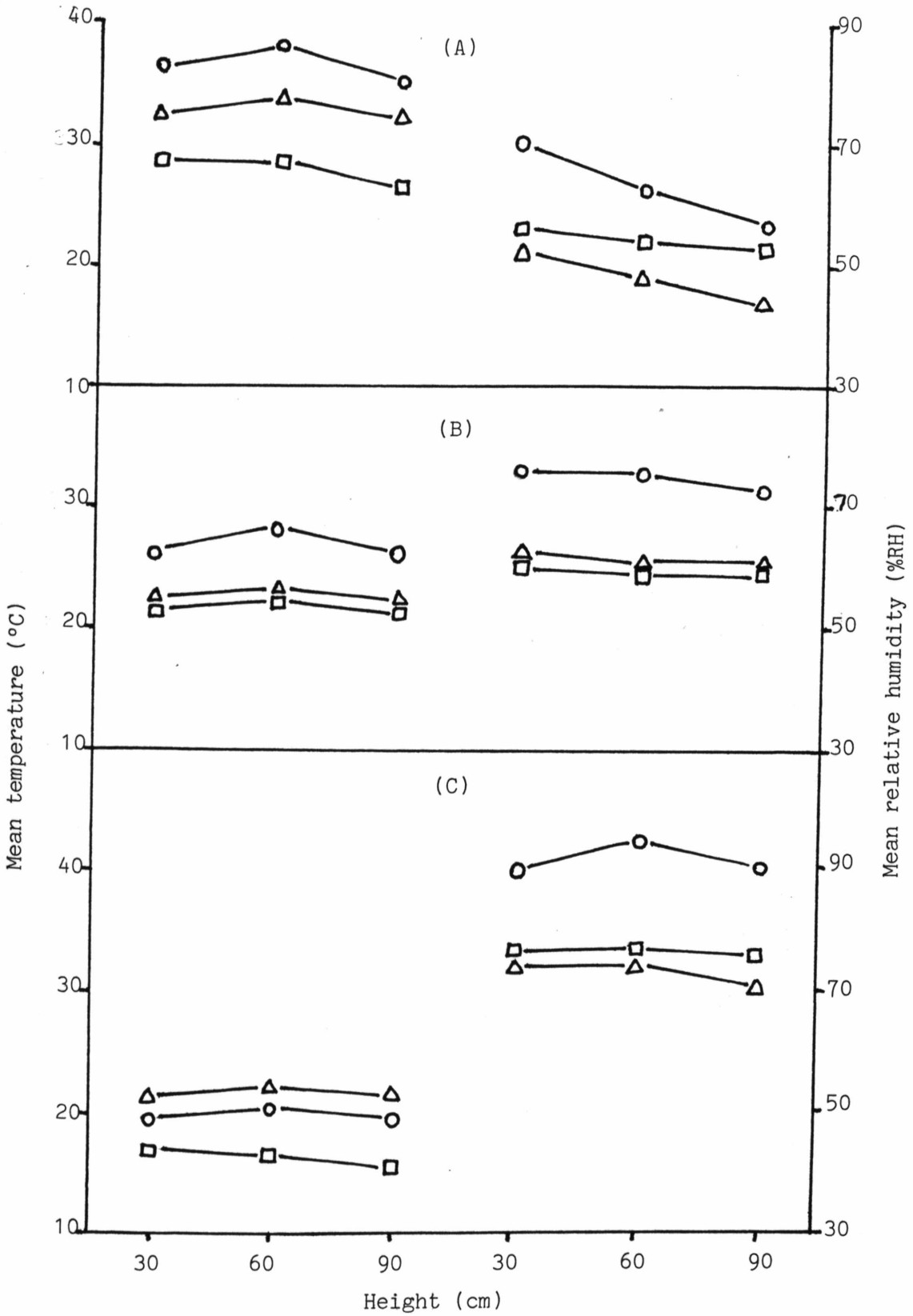


Figure 3A.2 Mean temperature and humidity at the three different heights in July (A), August (B) and September (C) 1983 in field (□), tube (○) and glasshouse (△), sampled over a 3 day period at 3 different times of day using a Latin square design.

the humidity was similar at 30cm, 60cm and 90cm but in September it was lower at 90cm. In absolute terms, only the tube environment attained very high humidities while glasshouse and field remained within the "normal" limits.

Table 3A.3

Spot readings of mean humidity (%RH) in field, tube and glasshouse and at three heights above ground level for July, August and September 1983, sampled over a 3 day period at 3 different times of day using a Latin square design.

	JULY	AUGUST	SEPTEMBER
FIELD	54.9	59.8	77.1
TUBE	63.9	75.5	92.1
GLASSHOUSE	48.5	61.4	73.8
SIGNIFICANCE	***	***	***
LSD (P0.05)	1.6	3.1	1.9
30CM	59.9	66.4	81.2
60CM	55.6	65.7	82.7
90CM	51.8	64.6	79.1
SIGNIFICANCE	***	NS	**
LSD (P0.05)	1.6	3.1	1.9
DAY	***	*	***
TIME	***	*	*

3A.3 Environment 1984

Spot measurements of temperature and humidity were taken in field, tube and glasshouse environments on eight occasions from February to July 1984. Readings were taken at a height of 60cm from ground level and five positions, each corresponding to a tree, sampled within each environment. Measurements were repeated at 2 hourly intervals throughout the day, and on each occasion the prevailing weather conditions were noted. Figures 3A.3 - 3A.10 give the results for temperature and humidity on the eight sampling days.

During the winter months, when conditions were overcast or there

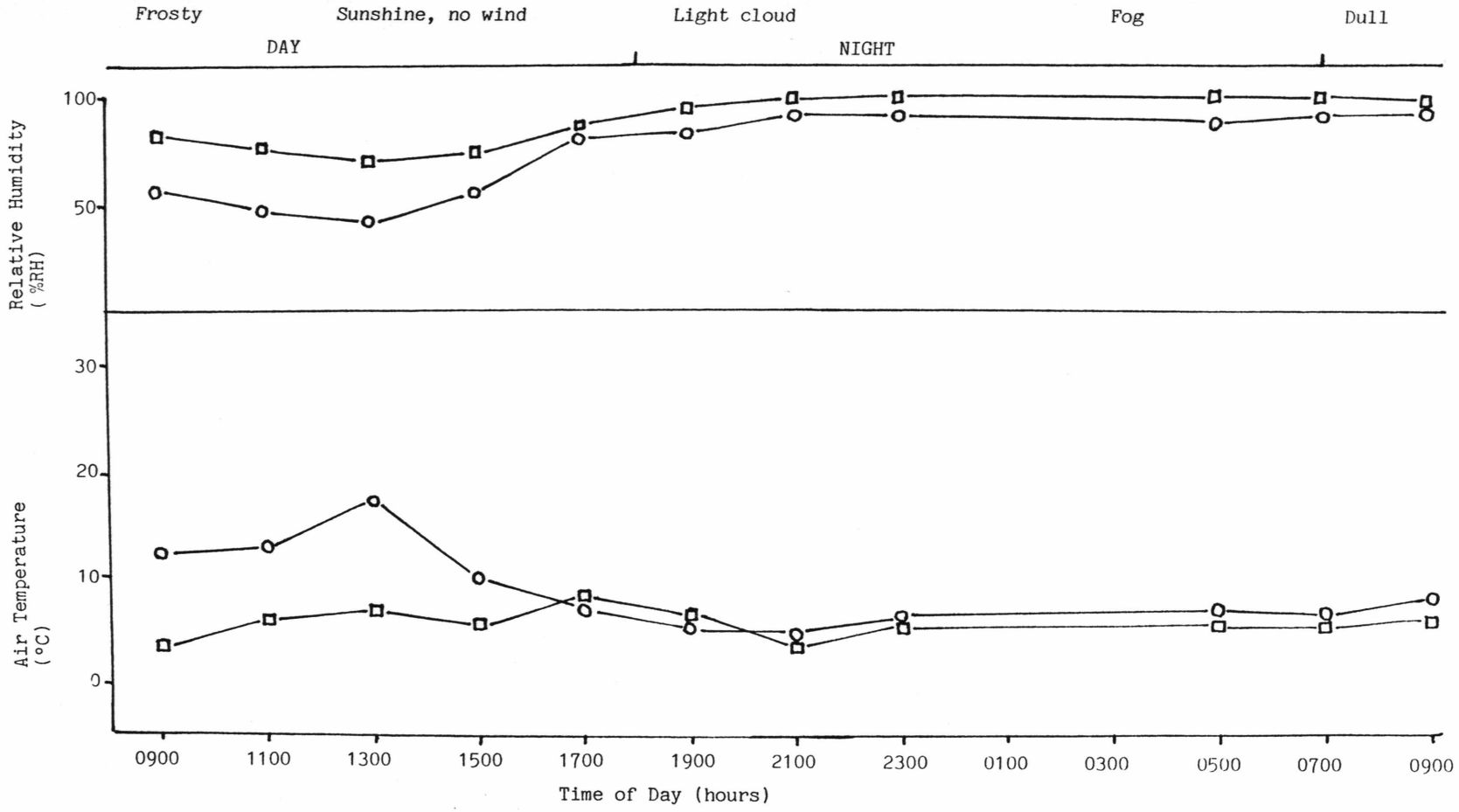


Figure 3A.3 Mean air temperature and relative humidity (n=5) in field (□) and tube (○).
Spot measurements taken at 2 hourly intervals 14/2/84 - 15/2/84. (No glasshouse due to equipment failure)

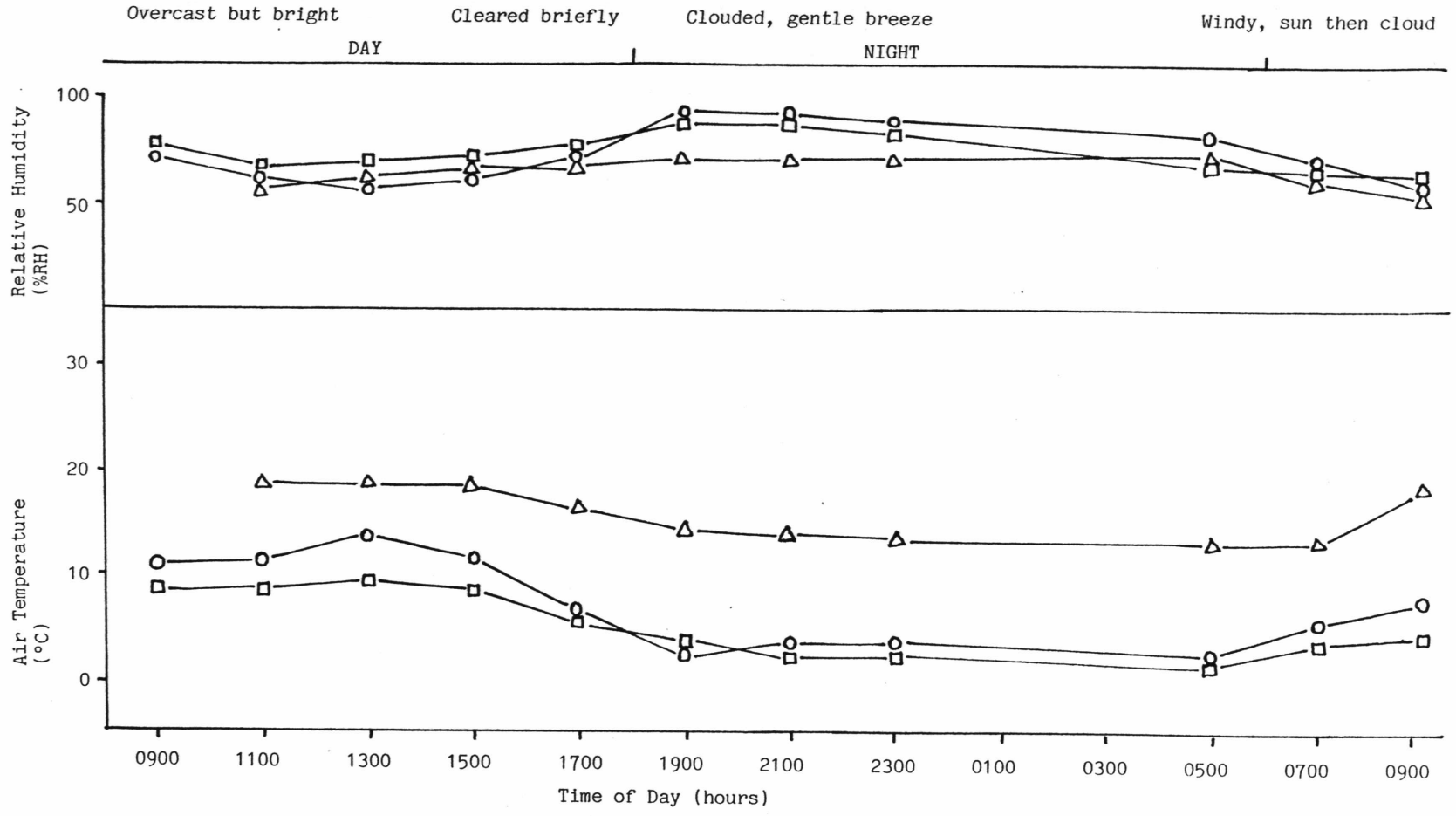


Figure 3A.4 Mean air temperature and humidity (n=5) in field (□), tube (○) and glasshouse (△). Spot measurements taken at 2 hourly intervals 7/3/84 - 8/3/84.

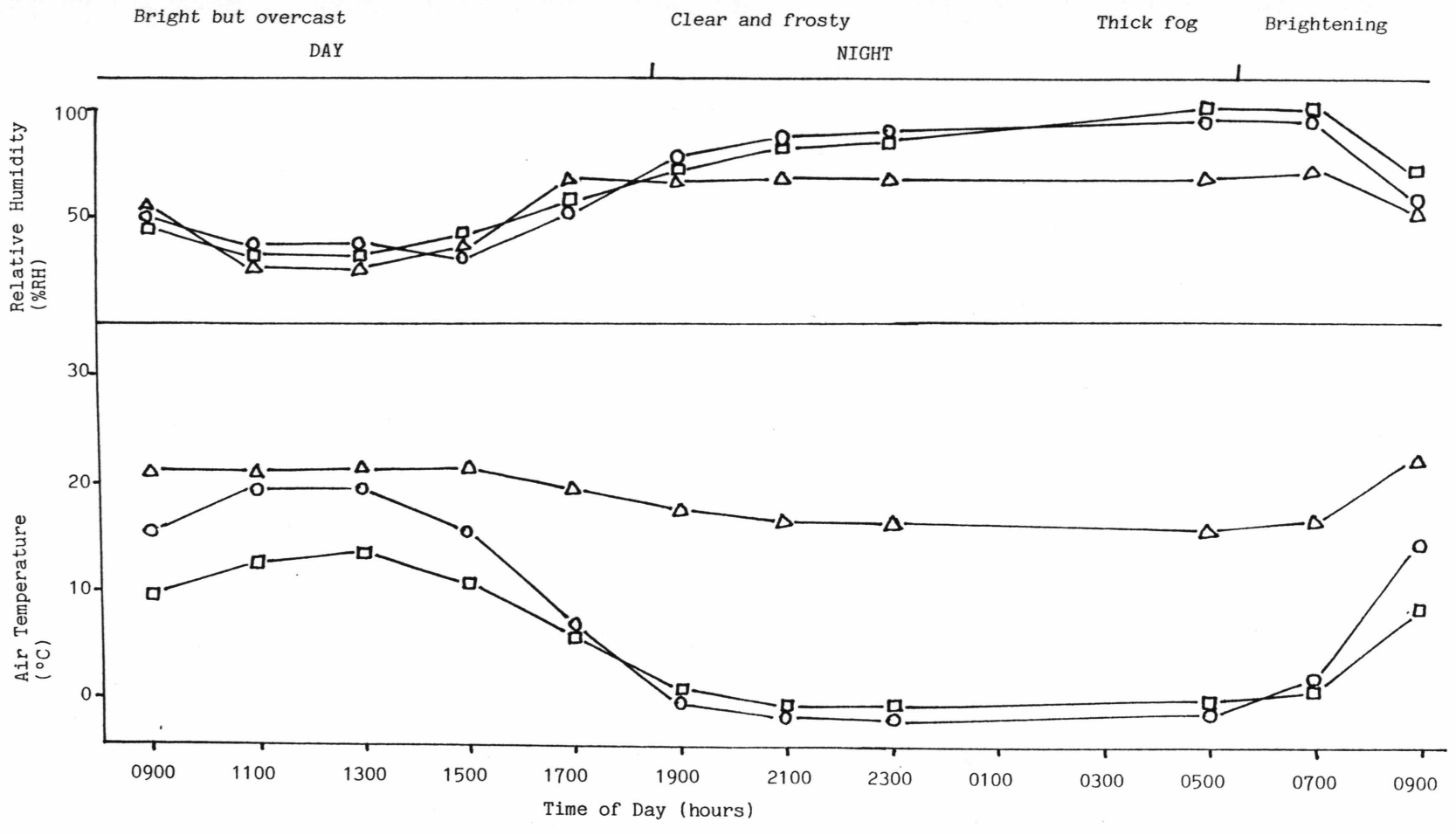


Figure 3A.5 Mean air temperature and humidity (n=5) in field (□), tube (○) and glasshouse (△). Spot measurements at 2 hourly intervals 22/3/84 - 23/3/84.

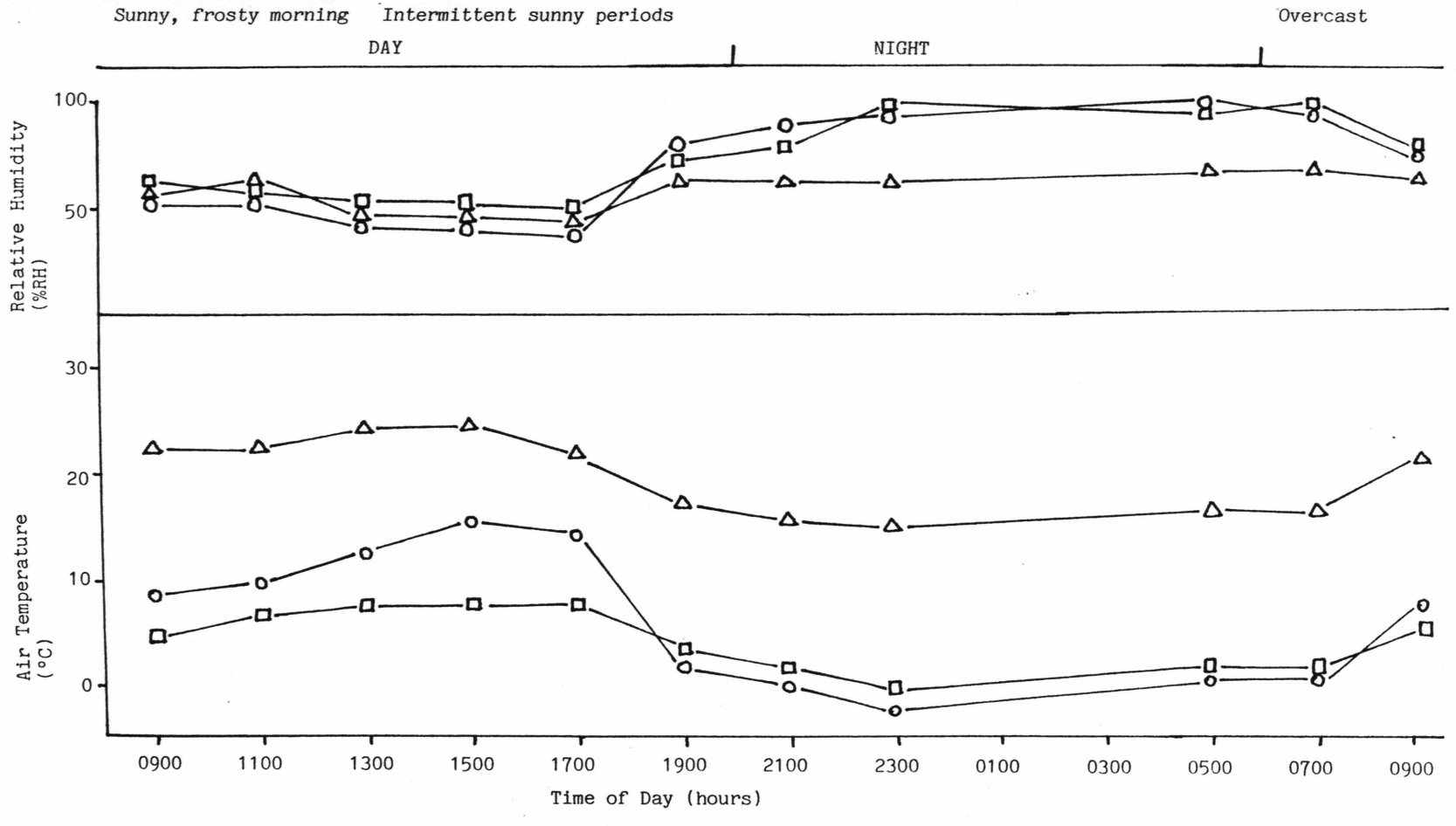


Figure 3A.6 Mean air temperature and humidity (n=5) in field (□), tube (○) and glasshouse (△). Spot measurements at 2 hourly intervals 4/4/84 - 5/4/84.

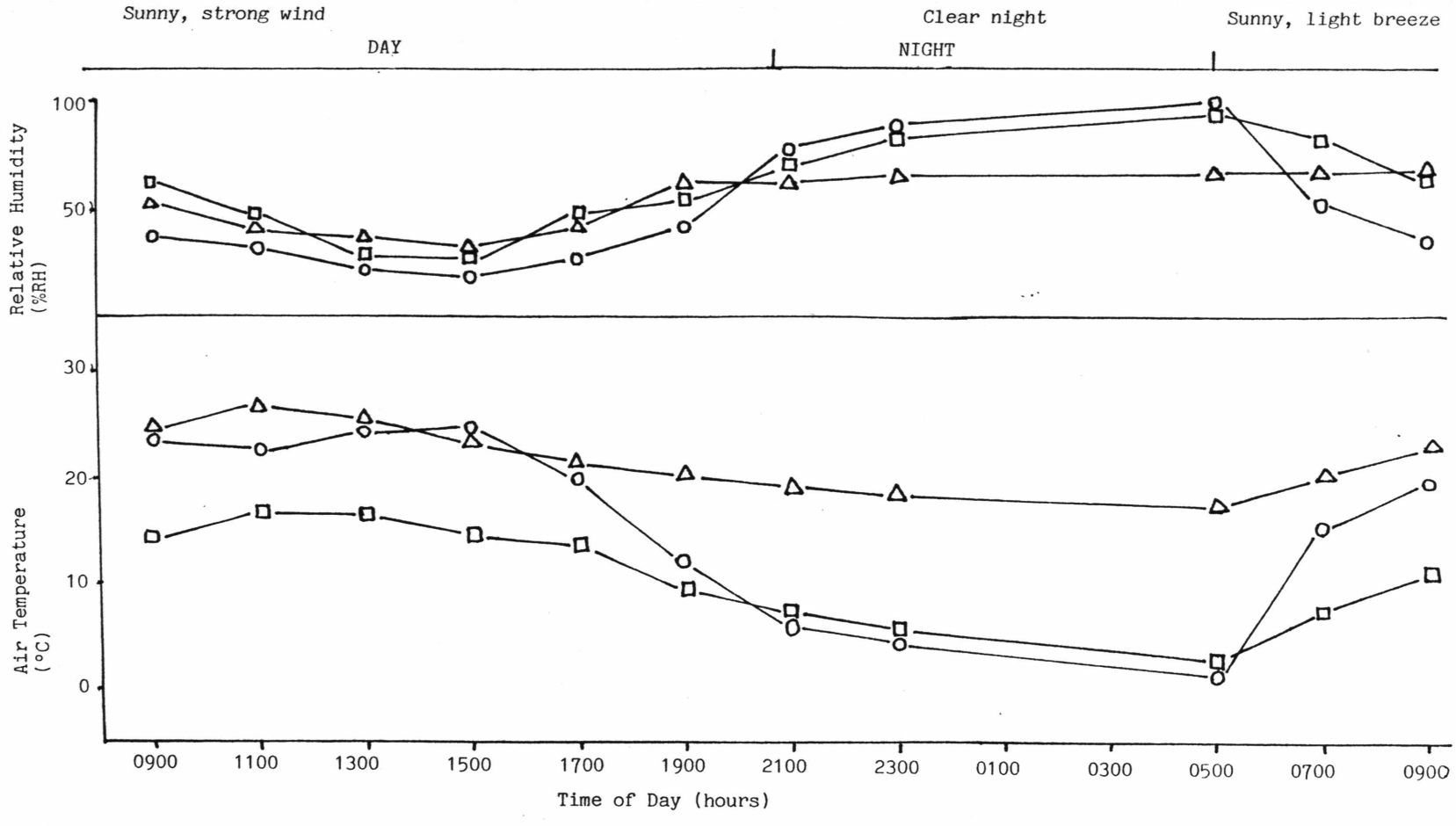


Figure 3A.7 Mean air temperature and relative humidity (n=5) in field (□), tube (○) and glasshouse (△). Spot measuremnts at 2 hourly intervals 27/4/84 - 28/8/84.

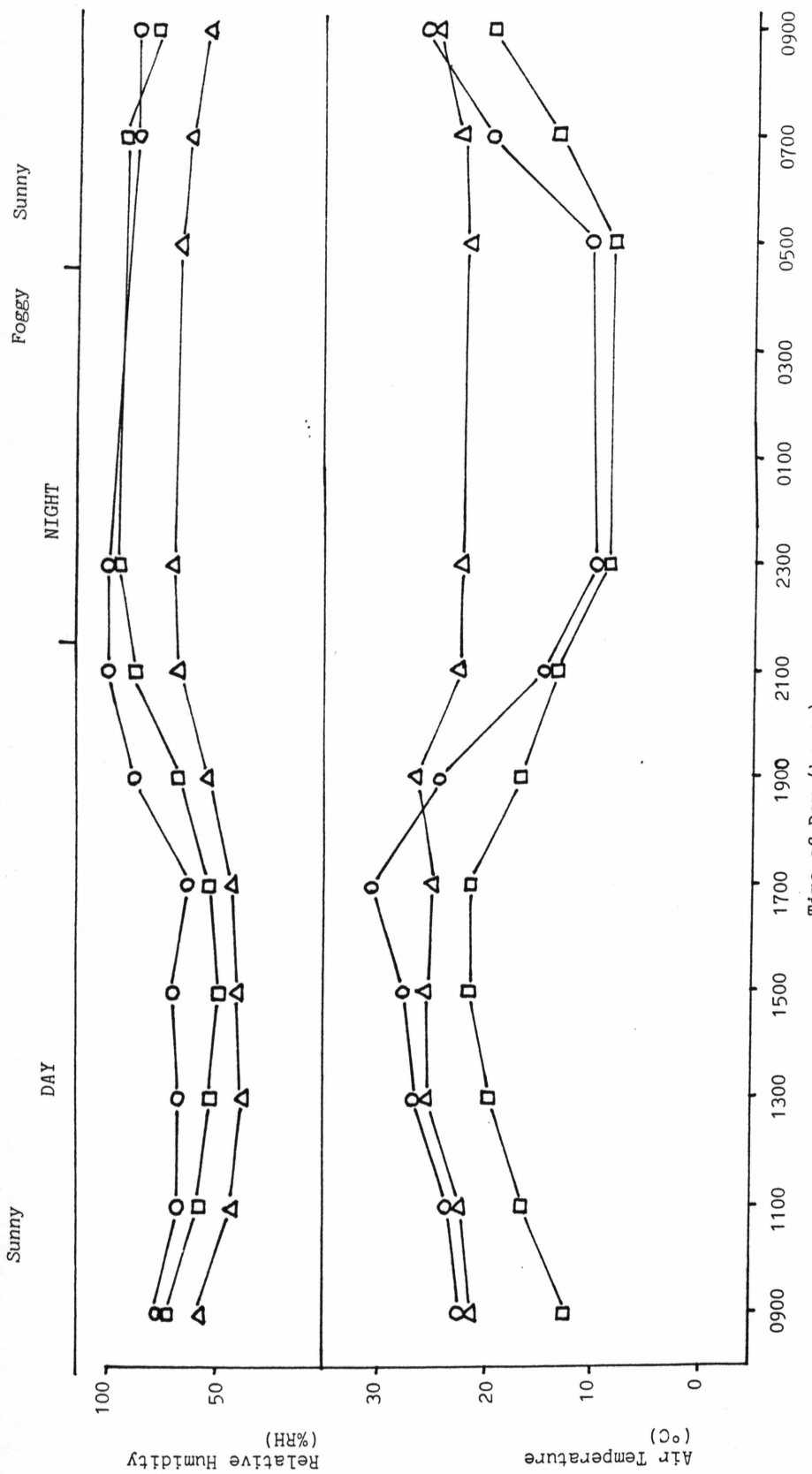


Figure 3A.8 Mean air temperature and relative humidity (n=5) in field (□), tube (○) and glasshouse (△). Spot measurements at 2 hourly intervals 30/5/84 - 31/5/84.

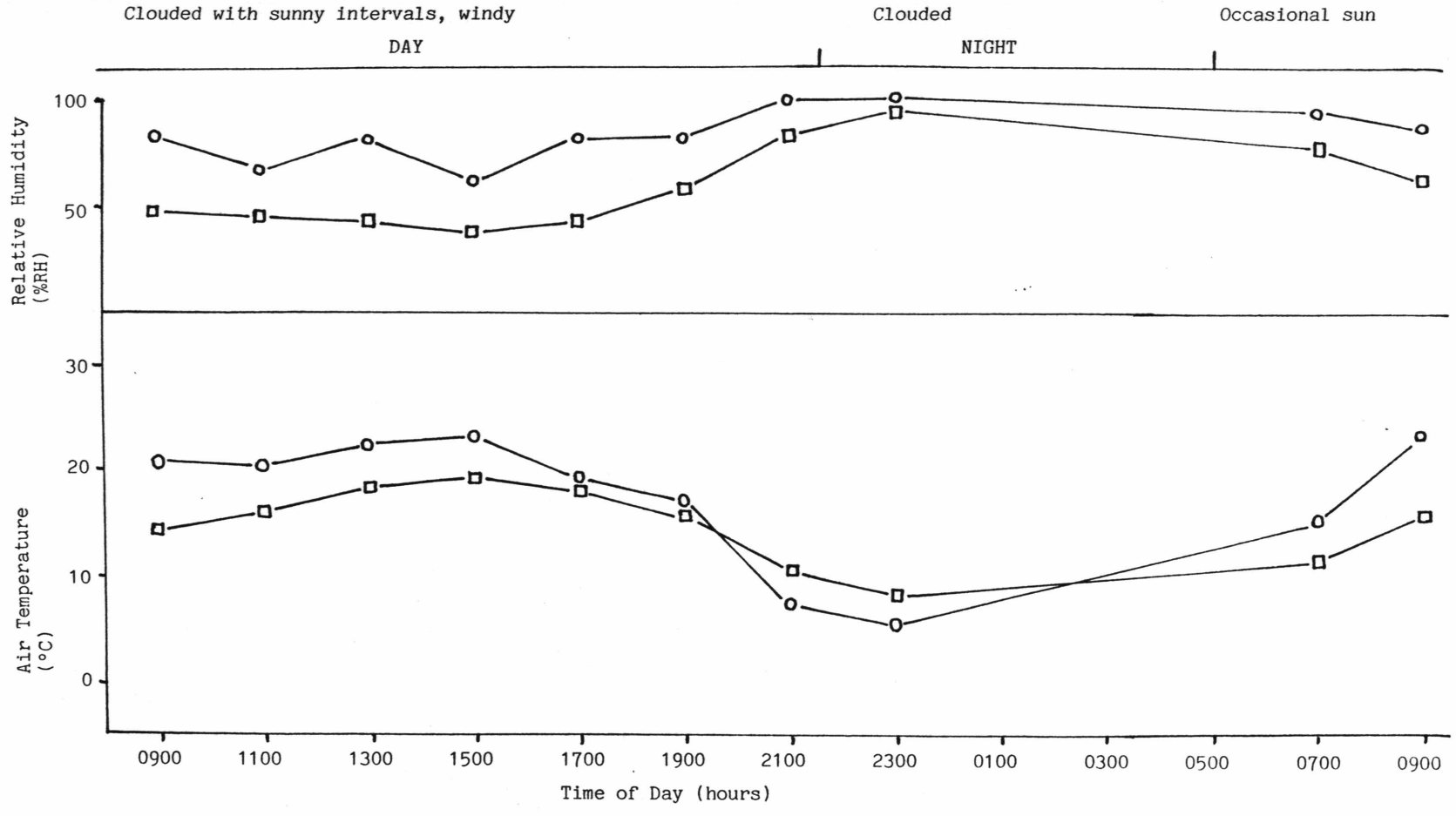


Figure 3A.9 Mean air temperature and relative humidity (n=5) in field (□) & tube (O). Spot measurements at 2 hourly intervals 3/7/84 - 4/7/84. (No glasshouse due to equipment failure).

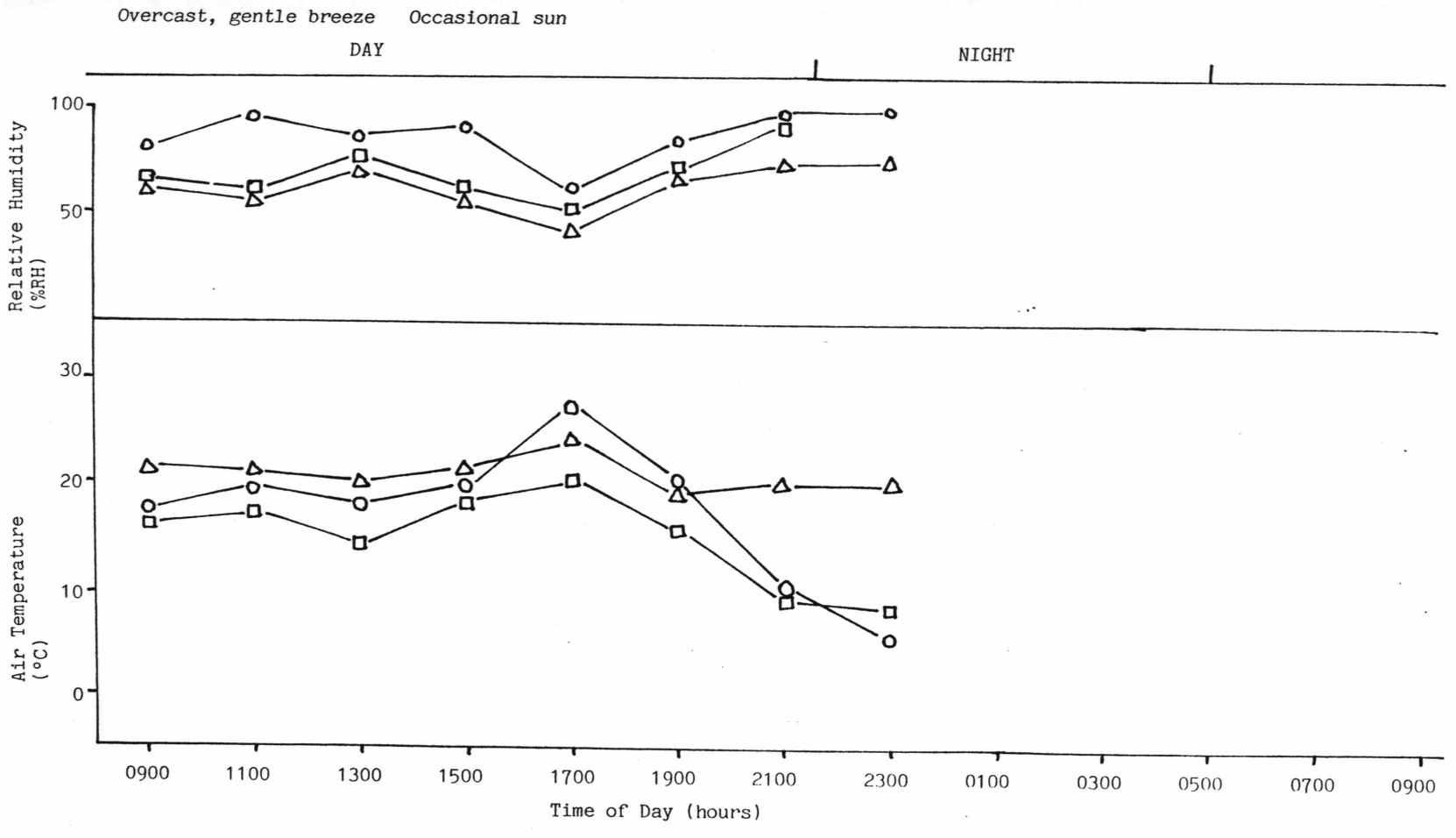


Figure 3A.10 Mean air temperature and relative humidity (n=5) in field (□), tube (○) and glasshouse (△). Spot measurements taken at 2 hourly intervals 19/7/84.

was a strong wind the relative humidity was similar in field, tube and glasshouse environments. Sunny conditions on the day in February increased the tube temperature to 10°C above that in the field, with a corresponding decrease in tube humidity, 42.9%RH compared with field humidity 71.2%RH. Tube temperature also increased above that in the field on overcast but bright winter days, on the day sampled at the end of March the maximum tube temperature, 19.9°C, was similar to the glasshouse temperature, 21.7°C. During frosty nights the tube temperature fell about 1.5°C below that in the field. Humidity in the field and tube was similar at night, both higher than in the glasshouse. For the days sampled in February and March the mean glasshouse temperature, 16.6 ±0.6°C, was about twice that in the field (4.6 ± 0.7°C) and tube (6.9 ± 1.2°C) environments. The mean humidity in field and tube environments, 76.7 ± 3.4%RH and 71.4 ± 3.5%RH respectively, were slightly higher than in the glasshouse (61.9 ± 2.8%RH).

On the day sampled at the end of April the maximum tube temperature, 24.5°C, was similar to that in the glasshouse, 26.7°C. Tube temperatures during the day continued to be similar to or greater than in the glasshouse during the summer months. Mean temperatures for the days sampled in May and July were as follows: field 15.2 ± 0.8°C, tube 19.0 ± 1.3°C, and glasshouse 22.3 ± 0.4°C. The tube temperature rose quickly after sunrise on sunny days but could fall below field temperature at sunset. For example on the day sampled at the end of April over the two hour period after sunrise the tube temperature rose by 12.4°C to 14.9°C, whereas the field temperature rose only 4.5°C to 7.3°C. At the beginning of July the tube temperature at night fell to over 2°C below field temperature.

During the summer days recorded humidity was higher in the tube than in the field and glasshouse. Trees were in leaf by mid-May and on days sampled after this time a rise in tube temperature was not accompanied by a corresponding decrease in humidity as seen in February. Humidity in the field and glasshouse were either similar or the humidity higher in the field. Mean humidity for tube, field and glasshouse environments for the days sampled in May and July were 84.6 ± 2.3%RH, 66.8 ± 3.4%RH and 58.4 ± 2.8%RH respectively. At night the field and tube humidity were similar and greater than in the glasshouse environment.

3A.4 Comparison Between Field, Tube and Glasshouse Environments.

3A.4a Radiation

Using data logging results for 54 days between August 1984-July 1985 the total daily radiation and maximum radiation for each day were compared for field and tube environments (table 3A.4). Comparison between field and glasshouse environments is discussed below. The mean difference between total daily radiation in the field and tube environments was 868 ±113$Wm^{-2}day^{-1}$. The actual reduction in radiation was seen to increase with increasing light intensity in the field (fig. 3A.11). The mean difference between maximum radiation in the field and tube environments was 129 ±18$Wm^{-2}hr^{-1}$, at radiation levels above about 500$Wm^{-2}hr^{-1}$ the difference appeared to increase with increasing light intensity in the field (fig. 3A.12).

Table 3A.4

Overall mean (±SE) total daily and maximum hourly radiation level for each day in field and tube environments (n=53).

	FIELD	TUBE	SIG.	TUBE AS % OF FIELD
DAILY TOTAL ($Wm^{-2}day^{-1}$)	3131±280	2263±188	*	73.5 ± 2.3
MAXIMUM ($Wm^{-2}hr^{-1}$)	473±32	344±20	***	75.7 ± 2.6

More limited data are available to compare the radiation levels in field and glasshouse; the data-logging results are confined to 23 days from June and July 1985. The total daily radiation was significantly ($P<0.05$) higher in the field (4806 ±337$Wm^{-2}day^{-1}$) than in the glasshouse (3811 ± 282$Wm^{-2}day^{-1}$). However the maximum radiation levels for each day in field (670 ± 36$Wm^{-2}hr^{-1}$) and glasshouse (596 ± 36$Wm^{-2}hr^{-1}$) were not significantly different. There was a 21.1 ± 0.8% decrease in total radiation and 11.2 ±1.6% decrease in maximum radiation in the glasshouse compared with the field.

3A.4b Temperature

The daily mean, maximum and minimum temperatures and the range in temperature i.e. the difference between maximum and minimum temperatures in field and tube were compared for 98 days between August 1984-July 1985 (table 3A.5). The mean daily and maximum temperature in the tube environment were significantly greater than in the field,

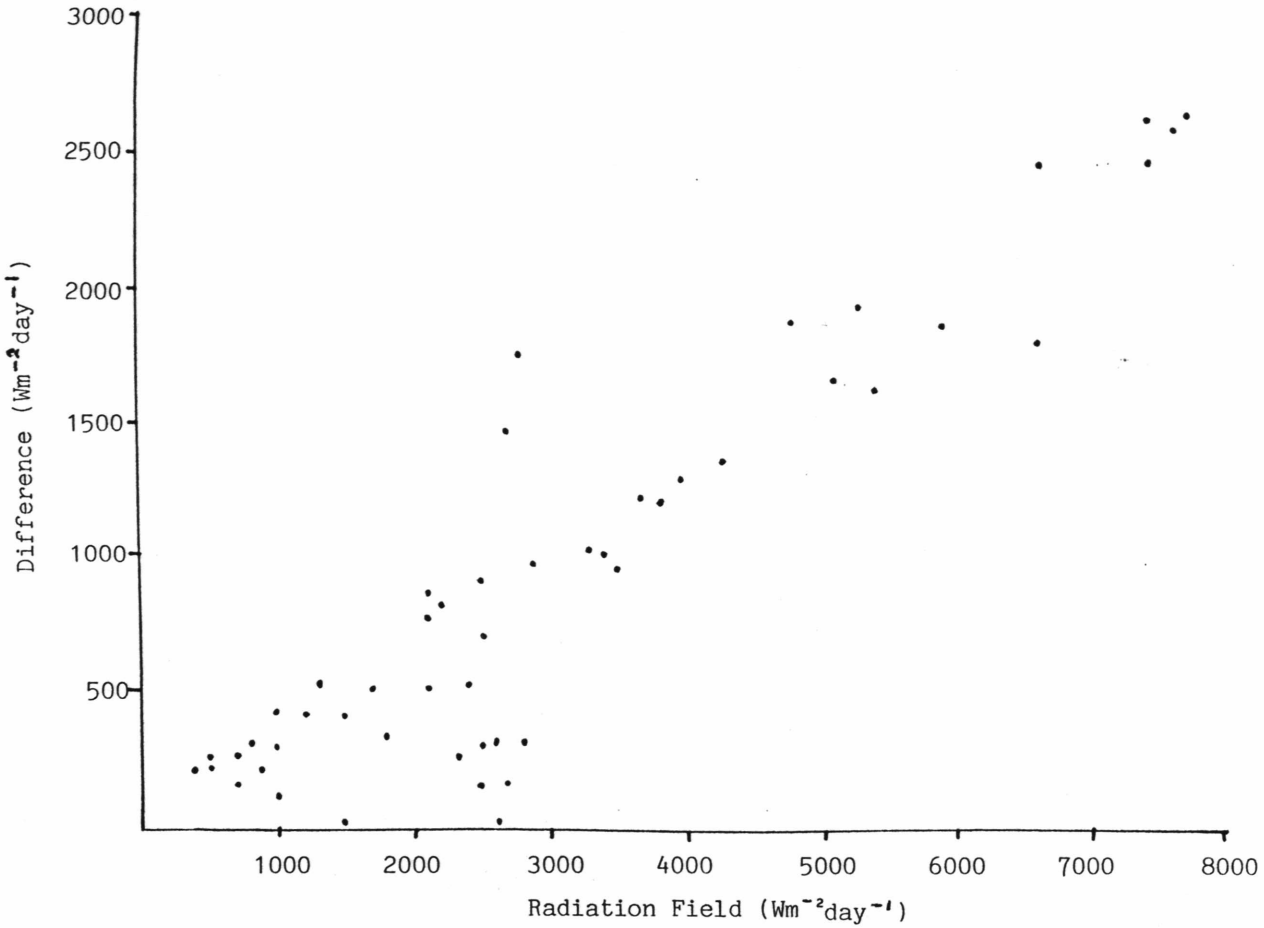


Figure 3A.11 Difference between total daily radiation in field and tube plotted against total daily radiation in the field. y= -150.0 + 0.348x *** r=0.917 83.8% of variance accounted for.

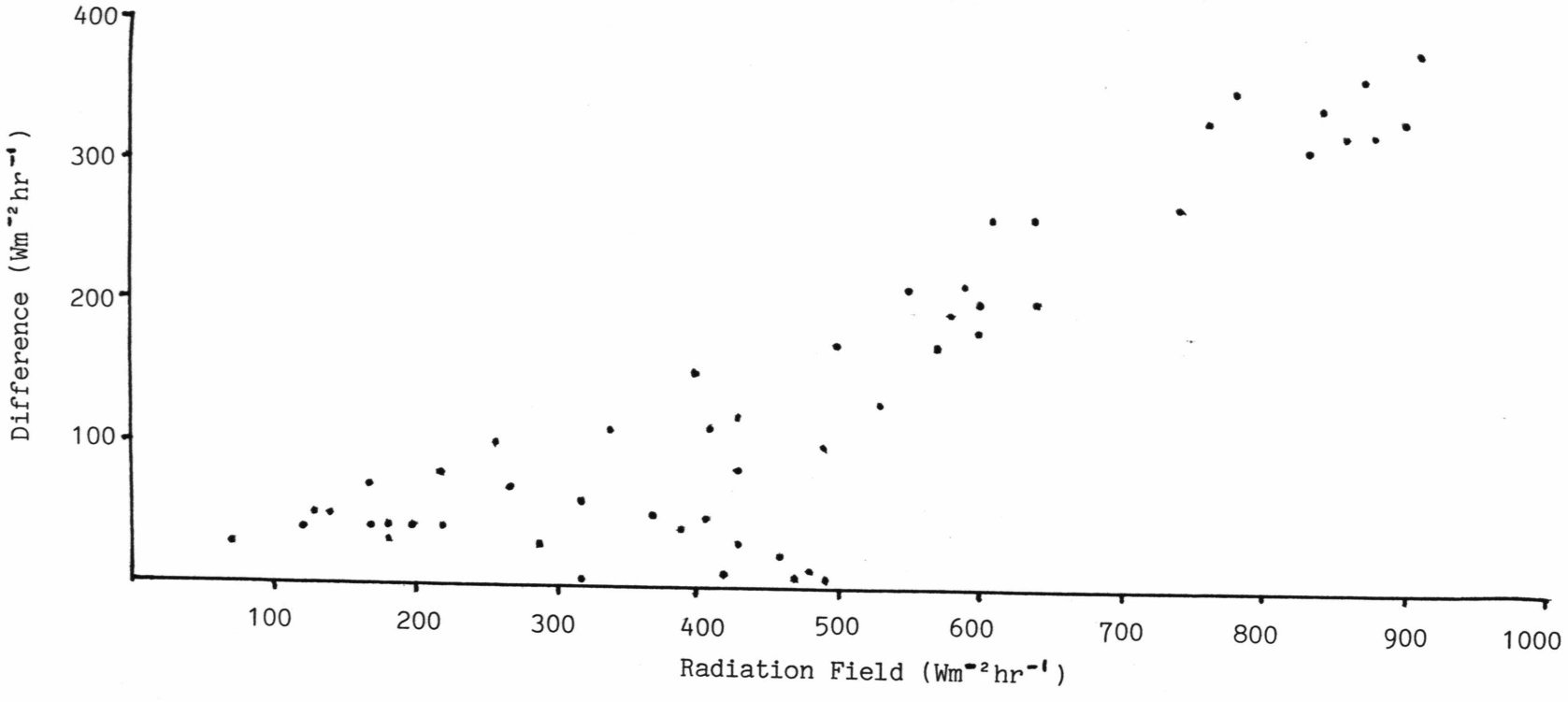


Figure 3A.12 Difference between maximum hourly radiation in field and tube plotted against maximum radiation in the field. For all readings: y = -63.2 + 0.433x *** r=0.869. For readings >500$Wm^{-2}hr^{-1}$: y = -100.1 + 0.516x*** r=0.938. For readings <500$Wm^{-2}hr^{-1}$: no significant linear relation r=0.009.

however the minimum temperatures were not significantly different. The range in temperature in the tube was approximately twice that in the field.

Table 3A.5

Mean daily temperature, mean maximum and minimum temperatures and mean range in temperature (±SE) in field and tube environments (n=98).

	FIELD	TUBE	SIGNIFICANCE
MEAN DAILY TEMP. (°C)	10.8 ±0.6	13.1 ± 0.7	*
MEAN MAXIMUM (°C)	15.5 ± 0.7	22.6 ± 0.9	***
MEAN MINIMUM (°C)	6.7 ± 0.5	6.1 ± 0.6	NS
MEAN RANGE (°C)	8.8 ± 0.3	16.5 ± 0.6	***

The data were then divided into two periods the winter and spring months, February to May (n=52) and the summer months June to September (n=46) (table 3A.6). In both periods the maximum temperature in the tube was significantly greater than in the field, and again the minimum temperatures were not significantly different. ~~A difference however can be seen in the mean range in temperature which was not significantly different between field and tube for the period February to May but during the summer months, June to September, the mean range was 8.9°C greater in the tube~~.

Table 3A.6

Mean daily temperature, mean maximum and minimum temperatures and mean range in temperature (±SE) in field and tube for two periods February-May (n=52) and June-September (n=46).

PERIOD		MEAN DAILY TEMP (°C)	MEAN MAXIMUM (°C)	MEAN MINIMUM (°C)	MEAN RANGE IN TEMP (°C)
FEB - MAY	FIELD	6.7±0.5	10.8±0.6	3.2±0.6	7.6±0.4
	TUBE	8.4±0.7	16.8±0.9	2.5±0.6	14.3±0.8
SIGNIFICANCE		NS	***	NS	***
JUNE - SEPT	FIELD	15.5±0.5	20.8±0.6	10.6±0.5	10.1±0.5
	TUBE	18.5±0.6	29.1±0.8	10.1±0.5	19.0±0.7
SIGNIFICANCE		***	***	NS	***

A similar comparison was made between field, tube and glasshouse environments for 35 days in June and July 1985 (table 3A.7). Mean temperature over this period was highest in the glasshouse and lowest in the field. The mean maximum temperatures in the tube and glasshouse were similar, however the mean minimum temperature in the glasshouse was much higher than in field and tube. The mean range in temperature in field and glasshouse were similar, however mean glasshouse temperatures were about 9°C higher than in the field. The range in temperature in the tube was 8-9°C greater than in the other two environments.

Table 3A.7

Mean daily temperature, mean maximum and minimum temperatures and mean range in temperature (±SE) in field, tube and glasshouse in June and July 1985 (n=35).

	FIELD	TUBE	GLASSHOUSE	SIG.	LSD (P0.05)
MEAN DAILY TEMP (°C)	15.7±0.5	18.8±0.6	23.6±0.3	***	1.4
MEAN MAXIMUM (°C)	20.6±0.6	28.9±0.8	30.0±0.7	***	2.0
MEAN MINIMUM (°C)	10.8±0.4	10.2±0.5	19.4±0.1	***	1.1
MEAN RANGE (°C)	9.8±0.5	18.7±0.8	10.6±0.7	***	1.9

3A.4c Humidity

The mean humidity in field and tube were also compared over a similar period, August 1984-July 1985. Overall the tube humidity was significantly higher than in the field, however division of the data into two periods, February to May and June to September, revealed that the difference in humidity occurred during the summer months only (table 3A.8), i.e. when the trees were in leaf. During the earlier period the trees came into leaf between the end of April and mid-May.

Humidity in field, tube and glasshouse were compared in June and July 1985 (n=35 days). The mean humidity in field (58.1±2.6%), glasshouse (64.5±1.5%) and tube (92.6±1.6%) were very significantly different (LSD(P0.05)5.6).

Table 3A.8

Mean daily humidity (%RH) in field and tube environments.

MONTHS	n	FIELD	TUBE	SIG.
AUGUST - JULY	98	74.6 ± 1.8	88.7 ± 1.0	***
FEBRUARY - MAY	52	83.0 ± 1.8	85.4 ± 1.5	NS
JUNE - SEPTEMBER	46	65.1 ± 2.7	92.4 ± 1.3	***

3A.5 Relationship Between Microclimate and Meteorological Data (August 1984 - July 1985)

In addition to the spot readings data for shortwave radiation (Wm^{-2}), temperature (°C) and humidity (%RH) recorded using the microcomputer data-logging system were related to meteorological records collected at the Meteorological Station, Wye College, using the least squares linear regression analysis. From the relationships thus obtained it was possible to derive estimates of the three environmental variables, total daily radiation, mean daily temperature and mean daily humidity for the experimental periods. Data for the field, tube and glasshouse environments are in the form of hourly means,for temperature and humidity these were averaged to obtain the daily mean value for the period midnight - midnight, for shortwave radiation the daily total was calculated over the same period.

3A.5a Radiation

Data for daily total shortwave radiation for the field environment covers 76 days during the period 25/8/84-19/7/85, for tube 53 days from a similar period 25/8/84-6/6/85 and glasshouse 23 days between 8/6/85-19/7/85. The Meteorological Station records total shortwave radiation in $mWcm^{-2}day^{-1}$, this had to be multiplied by 10 to give Wm^{-2} to make it compatible with data-logging results.

For each environment there was a strong positive linear relationship between the total daily radiation recorded and meteorological data (fig. 3A.13). The linear regression coefficients used in predictive equations are given in table 3A.9.

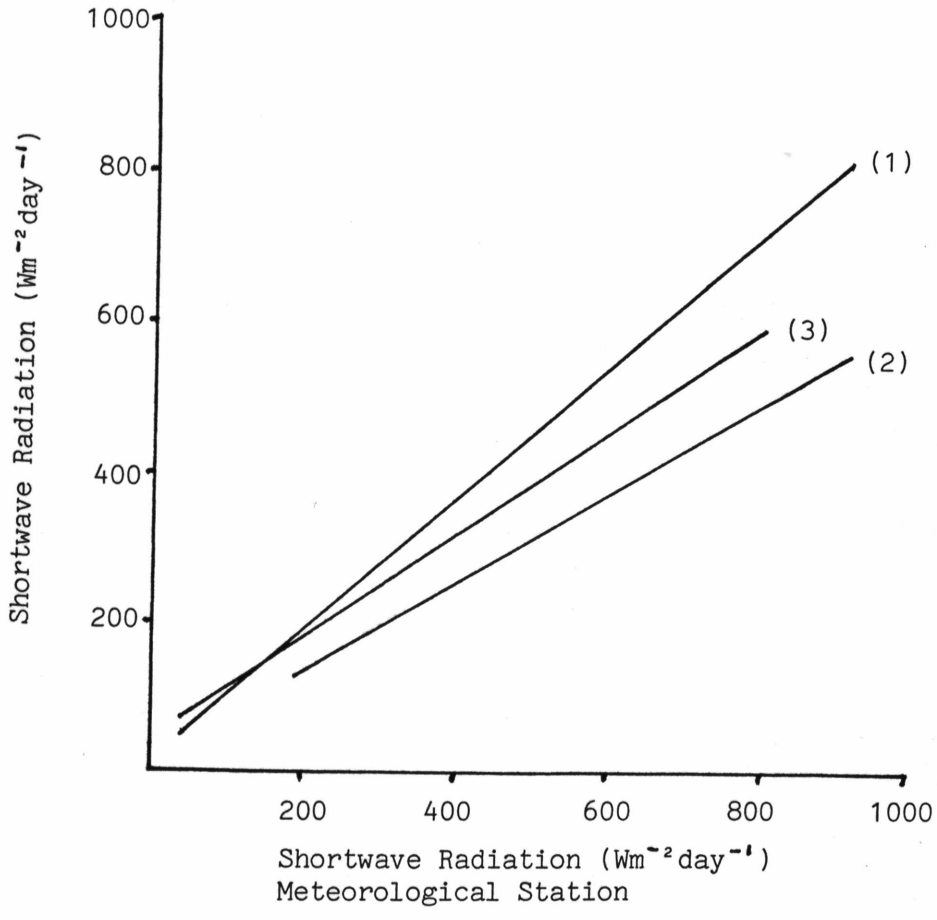


Figure 3A.13 Relationship between total shortwave radiation in field (1), tube (2) and glasshouse (3) and shortwave radiation recorded at the Meteorological station, Wye.

Table 3A.9

Linear regression coefficients relating total radiation ($Wm^{-2}day^{-1}$) in the field, tube and glasshouse (y) to shortwave radiation recorded at the Meteorological Station, Wye (x) where y=a+bx.

ENVIRONMENT	n	CONSTANT (a)	SLOPE (b)	r	t_{n-2}
FIELD	76	142 ± 121	0.880 ± 0.027	0.968	***
TUBE	53	340 ± 127	0.569 ± 0.032	0.930	***
GLASSHOUSE	23	-226 ± 318	0.756 ± 0.057	0.945	***

3A.5b Temperature

Daily mean temperature in field and tube, derived from data-logging data for 98 days between August 1984-July 1985, were related to the dry bulb temperature (°C) taken at 0900hr GMT at the Meteorological Station. A similar analysis was carried out for the mean daily temperature in the glasshouse for 35 days from June and July 1985 (fig. 3A.14). There was a strong positive relationship between field, tube and glasshouse temperature and the Meteorological data (table 3A.10), for field 96.2%, tube 93.7% and glasshouse 68.0% of the variation was accounted for by these regression equations.

Table 3A.10

Linear regression coefficients relating mean daily temperature (°C) in field, tube and glasshouse (y) to dry bulb temperature 0900hr GMT (x) recorded at the Meteorological Station, Wye where y=a+bx.

ENVIRONMENT	n	CONSTANT (a)	SLOPE (b)	r	t_{n-2}
FIELD	98	0.794 ± 0.230	0.926 ± 0.019	0.981	***
TUBE	98	1.460 ± 0.352	1.075 ± 0.028	0.968	***
GLASSHOUSE	35	15.447 ± 0.978	0.515 ± 0.060	0.830	***

3A.5c Humidity

Daily mean humidity for field and tube was related to several meteorological variables for 98 days between August 1984-July 1985. For the field environment the mean humidity was most closely related to humidity at 0900hr GMT, total shortwave radiation, evaporation and

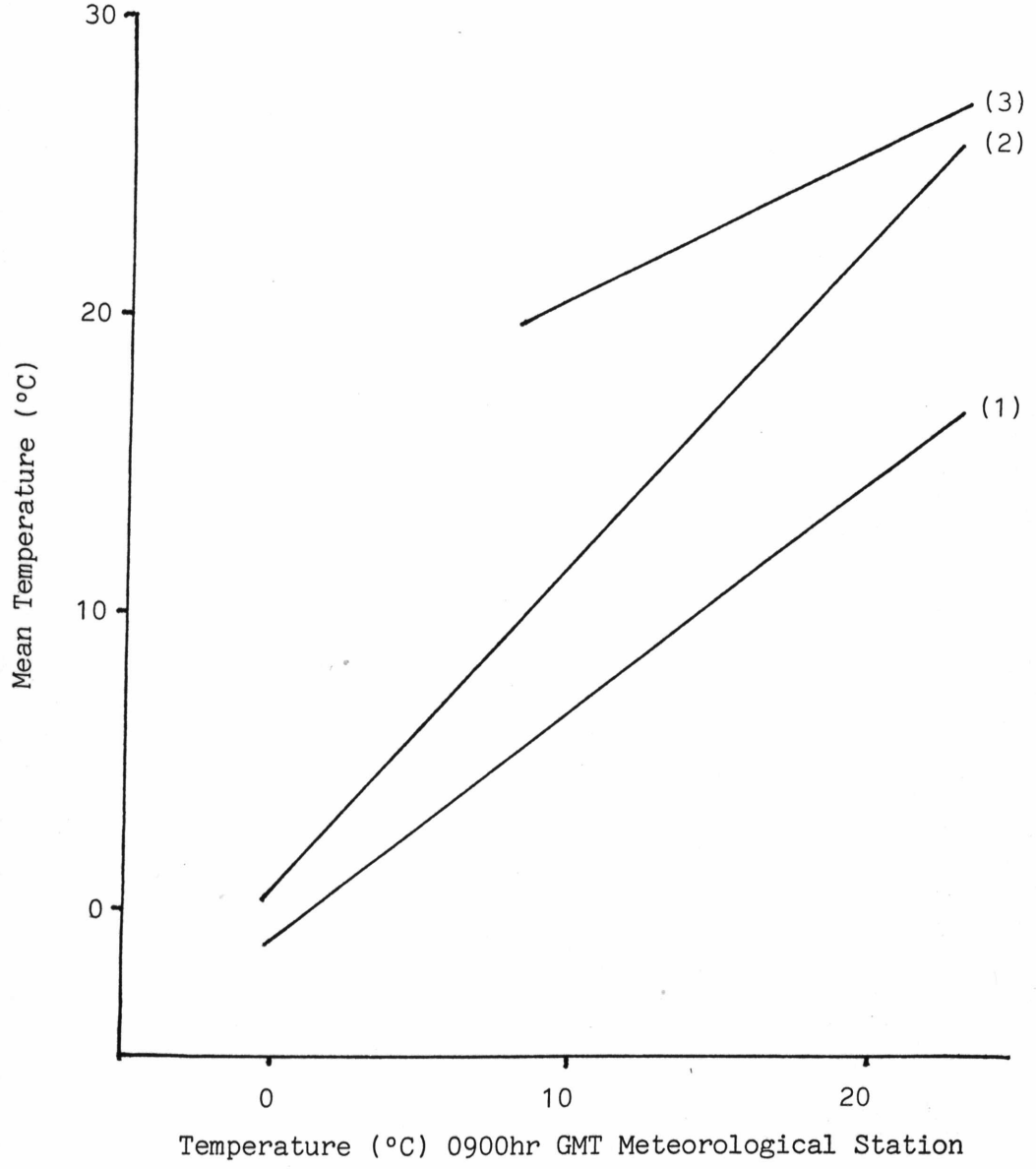


Figure 3A.14 Relationship between mean temperature in field (1), tube (2) and glasshouse (3) and temperature 0900hr GMT recorded at the Meteorological Station, Wye.

the hours of sunshine (table 3A.11). A slight improvement can be made in determining mean humidity in the field when humidity at 0900hr and total shortwave radiation are considered together, with the resulting multiple regression equation as follows:

$y = 38.990 + 0.631x_1 - 0.0033x_2 \quad r = 0.863$

where y = mean humidity in the field (%RH)

x_1 = humidity 0900hr GMT (%RH)

x_2 = total shortwave radiation ($Wm^{-2}day^{-1}$)

The addition of further variables e.g. evaporation, hours of sunshine and temperature at 0900hr to the regression equation gave no further increase in the correlation coefficient (r). Mean tube humidity was not closely related ($r<0.5$) to any of the meteorological variables chosen for study (table 3A.12).

Daily mean humidity in the glasshouse for 35days from June and July 1985 was related to the same meteorological variables (table 3A.13). The mean humidity in the glasshouse was most closely related to the humidity at 0900hr GMT. There were also weak correlations with shortwave radiation, hours of sunshine and minimum temperature.

3A.6 Microclimate Data Derived from Meteorological Data for the Period May 1983 - August 1985

A summary of the meteorological data for the period May 1983 to August 1985 is given in table 3A.14. Using the relationships derived in the preceeding sections between microclimate and meteorological data estimates were made of monthly means for total daily radiation (table 3A.15) and mean daily air temperature (table 3A.16) for field, tube and glasshouse environments, as well as for mean daily humidity for the field and glasshouse environments (table 3A.17). During some of the winter months the estimated monthly mean total daily radiation in the tube is slightly higher than in the field. This apparent anomaly in radiation level (fig. 3A.15) occurred only during the winter months and may have been due to a combination of the low angle of the sun in the sky and the corrugated structure of the tube material, possibly giving rise to a light scattering effect.

Caution must be applied to the use of such computed values. Errors arise in the calculation of the regression equation, thus 95% confidence intervals are given for each calculated value. Care must also be taken to apply the equations to data within the range used to calculate the regression equations. Tabulated values marked * have been calculated including values outside the appropriate range, and must therefore be

	Constant	Slope	r	t	% Variance accounted for
Humidity 0900hr (%RH)	3.16	0.936	0.811	***	65.4
Temperature 0900hr (°C)	91.06	-1.519	0.506	***	24.8
Maximum Temperature (°C)	93.71	-1.322	0.454	***	19.8
Minimum Temperature (°C)	81.22	-0.982	0.282	**	7.0
Shortwave Radiation ($Wm^{-2}day^{-1}$)	98.29	-0.0063	0.749	***	55.6
Rainfall (mm)	73.94	0.435	0.101	NS	
Hours of Sunshine	89.95	-2.887	0.688	***	46.8
Evaporation (mm)	91.2	-8.25	0.710	***	49.9

Table 3A.11 Linear regression coefficients relating mean daily humidity in the field to several meteorological parameters, recorded at the Meteorological station, Wye.

	Constant	Slope	r	t	% Variance accounted for
Humidity 0900hr (%RH)	76.78	0.156	0.237	*	4.7
Temperature 0900hr (°C)	82.0	0.614	0.360	***	12.0
Maximum Temperature (°C)	81.06	0.526	0.318	**	9.2
Minimum Temperature (°C)	82.32	0.955	0.482	***	22.4
Shortwave Radiation ($Wm^{-2}day^{-1}$)	89.33	-0.0002	0.037	NS	
Rainfall (mm)	88.01	0.456	0.178	NS	2.2
Hours of Sunshine	91.55	-0.542	0.228	*	4.2
Evaporation (mm)	91.22	-0.566	0.091	NS	

Table 3A.12 Linear regression coefficients relating mean daily humidity in the tube to several meteorological parameters, recorded at the Meteorological station, Wye.

	Constant	Slope	r	t	% variance accounted for
Humidity 0900hr	27.22	0.546	0.847	***	70.9
Temperature 0900hr	69.91	-0.342	0.131	NS	
Maximum Temperature (°C)	72.73	-0.432	0.158	NS	
Minimum Temperature (°C)	47.26	1.655	0.526	**	25.5
Shortwave Radiation (Wm^{-2} day^{-1})	81.86	-0.0032	0.630	***	37.9
Rainfall (mm)	63.74	0.296	0.209	NS	1.5
Hours of Sunshine	72.33	-1.042	0.543	***	27.4
Evaporation (mm)	70.11	-1.740	0.268	NS	4.3

Table 3A.13 Linear regression coefficients relating mean daily humidity in the glasshouse to several meteorological parameters, recorded at the Meteorological station, Wye.

1983	A	B	C	D	E	F	G	H	I
May	4442	11.3	14.7	6.8	75.7	11.2	11.6	3.4	4.9
June	5912	15.4	18.9	11.2	73.7	16.5	15.4	1.4	6.8
July	7634	20.5	24.7	14.0	71.9	20.6	18.4	0.9	8.6
Aug	4425	18.6	21.8	13.6	71.8	18.5	17.5	0.5	6.6
Sept	2262	14.9	18.4	10.6	77.7	14.0	15.5	1.4	4.0
Oct	1346	11.3	14.6	7.2	83.6	10.1	13.2	1.6	3.8
Nov	487	7.6	10.8	4.9	89.0	7.4	9.9	1.2	1.9
Dec	189	5.8	8.4	3.0	87.1	4.7	7.0	2.6	2.0
1984									
Jan	344	4.4	7.4	1.4	85.1	3.4	5.8	4.2	2.8
Feb	542	3.7	6.7	1.4	82.8	3.4	5.1	0.9	2.8
March	713	5.4	7.6	2.2	82.1	4.4	5.7	2.6	2.4
April	2722	9.2	12.2	3.0	61.1	8.1	7.8	0.3	6.8
May	4173	9.8	12.8	6.7	77.8	11.3	10.8	1.8	4.5
June	5466	15.8	19.3	9.2	71.9	16.8	15.0	0.9	7.2
July	4822	17.7	21.6	11.4	67.0	18.5	16.6	0.6	6.7
Aug	4138	17.8	22.3	12.8	78.4	18.0	17.3	0.9	5.9
Sep	2344	14.3	17.4	11.0	81.0	13.6	15.4	1.6	3.1
Oct	1649	11.7	15.0	7.7	87.3	10.8	12.9	4.0	3.1
Nov	936	9.3	12.1	6.7	86.5	8.2	11.0	3.3	2.1
Dec	566	5.3	8.6	2.5	90.3	4.8	8.0	3.0	1.7
1985									
Jan	703	-0.3	3.0	-3.2	99.6	1.6	4.2	1.9	1.4
Feb	1649	1.7	4.7	-1.1	80.3	1.2	3.8	3.8	3.3
March	2209	4.1	8.0	1.4	84.1	3.5	5.2	1.7	3.0
April	3721	9.1	12.8	4.7	73.3	7.8	8.8	1.5	4.7
May	4476	12.1	15.2	7.4	72.2	11.5	11.1	1.1	5.2
June	4688	13.9	17.1	9.6	71.7	14.2	14.3	3.3	5.2
July	5306	18.0	21.1	12.4	69.4	17.9	16.9	1.4	7.8
Aug	3675	16.0	19.1	11.3	76.3	14.9	16.0	2.8	6.4

A Shortwave radiation ($Wm^{-2}day^{-1}$)
B Dry bulb temperature 0900hr GMT (°C)
C Maximum temperature (°C)
D Minimum temperature (°C)
E Humidity 0900hr GMT (%RH)
F Soil temperature 10cm (°C)
G Earth temperature 50cm (°C)
H Rainfall (mm)
I Hours of sunshine

Table 3A.14 Monthly means of meteorological data for the three year study period.

	FIELD		TUBE		GLASSHOUSE	
1983						
May	4051 ± 119		2867 ± 155		3132 ± 222	
June	5344 ± 156		3704 ± 213		4243 ± 206	
July	6860 ± 226		4684 ± 303		5545 ± 334	
Aug	4036 ± 121		2858 ± 155		3119 ± 222	
Sep	2132 ± 149		1627 ± 157		1484 ± 412	
Oct	1326 ± 182		1106 ± 190		791 ± 510	*
Nov	570 ± 218		617 ± 230		142 ± 604	*
Dec	380 ± 231	*	447 ± 245	*		
1984						
Jan	445 ± 224	*	536 ± 237	*	34 ± 620	*
Feb	619 ± 216		648 ± 228		184 ± 598	*
March	769 ± 208		756 ± 219		313 ± 579	*
April	2537 ± 135		1889 ± 146		1832 ± 365	
May	3814 ± 119		2714 ± 149		2929 ± 238	
June	4952 ± 142		3450 ± 192		3906 ± 195	
July	4385 ± 126		3084 ± 167		3419 ± 196	
Aug	3783 ± 119		2694 ± 148		2902 ± 241	
Sep	2205 ± 146		1674 ± 154		1546 ± 403	
Oct	1593 ± 170		1278 ± 178		1021 ± 477	*
Nov	966 ± 199		872 ± 208		482 ± 555	*
Dec	640 ± 215		662 ± 226		202 ± 596	*
1985						
Jan	761 ± 209		740 ± 220		305 ± 580	*
Feb	1593 ± 170		1278 ± 178		1021 ± 477	*
March	2086 ± 150		1597 ± 158		1444 ± 417	
April	3416 ± 119		2457 ± 142		2587 ± 273	
May	4081 ± 121		2887 ± 156		3158 ± 220	
June	4267 ± 124		3007 ± 163		3318 ± 209	
July	4811 ± 137		3359 ± 186		3675 ± 195	
Aug	3376 ± 119		2431 ± 141		2552 ± 276	

Table 3A.15 Total daily shortwave radiation ($Wm^{-2}day^{-1}$) in the field, tube and glasshouse environments; computed monthly mean values and 95% confidence limits. * - see text.

	FIELD	TUBE	GLASSHOUSE	
1983				
May	11.2 ± 0.2	17.3 ± 0.3	23.0 ± 0.7	
June	15.0 ± 0.3	21.8 ± 0.4	25.2 ± 0.4	
July	19.8 ± 0.4	28.0 ± 0.6	28.2 ± 0.7	
Aug	18.0 ± 0.3	24.9 ± 0.5	26.7 ± 0.5	
Sep	14.6 ± 0.2	21.2 ± 0.4	24.9 ± 0.4	
Oct	11.2 ± 0.2	17.1 ± 0.3	22.9 ± 0.7	
Nov	7.8 ± 0.2	13.1 ± 0.4	21.0 ± 1.1	*
Dec	6.2 ± 0.3	10.5 ± 0.4	19.8 ± 1.3	*
1984				
Jan	4.9 ± 0.3	9.4 ± 0.5	19.2 ± 1.5	*
Feb	4.2 ± 0.3	8.7 ± 0.5	18.9 ± 1.5	*
March	5.8 ± 0.3	9.6 ± 0.4	19.4 ± 1.3	*
April	9.3 ± 0.2	14.6 ± 0.3	21.7 ± 0.9	
May	9.9 ± 0.2	15.2 ± 0.3	22.0 ± 0.8	
June	15.4 ± 0.3	22.2 ± 0.4	25.4 ± 0.4	
July	17.2 ± 0.3	24.7 ± 0.5	26.6 ± 0.4	
Aug	17.3 ± 0.3	25.4 ± 0.5	26.9 ± 0.5	
Sep	14.0 ± 0.2	20.2 ± 0.4	24.4 ± 0.4	
Oct	11.6 ± 0.2	17.6 ± 0.3	23.2 ± 0.6	
Nov	9.4 ± 0.2	14.5 ± 0.3	21.7 ± 0.9	
Dec	5.7 ± 0.3	10.7 ± 0.4	19.9 ± 1.4	*
1985				
Jan	0.5 ± 0.4	4.7 ± 0.7	17.0 ± 2.0	*
Feb	2.4 ± 0.4	6.5 ± 0.6	18.8 ± 1.8	*
March	4.6 ± 0.3	10.1 ± 0.5	19.6 ± 1.5	*
April	9.2 ± 0.2	15.2 ± 0.3	22.0 ± 0.9	
May	12.0 ± 0.2	17.8 ± 0.3	23.3 ± 0.6	
June	13.7 ± 0.2	19.8 ± 0.3	24.2 ± 0.5	
July	17.5 ± 0.3	24.1 ± 0.5	26.3 ± 0.5	
Aug	15.6 ± 0.3	22.0 ± 0.4	25.3 ± 0.4	

Table 3A.16 Mean daily air temperature (°C) in field, tube and glasshouse environments; computed monthly mean values and 95% confidence limits. * - see text.

	FIELD		GLASSHOUSE	
1983				
May	72.1	2.1	68.5	1.8
June	66.0	3.1	67.5	1.7
July	59.2	4.8	66.5	1.7
August	69.7	2.1	66.4	1.7
September	80.5	2.9	69.6	2.0
October	87.3	3.4	72.9	2.5
November	93.5	4.0 *	75.8	3.0
December	93.3	4.4 *	74.8	2.8
1984				
January	91.5	4.4 *	73.7	2.6
February	89.4	4.3 *	72.4	2.4
March	88.4	4.2	72.0	2.3
April	68.6	4.5	60.6	1.8
May	74.3	2.1	69.7	2.0
June	66.3	2.5	66.5	1.7
July	65.3	2.3	63.8	1.6
August	74.8	2.1	70.0	2.0
September	82.4	2.6	71.4	2.2
October	88.6	3.0	74.9	2.8
November	90.5	3.7	74.4	2.7
December	94.1	3.9 *	76.5	3.1
1985				
January	99.5	3.9	81.6	4.1 *
February	84.2	3.3	71.1	2.2
March	84.4	2.7	73.1	2.5
April	72.9	2.2	67.2	1.7
May	69.8	2.1	66.6	1.7
June	68.8	2.1	66.4	1.7
July	65.3	2.4	65.1	1.6
August	75.0	2.1	68.9	1.9

Table 3A.17 Mean daily relative humidity (%RH) in field and glasshouse environments; computed monthly mean values and 95% confidence limits. * - see text.

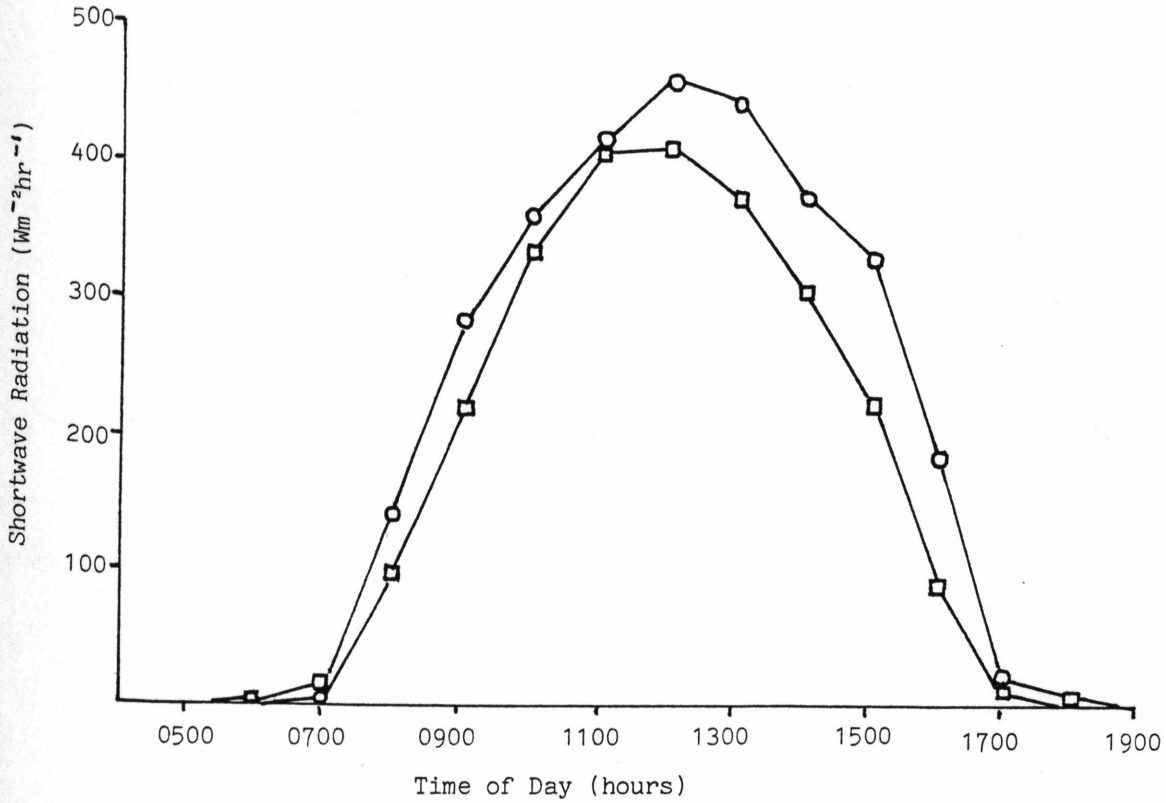


Figure 3A.15 Radiation levels ($Wm^{-2}hr^{-1}$) in field (□) and tube (○) on a day in February 1985.

treated with caution. This applies particularly to the glasshouse environment, since microclimate data were available for the summer months only. Other sources of error include the calibration and sensitivity of the instruments used in sampling the microclimate. Only one sensor could be used in each of the field, tube and glasshouse environments.

3A.7 Leaf Temperature

Measurements of temperature discussed so far have been of air temperatures, however leaf temperature can vary from air temperature and also from leaf to leaf depending upon conditions. Figures 3A.16 and 3A.17 give the mean leaf and air temperatures in the field and tube for 12days in August 1984 and 16days in July 1985 respectively. Soil temperatures shown for the first series of measurements may have been raised somewhat due to the heating effect of radiation since the tops of the thermometers were not protected from radiation during these measurements. However, the soil thermometers were covered for the second series of measurements.

For the days recorded in August 1984 the difference between mean leaf temperature and air temperature in the field (-1.25 ± 0.29°C) was greater than the difference in the tube environment (-0.68 ± 0.20°C). In July 1985 there was a greater mean difference between the leaf and air temperature in the field, -3.54 ± 0.17°C, and the mean difference between leaf and air temperature in the tube was slightly positive, 0.96 ± 0.34°C.

3A.8 Carbon Dioxide Profiles in Field, Tube and Glasshouse Environments

3A.8a Study I

The CO_2 concentrations (ppm) in the field, tube and glasshouse were sampled on nine occasions over a three day period 19/7/83-21/7/83. One position was sampled in each environment, each corresponding to a particular tree. The tube sampled contained a tree which was approximately 75cm in height. From each position two 50ml samples were taken from amongst the leaves of the tree at five heights above soil level (20cm, 40cm, 60cm, 80cm and 100cm), and the mean value for the two samples calculated.

The changes in CO_2 concentration with height in each of the three environments are shown in figure 3A.18. The CO_2 profiles in the field and glasshouse environments were similar, with the concentration in

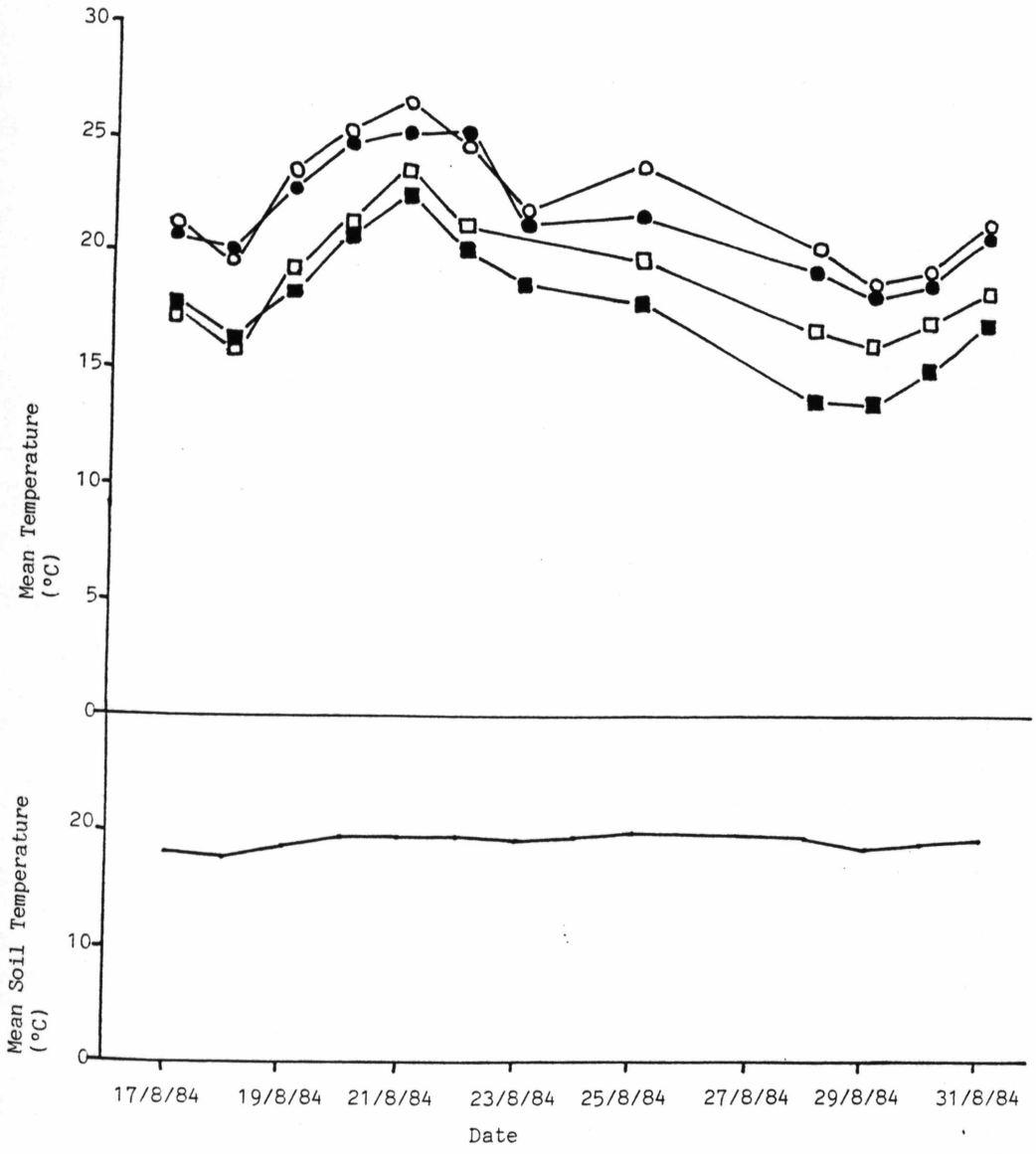


Figure 3A.16 Mean air and leaf temperatures in field and tube environments, August 1984.

□ Field air temperature

○ Tube air temperature

■ Field leaf temperature

● Tube leaf temperature

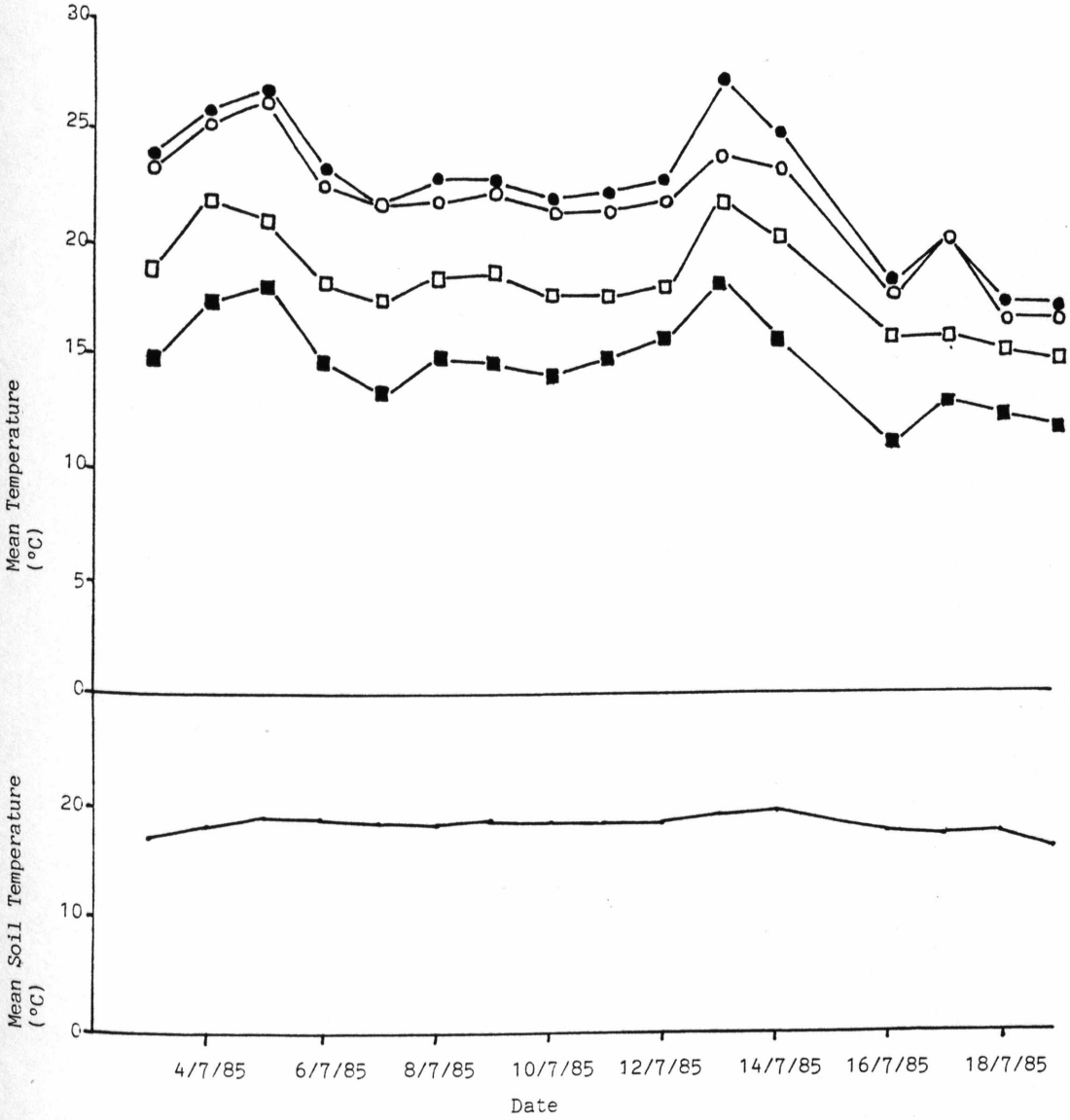


Figure 3A.17 Mean air and leaf temperature in field and tube environments, July 1985.

□ Field air temperature ■ Field leaf temperature

○ Tube air temperature ● Tube leaf temperature

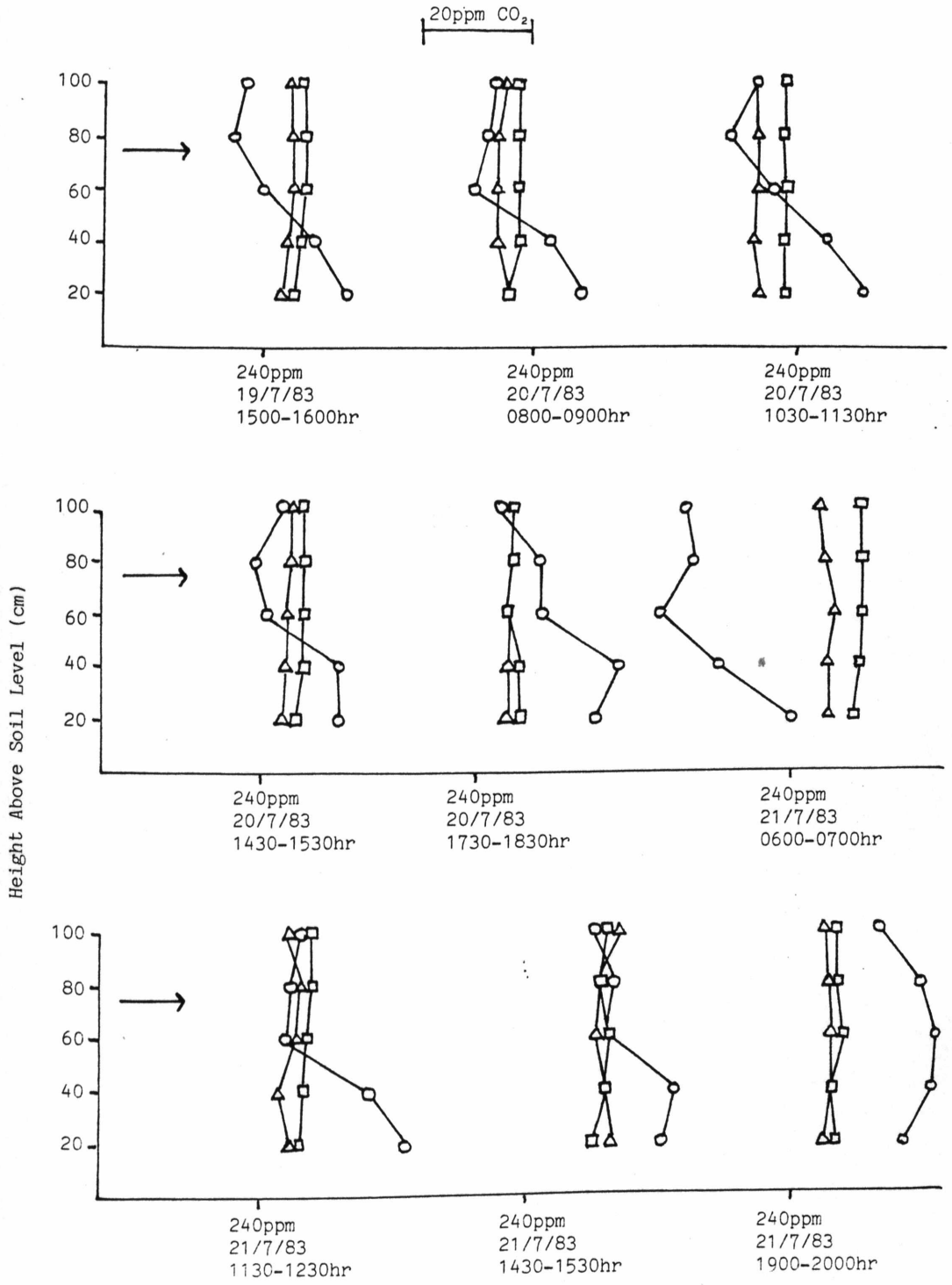


Figure 3A.18 CO_2 profiles in field (□), tube (○) and glasshouse (△) at 9 different times over three days 19/7/83 - 21/7/83.
(⟶ shows height of tree within tube)

the glasshouse tending to be slightly lower than in the field. The CO_2 profiles in the tube however differed markedly from those in the field. There was a higher CO_2 concentration below 40cm in the tube than above 60cm, the CO_2 level below 40cm tending to be greater than in the field during the day. Samples taken very early in the morning (0600-0700hr) showed a different pattern when there was a decrease in CO_2 throughout the tube compared with the field environment. However the CO_2 level was still higher in the lower part of the tube. The maximum decrease in CO_2 concentration at this time occurred in the centre of the tube. Samples taken late in the day (1730-1830hr, 1900-2000hr) showed an increase in CO_2 in the tube compared with the field.

3A.8b Study II

CO_2 concentrations (ppm) at 30cm 60cm and 90cm above soil level were sampled at five positions in the field, tube and glasshouse environments, each position corresponding to a tree taken at random. One 50ml sample was taken from each sampling point and five series of samples were taken at different times of day during the period 15/8/83-23/8/83. Mean height of trees used for sampling in the field was 35.1 ± 4.5cm, tube 75.0 ±13.0cm and glasshouse 46.8 ± 10.3cm. Simultaneous spot readings (3 replicates per environment) of air temperature (°C), relative humidity (%RH) and light level, PAR ($\mu molm^{-2}s^{-1}$) were also taken at heights of 30cm, 60cm and 90cm. Due to the time taken to complete a series of measurements the order in which the FTG-environments were sampled was determined using random numbers.

On each occasion there were no significant differences in temperature, humidity and light level at the three heights sampled. The interaction between FTG-environment and height was also not significant. For this reason the results for the field, tube and glasshouse environments are averaged over the three heights sampled (fig. 3A.19).

The concentration of CO_2 was significantly affected by main effects FTG-environment and height (table 3A.18). On each occasion there was a consistently lower level of CO_2 in the tube than in either field or glasshouse environments. The mean CO_2 concentration in the glasshouse was not significantly different from that in the field, except for the sample taken early in the morning (0630-0930hr) when the CO_2 level in the glasshouse was higher than that in the field. The relationship between CO_2 level and height above soil level varied on each sampling occasion, this reflected differences between the three environments. The interaction between FTG-environment and height was significant

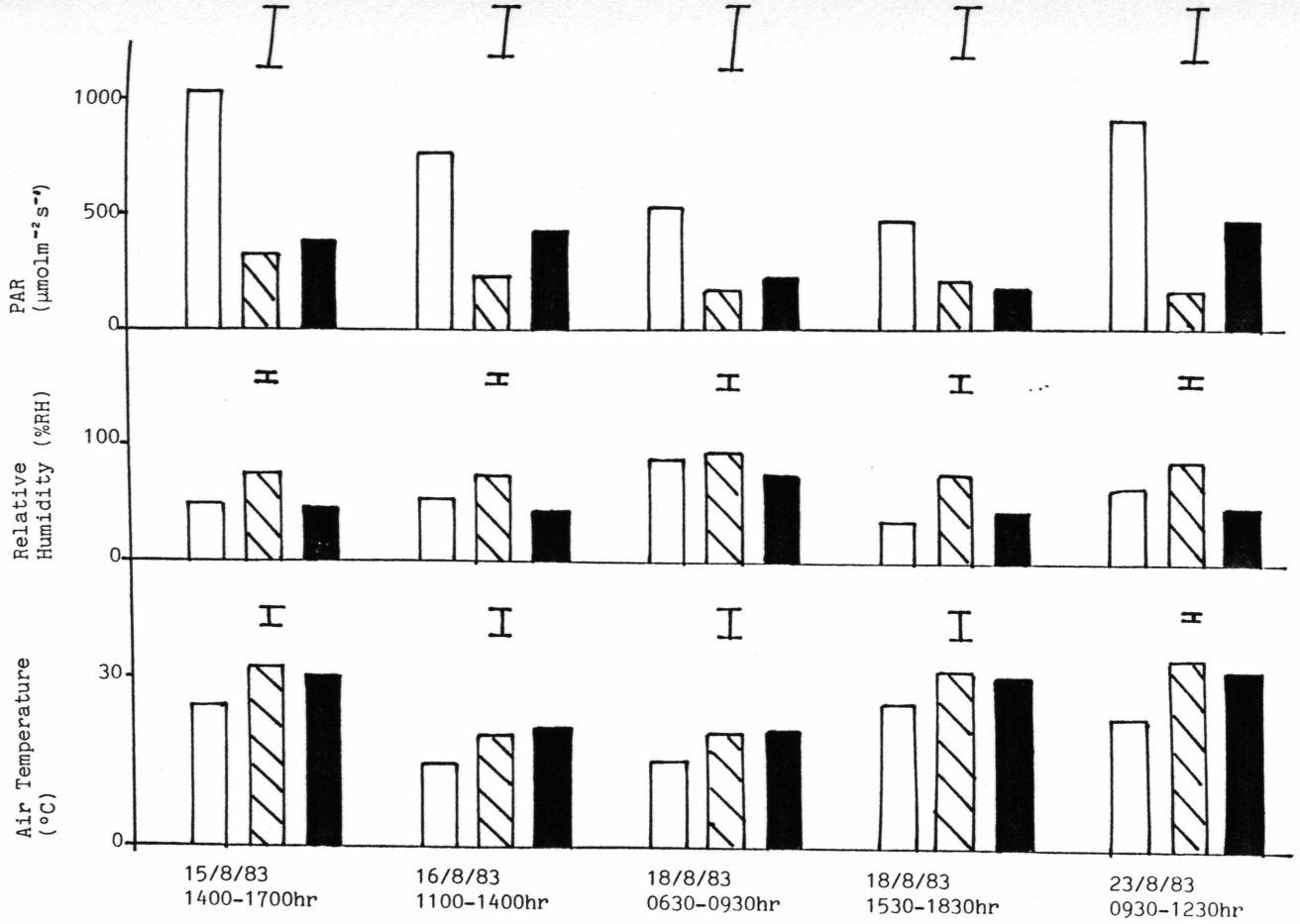


Figure 3A.19 Temperature (°C), relative humidity (%RH) and light level PAR ($\mu molm^{-2}s^{-1}$), averaged over three heights, in field (□), tube (▨) and glasshouse (■) on five occasions 15/8/83 - 23/8/83.

on each sampling occasion (fig. 3A.20).

Table 3A.18

The effect of FTG-environment and height on the mean concentration of CO_2 (ppm) (n=5) on five occasions 15/8/83-23/8/83.

	15/8/83 1400-1700hr	16/8/83 1100-1400hr	18/8/83 0630-0930hr	18/8/83 1530-1830hr	23/8/83 0930-1230hr
FIELD	264.5	269.1	272.6	284.0	288.6
TUBE	254.1	264.9	258.9	268.6	264.4
GLASSHOUSE	266.7	272.0	285.5	286.6	291.8
SIGNIFICANCE	***	**	***	***	***
LSD (P0.05)	3.3	3.6	5.6	4.0	6.1
30CM	263.1	273.0	266.8	277.9	288.7
60CM	258.9	275.0	275.9	273.9	278.1
90CM	263.3	258.0	274.3	287.3	278.0
SIGNIFICANCE	*	***	*	**	**
LSD (P0.05)	3.3	3.6	5.6	4.0	6.1
COEFFICIENT OF VARIATION (%)	1.7	1.8	2.8	2.0	2.9

On 15/8/83 the CO_2 concentration was similar at each height in the field and glasshouse environments. In the tube however the CO_2 level decreased with height, with the level at 30cm not significantly different from that in the field. On 16/8/83 there was a decrease in CO_2 at 90cm in each environment. Large differences in CO_2 level were seen for the period 0630-0930hr on 18/8/83. There were no significant differences between environments at 30cm, however at 60cm and 90cm the level in the glasshouse was 13.5-17.6ppm higher, and that in the tube 23.2-26.6ppm lower than in the field. In the field and glasshouse the CO_2 level increased with height but in the tube there was a decrease with height. The second series of samples taken during the afternoon of 18/8/83 showed a sharp decrease in CO_2 level in the tube at 60cm, but the levels at 30cm and 90cm were similar to those in the field and glasshouse environments. On 23/8/83 the pattern of CO_2 concentration with height in each environment was similar to that seen on 15/8/83. There were no significant differences between field and glasshouse, nor

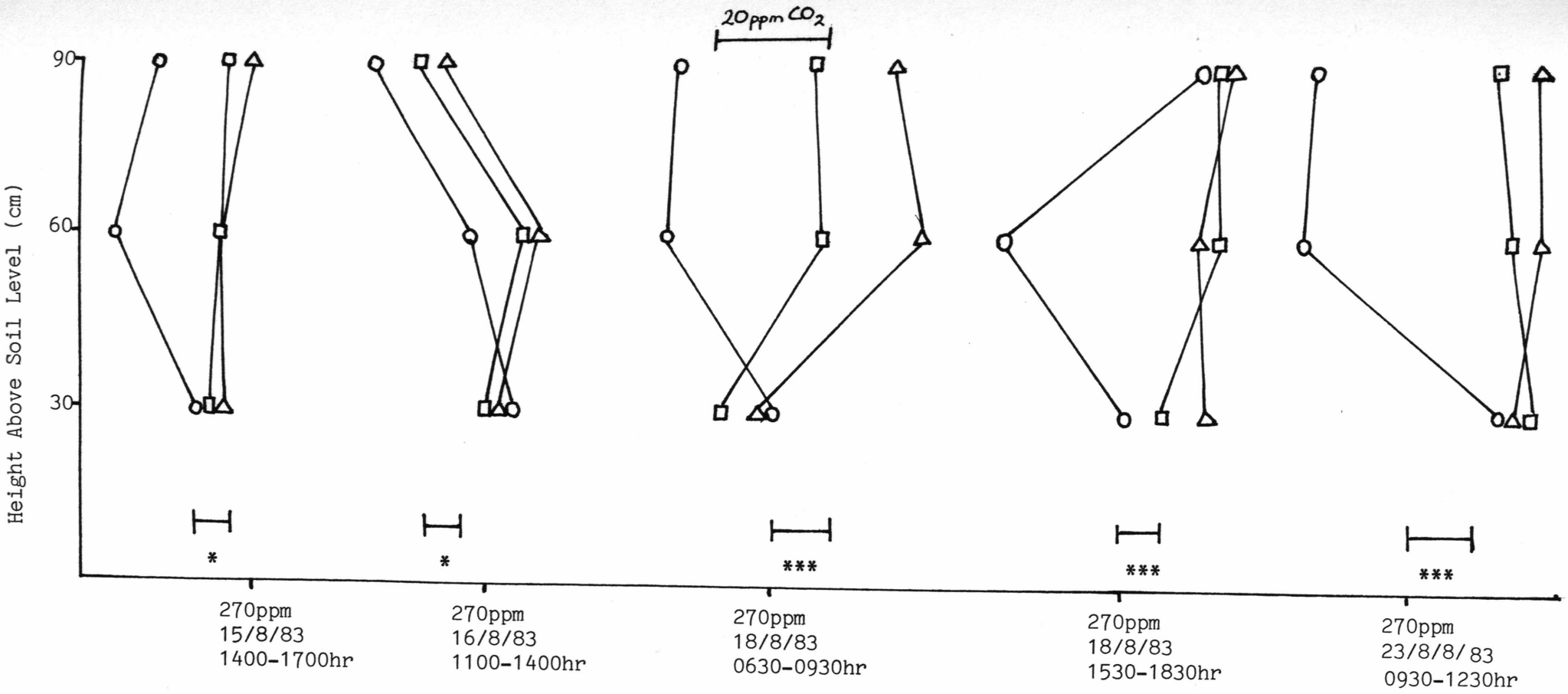


Figure 3A.20 Profiles of CO_2 concentrations (ppm) in field (□), tube (○) and glasshouse (△) environments at 30cm, 60cm and 90cm on five occasions, 15/8/83 - 23/8/83.

between the three heights in these two environments. However the levels of CO_2 in the tube at 60cm and 90cm were 32.5-34.4ppm lower than at 30cm in the tube and significantly lower (32.1-36.2ppm) than at 60cm and 90cm in the field.

3A.8c Study III

The CO_2 concentration (ppm) at three heights above soil level (30cm, 60cm and 90cm) was measured at five positions in the field and tube environments. One 50ml syringe sample was taken from each height at each position, a series of samples taking approximately one hour to complete and pass through the IRGA. Measurements were made on two groups of plants, the first group consisted of trees in their first year of growth, with a mean height of 30.0 ±3.7cm, samples taken on 31/7/84 and 7/8/84. The second group consisted of trees in their second year's growth, with a mean height of 151.5 ±18.4cm, the samples being taken on 5/7/84 and 17/7/84.

For the first group of trees there were significant differences between the field and tube environments on three occasions but no significant differences between different heights (table 3A.19). Where a significant difference was recorded the mean concentration of CO_2 in the tube was lower than in the field, but the interaction between environment and height was statistically not significant.

Larger differences in CO_2 concentration were found with the second group of trees. On 5/7/84 significant differences were recorded between the field and tube environments and between the three heights above soil level (table 3A.20). The level of CO_2 in the tube was lower than in the field during most of the day, until 1700hr. Samples taken between 1800-2100hr showed no significant differences between environments, but after dark the level of CO_2 in the tube rose above that in the field. The concentration of CO_2 at 90cm above soil level tended to be lower than at 30cm and 60cm.

There were no significant differences in concentration of CO_2 at the three heights above soil level in the field. However in the tube environment there was a significant decrease in CO_2 with height until 2000hr (fig. 3A.21). The level of CO_2 at 30cm was similar to that in the field, except for the final sample at 2200hr when there was a general increase (30.4-37.0ppm) in CO_2 in the tube environment compared with that in the field. The mean concentration of CO_2 recorded at 60cm was up to 43.4ppm lower than in the field, and at 90cm the difference between tube and field could be as great as 52ppm, both occuring at

	← 31/7/84 →						← 7/8/84 →		
Time of day (Hours)	1000-1100	1400-1500	1600-1700	1800-1900	2000-2100	2145-2245	1000-1100	1430-1530	1800-1900
Field	285.9	279.3	269.9	275.0	284.2	288.5	283.5	274.7	274.8
Tube	280.6	277.8	268.7	271.6	285.3	289.9	279.1	271.5	270.1
Significance	***	NS	NS	NS	NS	NS	*	NS	**
LSD(P0.05)	2.4	7.1	2.3	3.4	2.0	4.0	3.7	5.7	2.6
30cm	283.4	276.9	269.7	271.8	284.3	289.5	282.1	273.7	272.3
60cm	282.8	277.1	269.0	272.7	284.8	289.2	280.8	273.6	272.4
90cm	283.6	281.7	269.2	275.4	285.1	289.0	280.9	272.0	272.6
Significance	NS	NS	NS	NS	NS	NS	NS	NS	NS
LSD(P0.05)	2.9	8.7	2.8	4.2	2.5	4.9	4.5	7.0	3.2
Coefficient of variation (%)	1.1	3.4	1.1	1.7	0.9	1.8	1.8	2.8	1.3

Table 3A.19 The effect of the two main factors, environment and height above soil level, on the mean CO_2 concentration (ppm) (n=5). Tubes containing trees in their first year of growth.

Time of day (hours)	1000-1100	1200-1300	1400-1500	1600-1700	1800-1900	2000-2100	2200-2300
Field	269.9	277.2	267.7	279.1	286.1	308.4	324.2
Tube	236.9	251.6	253.4	261.3	278.0	306.4	357.3
Significance	***	***	***	***	NS	NS	***
LSD(P0.05)	9.1	9.9	6.9	5.5	8.8	6.1	9.3
30cm	262.9	268.2	267.2	277.3	287.8	309.2	344.3
60cm	251.1	264.8	263.2	271.7	283.6	310.1	339.6
90cm	246.2	260.2	251.3	261.7	274.7	302.9	338.4
Significance	*	NS	**	***	NS	NS	NS
LSD(P0.05)	11.2	12.1	8.4	6.8	10.8	7.5	11.4
Coefficient of variation (%)	4.8	5.0	3.5	2.7	4.2	2.7	3.6

Table 3A.20 The effect of the two main factors, environment and height above soil level,on the mean CO_2 concentration (ppm) (n=5) on 5/7/84. Tubes containing trees in their second year of growth.

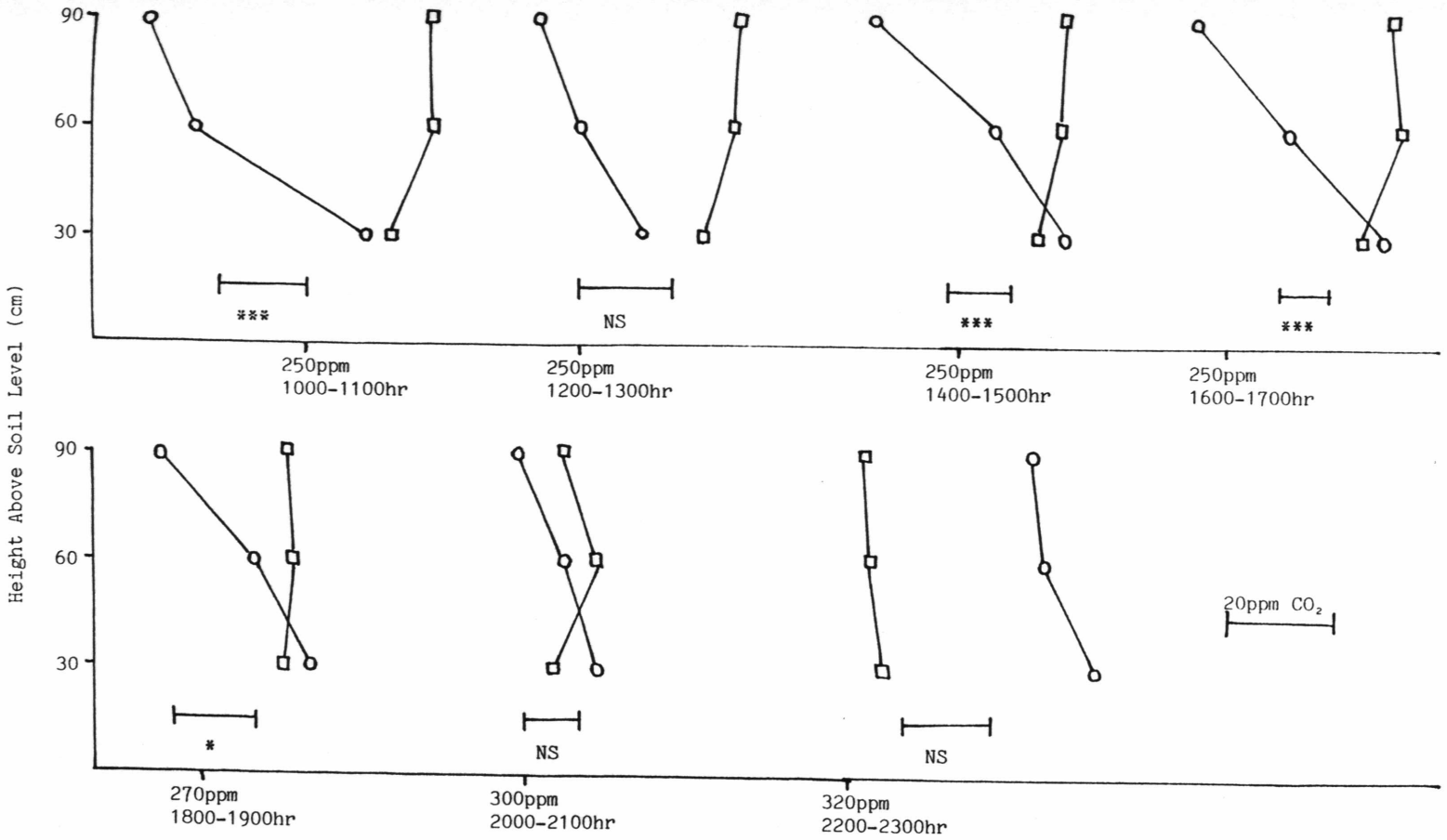


Figure 3A.21 Profiles of concentration of CO_2 (ppm) in field (□) and tube (○) environments, the interaction between environment and height above soil level at different times of day on 5/7/84. (Mean height of tube trees was 151 ±18.4cm).

1000-1100hr.

On 17/7/84 the concentration of CO_2 was sampled at two hourly intervals between 0600-2200hr. Significant differences between the field and tube environment were recorded throughout the day, and also between the three heights above soil level on 5 occasions (table 3A.21). The level of CO_2 in the tube was below that in the field until 2000hr, after which time it rose above that in the field.

The interaction between environment and height was also significant until 1900hr (fig. 3A.22). After this time there were no signficant differences in CO_2 concentration at the three heights above soil level in both field and tube environments. Throughout the day the level of CO_2 at 30cm in the tube was not significantly different from the level at this height in the field, but there was a sharp decrease in concentration with height within the tube. These results were thus similar to those recorded on 5/7/84. The difference between CO_2 concentration in the field and tube at 90cm was as great as 62.4ppm, recorded at 0600-0700hr. Also at this time there was the largest difference (51ppm) between the mean CO_2 level at 30cm and that at 90cm within the tube.

3A.9 Effect of Covering the Soil Surface on the Level of CO_2 Within the Tube Environment.

The previous experiments had shown not only differences in CO_2 with height in the tube, but also relatively high levels near the soil surface. The following experiments were designed to test to what extent such CO_2 was derived from the soil itself.

3A.9a Study I

CO_2 concentration at 30cm, 60cm and 90cm in the field environment and in tubes with and without "mats" covering the soil surface was measured by taking a single 50ml syringe sample from each height. Five replicates of the field and two tube environments were taken. Measurements were made on two groups of plants, 7 series of measurements were taken (22/8/84, 6/9/84) on the first group which consisted of plants in their first year of growth. The mean height of tube trees without mats was 32.7 ± 4.0cm and with mats 29.1 ± 2.6cm. The second group consisted of trees in their second year of growth, 5 series of measurements were made on 8/8/84 and 9/8/84. Mean heights of tube trees in this group were 180.5 ± 12.9cm (-mats) and 168.2 ± 8.8cm (+mats).

For the first group of trees there were significant differences

Time of day (hours)	0600-0700	0800-0900	1000-1100	1200-1300	1400-1500	1600-1700	1800-1900	2000-2100	2200-2300
Field	291.7	290.1	295.5	275.7	266.8	271.7	284.6	291.8	302.3
Tube	253.5	267.7	268.3	257.5	249.4	258.5	272.1	301.0	322.9
Significance	***	***	***	***	***	***	*	*	***
LSD(P0.05)	15.2	9.5	7.3	5.4	6.3	5.5	9.9	8.0	10.6
30cm	285.2	286.1	290.6	274.2	266.3	274.7	280.9	297.9	311.6
60cm	269.2	281.5	284.9	269.8	260.9	267.3	279.0	296.7	314.3
90cm	263.4	269.1	270.2	255.9	247.1	253.3	275.2	264.6	312.0
Significance	NS	*	***	***	***	***	NS	NS	NS
LSD(P0.05)	18.7	11.7	9.0	6.7	7.7	6.7	12.2	9.8	13.0
Coefficient of variation (%)	7.4	4.5	3.4	2.7	3.3	2.8	4.7	3.6	4.5

Table 3A.21 The effect of the two main factors, environment and height above soil level, on the mean CO_2 concentration (ppm) (n=5) on 17/7/84. Tubes containing trees in their second year of growth.

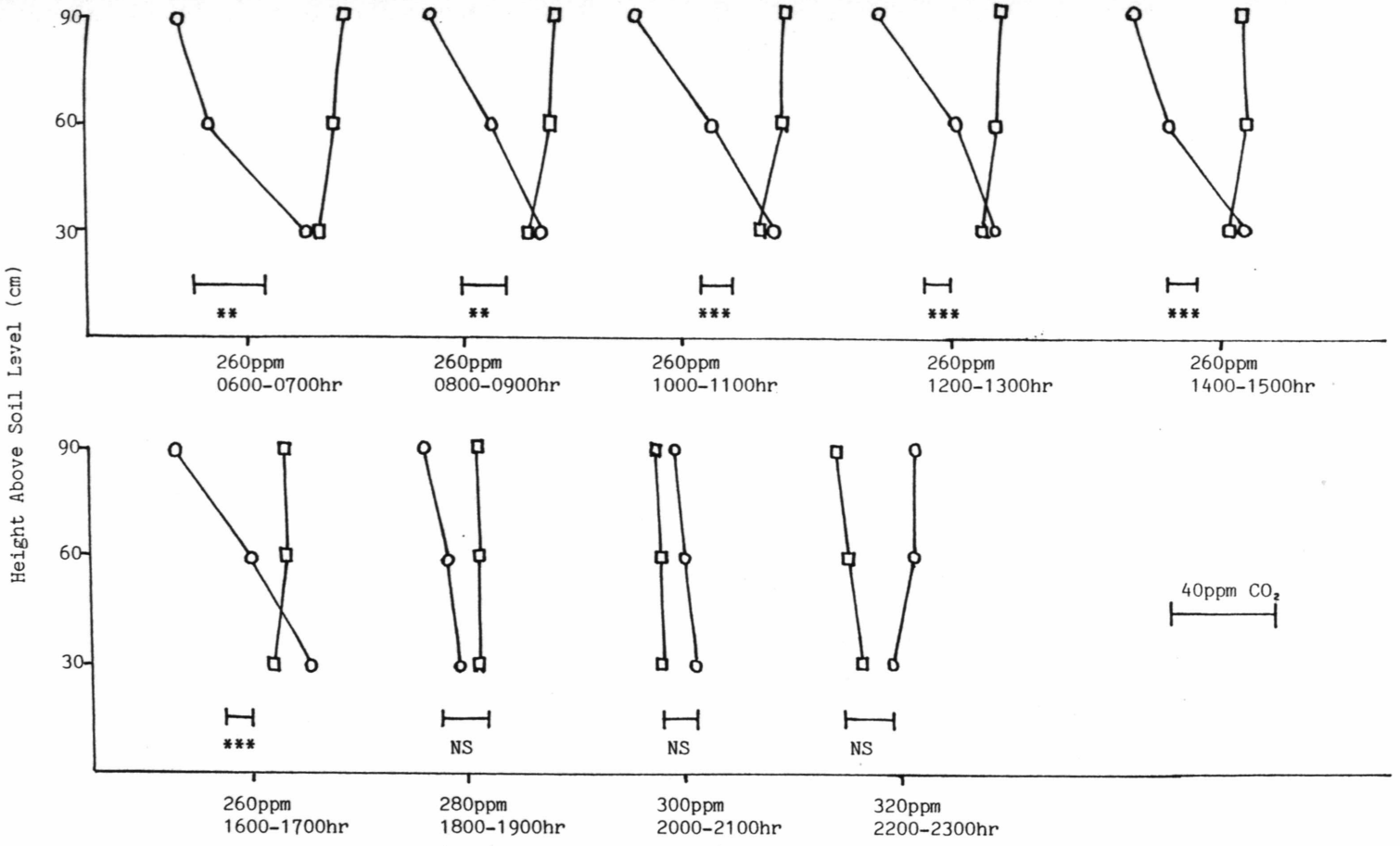


Figure 3A.22 Profiles of concentration of CO_2 (ppm) in field (□) and tube (○) environments, the interaction between environment and height above soil level at different times of day on 17/7/84. (Mean height of tube trees was 151.5 ±18.4cm).

Date	22/8/84			6/9/84			
Time of day (hours)	1000-1100	1400-1500	1800-1900	1000-1100	1200-1300	1430-1530	1700-1800
Field	276.9	275.6	280.7	282.1	302.3	283.1	294.8
Tube - mat	269.4	271.2	283.0	281.8	302.4	282.3	293.7
Tube + mat	259.2	259.1	277.7	275.9	293.3	278.7	285.1
Significance	***	***	*	**	***	NS	**
LSD(P0.05)	8.6	7.1	3.4	4.3	5.1	4.5	5.3
30cm	267.3	266.9	279.5	280.9	300.1	282.7	291.9
60cm	267.3	267.9	280.6	278.6	298.4	281.0	290.7
90cm	270.9	271.0	281.2	280.4	299.4	280.3	291.1
Significance	NS	NS	NS	NS	NS	NS	NS
LSD(P0.05)	8.6	7.1	3.4	4.2	5.1	4.5	5.3
Coefficient of variation (%)	4.3	3.6	1.6	2.1	2.3	2.2	2.5

Table 3A.22 Mean concentration of CO_2 (ppm) (n=5) in the field and in tubes with and without mats covering the soil surface, and at different heights above soil level. First group of tube plants.

between the field environment and tubes with and without mats covering the soil surface, but no significant differences between heights above soil level (table 3A.22). In each case the level of CO_2 was significantly lower in the tube when the soil surface was covered. By contrast there were no significant differences between the field and those tubes without mats. The interaction between environment and height was not significant.

No significant differences between field and tube environments were found using the second group of plants (table 3A.23), however height did have a significant effect on CO_2 concentration on three occasions. The level at 90cm was lower than at 30cm and 60cm. The interaction between environment and height was not significant.

Table 3A.23

Mean concentration of CO_2 (ppm) (n=5) in the field and in tubes with and without mats covering the soil surface, and at different heights above soil level. Second group of tube plants.

Date	8/8/84			9/8/84	
Time of Day (Hours)	1000-1100	1430-1530	1830-1930	1200-1300	1700-1800
Field	286.2	279.3	263.7	266.7	279.5
Tube -Mat	265.3	281.3	269.3	253.9	268.3
Tube +Mat	261.5	258.3	240.7	245.1	261.7
Significance	NS	NS	NS	NS	NS
LSD (P0.05)	22.4	20.5	28.5	28.4	18.5
30cm	284.3	288.3	269.8	264.7	281.3
60cm	274.3	277.3	262.7	260.1	273.8
90cm	254.5	253.3	241.2	240.9	254.3
Significance	*	**	NS	NS	*
LSD (P0.05)	22.4	20.5	28.5	28.4	18.5
Coefficient of Variation (%)	11.2	10.1	11.2	11.3	9.2

3A.9b Study II

In this study the concentration of CO_2 (ppm) was measured using the portable IRGA at heights of 30cm, 60cm and 90cm in the field and glasshouse environments and in tubes with and without covering the soil surface. Three replicates of the tube environments were taken, each corresponding to a particular tree chosen at random. However only one measurement was taken at each height in the field and glasshouse environments to reduce sampling time. In the statistical analysis the CO_2 concentration at each height in the tubes with and without covering the soil surface were compared as well as the mean results for the three heights in the field and glasshouse environments.

Two series of samples were taken (9/7/85-12/7/85, 15/7/85-17/7/85) with CO_2 measurements taken at 3 hourly intervals. During the second series of measurements the mats covering the soil surface were exchanged so that in those tubes, in which the soil had previously been exposed, the soil surface was covered and vice-versa. The computer data-logging system was used to record temperature (°C) and relative humidity (%RH) at hourly intervals throughout this study.

Using a single tree from each environment nail varnish impressions of the lower surface of leaves at approximately 60cm above soil level were taken at the same time as CO_2 measurements to allow estimates of stomatal apertures. These impressions were examined under the light microscope and photographed. The photographs were then examined to determine whether stomata were open or closed. Due to the limitation of the data no attempt was made to quantify the results e.g. in terms of number of open stomata. Only a qualitative assessment of stomatal opening is therefore given, with the degree of opening represented pictorially.

At the end of the study the tube trees were destructively sampled to determine fresh weight (g), dry weight (g), leaf number and leaf area (cm^2).

Mean air temperatures in the field, tube and glasshouse environments for the period 9/7/85-12/7/85 were 17.7 ± 0.4°C, 21.2 ± 0.8°C and 24.2 ± 0.5°C respectively. Mean relative humidity was close to saturation in the tube environment, 99.8 ± 0.05%, lowest in the field, 46.8 ± 2.8% and intermediate in the glasshouse, 65.4 ± 2.5%. Mean leaf temperature in the tube (21.9 ± 0.9°C) was substantially higher than in the field environment (14.6 ± 0.5°C).

Table 3A.24 gives the mean CO_2 concentrations in field and glasshouse environments and in tubes with and without mats covering the soil

surface.

Table 3A.24

Mean CO_2 concentration (ppm) in field, glasshouse and in tubes with and without mats covering the soil surface for the period 9/7/85-12/7/85.

ENVIRONMENT			MEAN ± SE (ppm CO_2)
FIELD			329.1 ± 2.8
GLASSHOUSE			341.9 ± 6.0
TUBE	-MAT	30CM	412.4 ± 7.0
		60CM	382.3 ± 12.0
		90CM	366.0 ± 11.5
TUBE	+MAT	30CM	302.1 ± 14.6
		60CM	265.4 ± 18.3
		90CM	285.4 ± 11.8

At each height the mean CO_2 concentration was lower in the tubes when the soil surface was covered than in those tubes without mats. Also in the tubes with mats the mean level of CO_2 at each height was below the mean level in the field, whereas in the tubes without mats the mean CO_2 level at each height was above that in the field.

Profiles of the CO_2 concentration in each environment on each sampling occasion (9/7/85-12/7/85) are given in figure 3A.23. The level of CO_2 in the glasshouse was similar to that in the field during the day but at night or in the early morning, before the glasshouse vents had opened, the mean CO_2 concentration in the glasshouse rose (up to 43ppm) above that in the field. During the day, in the tubes with mats the mean CO_2 level was lowest at 60cm, falling as low as 166.7ppmCO_2 on one occasion (0900-100hr 10/7/85). In tubes without mats the level at 30cm was higher (17.6-127ppm) than that at 60cm and 90cm. The range in CO_2 level within the tube environment (both with and without mats covering the soil surface) was reduced at night (2.0-72.7ppm) compared with the range of CO_2 concentrations which occurred within the tubes during the day (17-127ppm). The levels at 30cm and 60cm tending to be higher than at 90cm. Differences between tubes with and without mats were not significant at night.

The state of stomata in the field, tube and glasshouse environments is represented pictorially in figure 3A.24. This is only a qualitative assessment of the degree of opening of stomata, no data are available

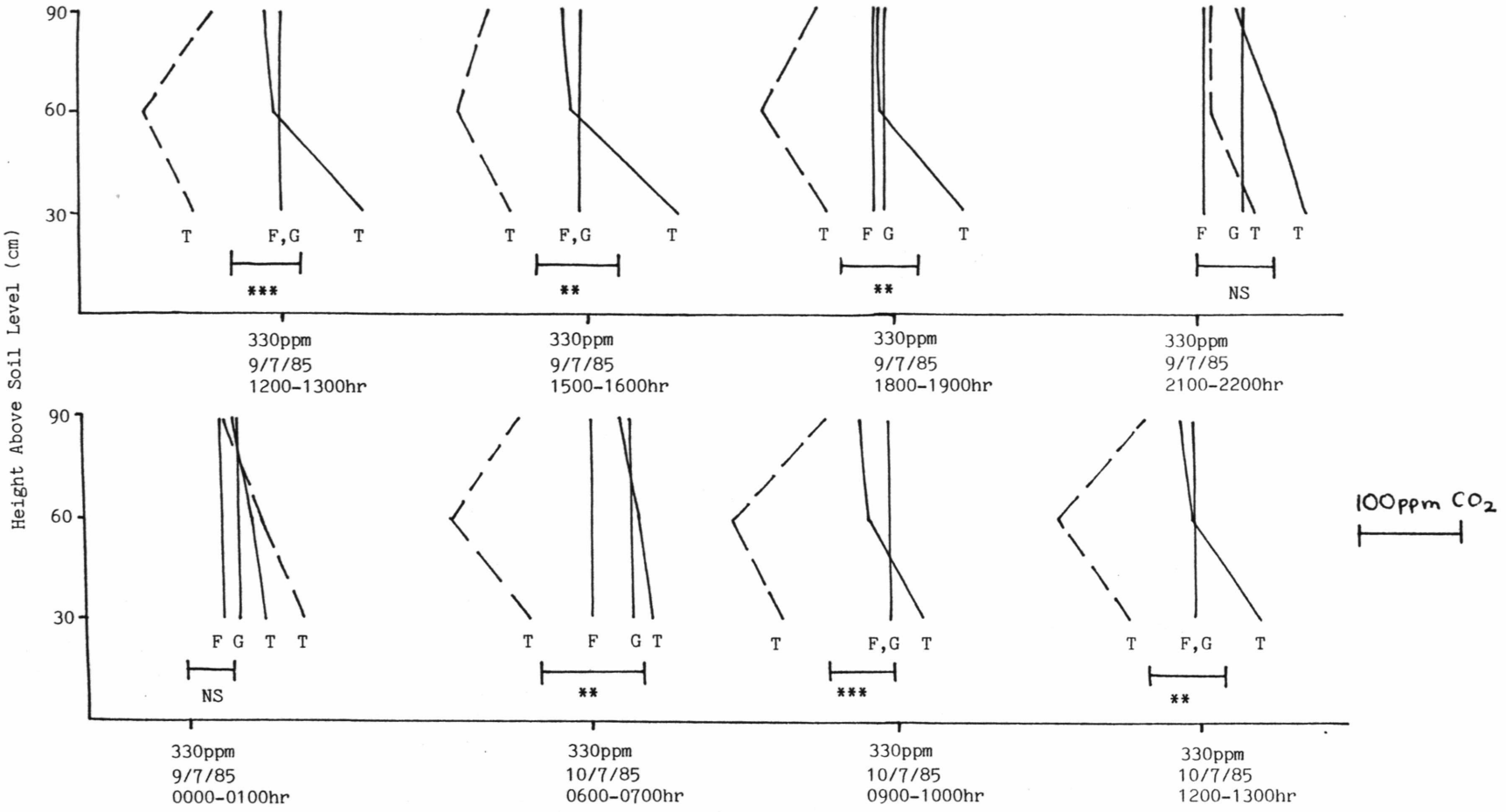


Figure 3A.23 Profiles of CO_2 concentration (ppm) in field (F) and glasshouse (G) environments (averaged over three heights) and at three heights in tubes (T) with (– – –) and without (———) mats covering the soil surface 9/7/85 - 12/7/85. Figure continued overleaf.

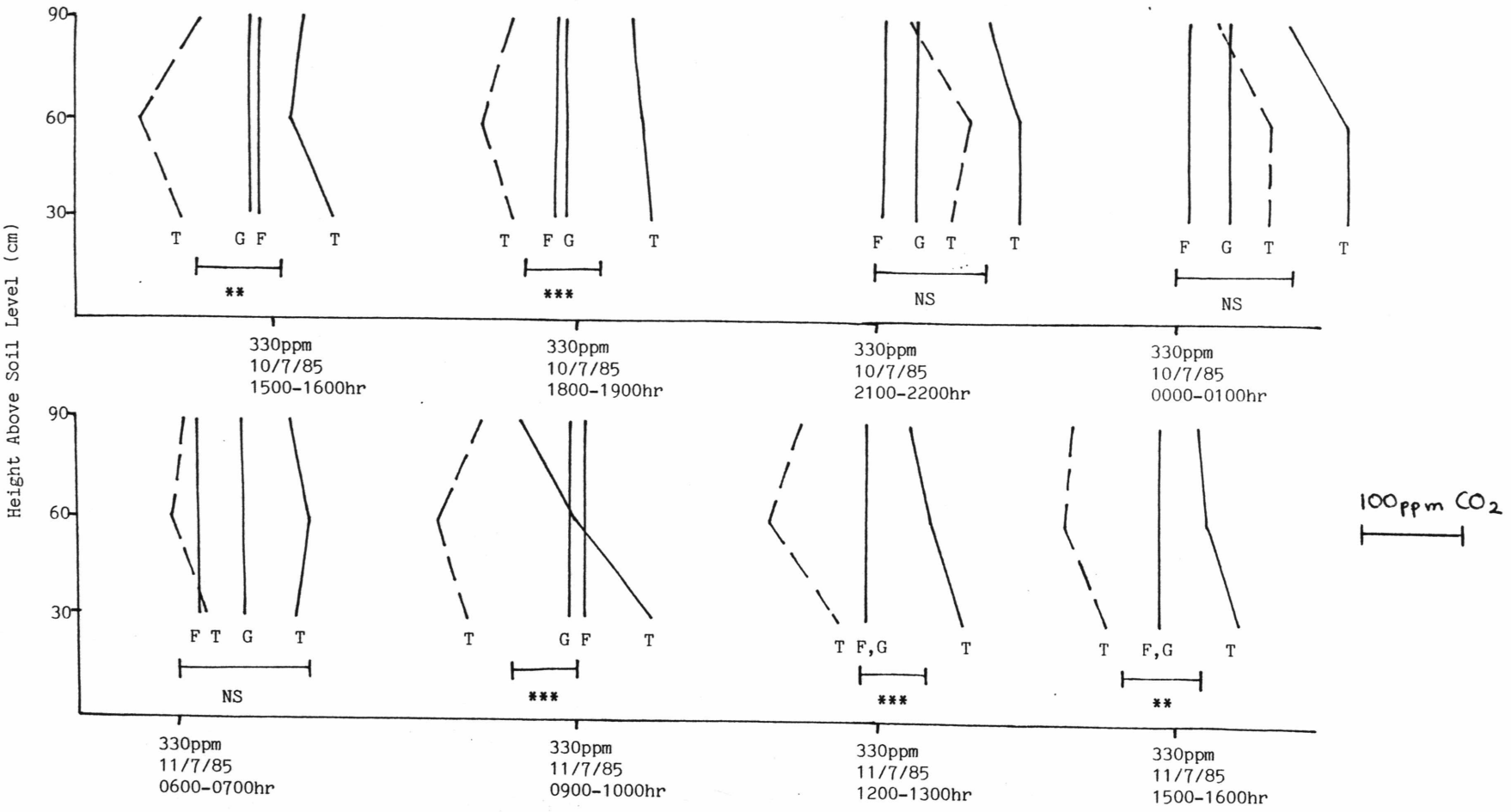


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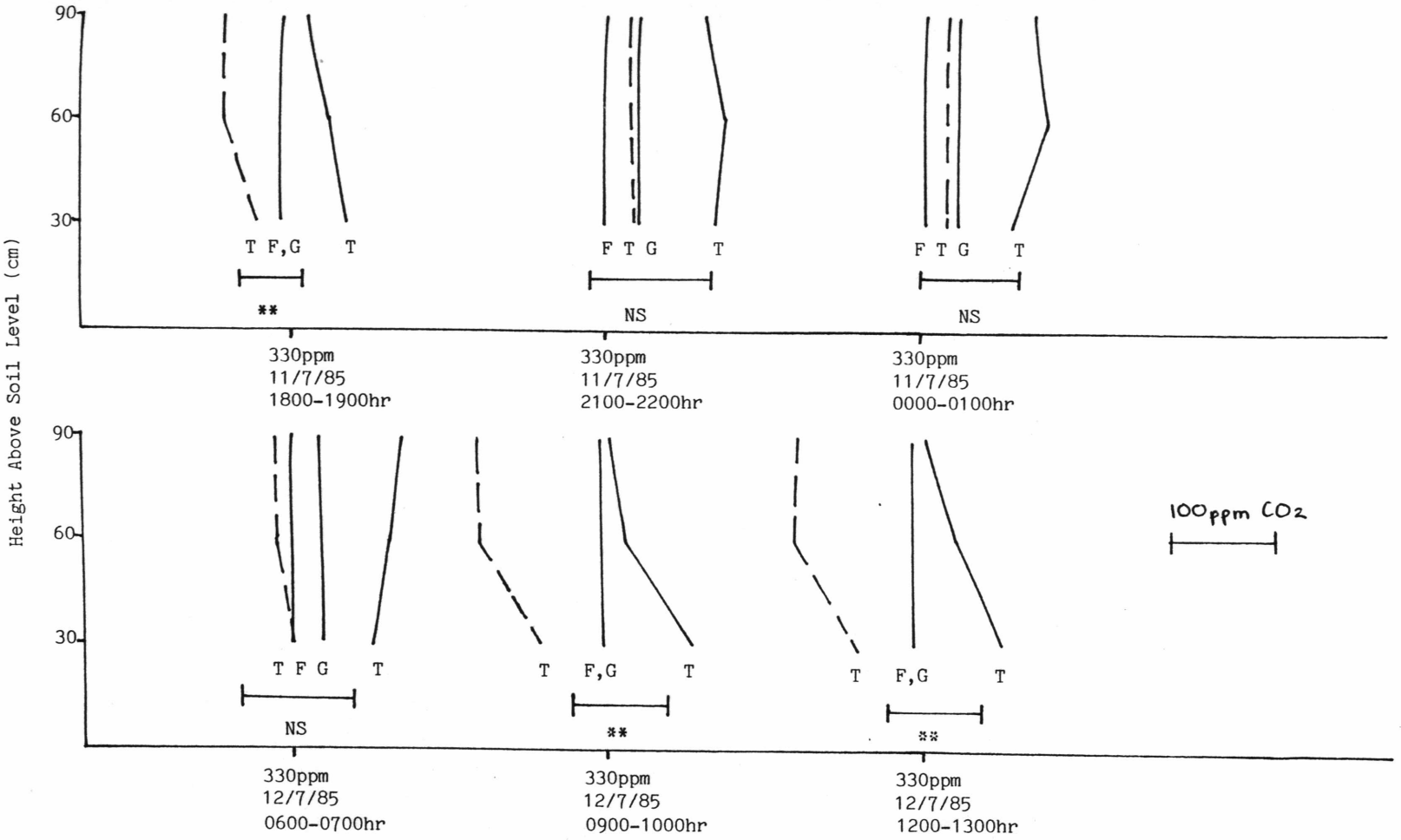


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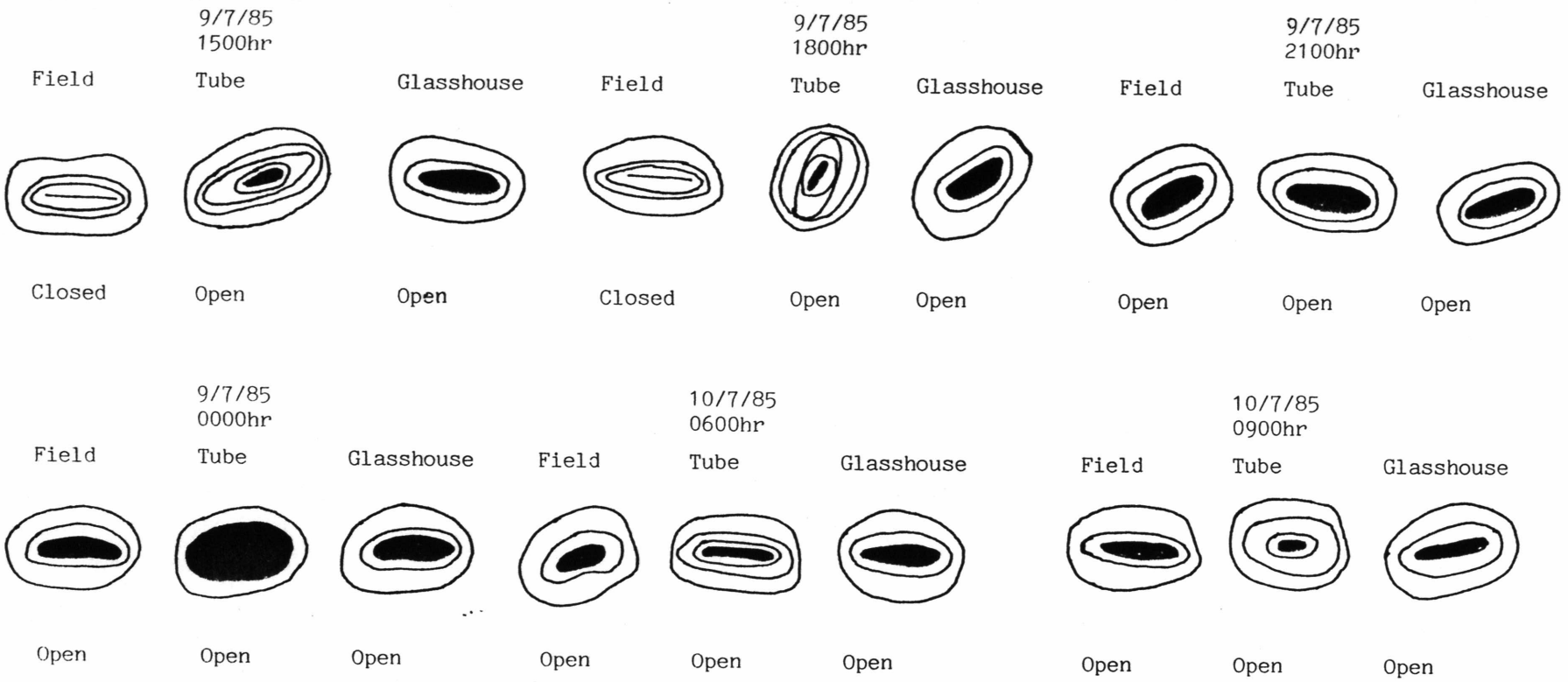


Figure 3A.24 State of stomata in field, tube and glasshouse environments at different times of day 9/7/85 - 11/7/85, drawn from photographs of nail varnish impressions of the leaf surface, shaded area represents stomatal opening. Figure continued overleaf.

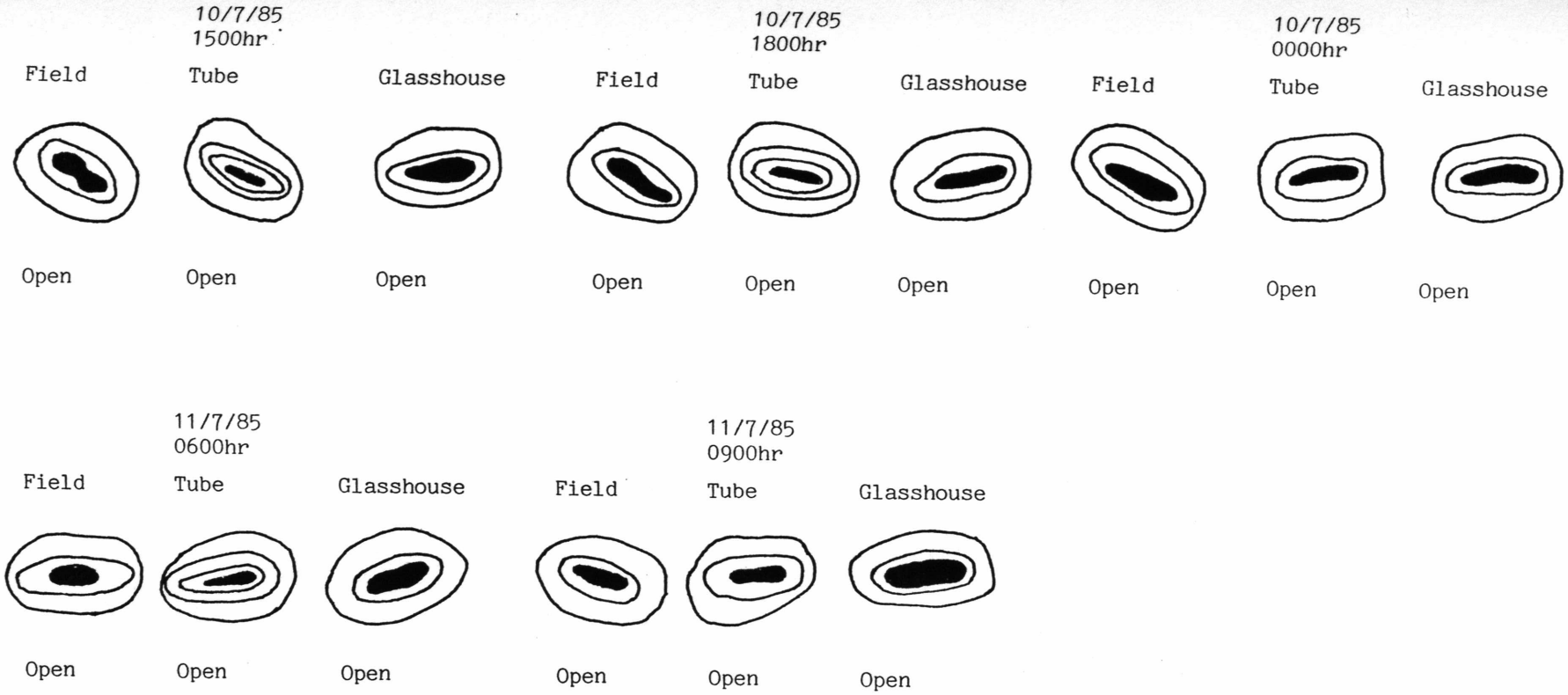


Figure 3A.24 continued from the previous page.

on the proportion of stomata which were open. Despite the paucity of the data there did appear to be a difference in stomatal opening between the three environments, though obviously a more detailed study is required to draw any firm conclusions. Basically stomata in the tubes appeared to be more widely open or more closed than field and glasshouse which resembled each other rather more, but it is not easy to correlate this with time of day.

During the second series of measurements, 15/7/85-17/7/85, mean air temperature was higher in the glasshouse, 23.5±0.4°C, than in the tube, 18.9±1.0°C and lowest in the field, 15.6±0.5°C. Mean relative humidity in the tube was again close to saturation, 99.8±0.1%, while mean humidity in the field and glasshouse environments were 55.2±4.0% and 64.0±2.6% respectively. There was also a similar difference between mean leaf temperature in the field and tube environments, 11.1±0.6°C and 19.2±1.1°C respectively.

The mean concentration of CO_2 in field, glasshouse and tube environments for the period 15/7/85-17/7/85 are given in table 3A.25. For the first half of this period the tubes with and without mats were set up as in the previous series of measurements, again the levels at all three heights in tubes without mats were above the mean level of CO_2 in the field and in those tubes with mats CO_2 concentration was reduced compared with the field level. Mean CO_2 concentration decreased with height in tubes without mats but was lower at 60cm than at 30cm and 90cm in tubes with mats.

Table 3A.25

Mean CO_2 concentration (ppm) in field, glasshouse and in tubes with and without mats covering the soil surface for the period 15/7/85-17/7/85.

		MATS AS BEFORE Mean±SE ppmCO_2	MATS REVERSED Mean±SE ppmCO_2
FIELD		335.8±10.2	344.3±10.6
GLASSHOUSE		337.0±8.5	356.3±17.2
TUBE -MAT	30CM	479.8±27.9	336.7±74.8
	60CM	429.2±28.6	313.9±63.4
	90CM	396.3±23.6	297.0±35.2
TUBE +MAT	30CM	295.8±21.3	375.9±13.4
	60CM	261.3±31.2	337.0±21.2
	90CM	279.4±22.5	332.1±20.0

For the second half of this series of measurements the mats covering the soil surfaces in the tubes were exchanged. In the tubes, previously without mats but now with the soil surface covered, the mean level of CO_2 decreased at each height so that the levels were below the mean concentration in the field. For those tubes from which the mats were removed there was an increase in CO_2. Whereas the level of CO_2 at 30cm was above field level, as found in the previous series of measurements, the mean levels at 60cm and 90cm were below the mean concentration of CO_2 in the field.

The pattern of CO_2 concentration in each environment on each occasion is given in figure 3A.25. Before the mats were exchanged the pattern of CO_2 in the tubes, with and without mats, was similar to that during the period 9/7/85-12/7/85. After the mats had been exchanged those tubes now without mats had higher (48.4-155.3ppm) CO_2 than those tubes now with mats until 1800-1900hr. At night however the mean level in those tubes now with mats rose to very high levels (692ppm at 30cm 0000-0100hr), significantly greater than in the tubes without mats. In the previous series of measurements the level of CO_2 in tubes without mats remained above that in the tubes with mats.

Such differences in results may be explained in part by differences between the two groups of tube trees. Table 3A.26 gives the mean fresh weight, dry weight, leaf number and leaf area for the tube trees used in this study. None of the tube trees had grown out of their tubes, therefore all stem and leaf material was contained within the tube. Although chosen at random there were large differences in the size of trees in the two groups of tubes, those in tubes originally with mats being approximately twice the size. They may therefore have exerted a greater influence on CO_2 within the tube and to some extent masked the effect of covering the soil surface.

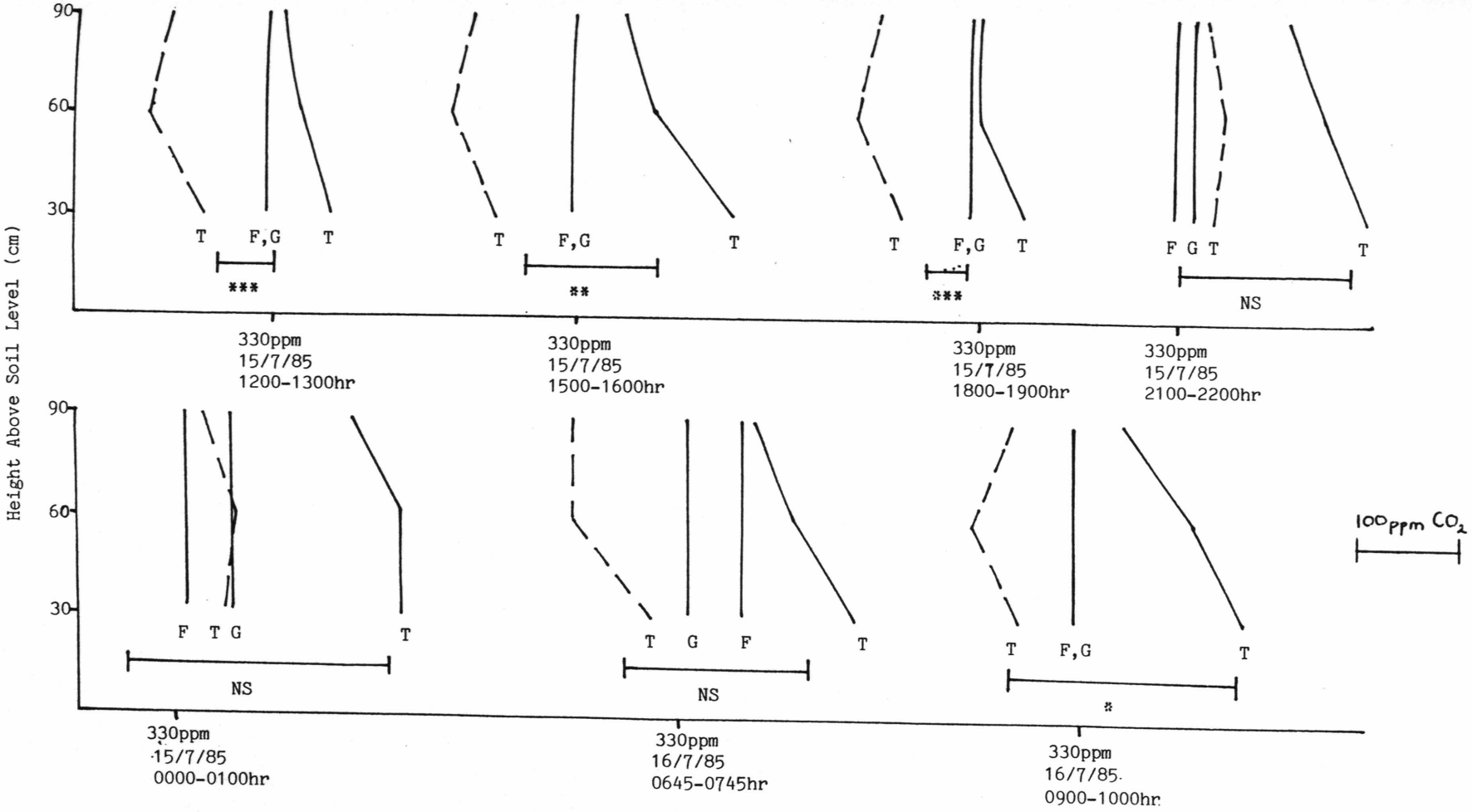


Figure 3A.25 Profiles of concentration CO_2 (ppm) in field (F) and glasshouse (G) environments (averaged over three heights) and in tubes (T) with (– – –) and without (——) covering of the soil surface 15/7/85-17/7/85. Figure continued overleaf.

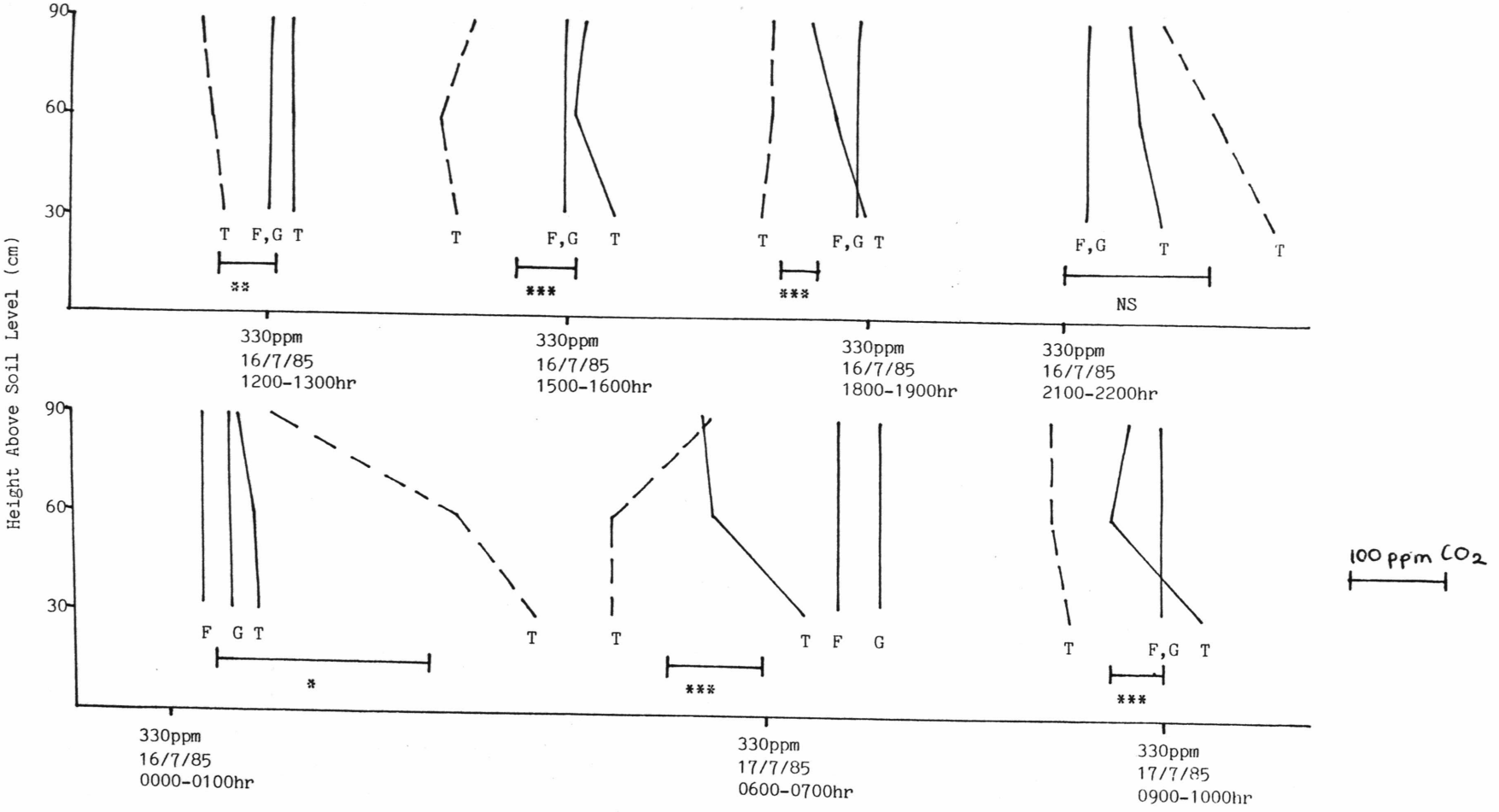


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Table 3A.26

Mean (±SE) fresh weight (g), dry weight (g), leaf number and leaf area (cm^2) of tube trees with and without mats (as for 9/7/85-12/7/85).

		TUBE -MAT (T_o)	TUBE +MAT (T_m)
HEIGHT (cm)		67.7±3.3	91.5±14.6
FRESH WEIGHT (g)	STEM	20.5±4.5	46.0±8.7
	LEAVES	20.9±4.6	45.5±6.5
	ROOT	35.2±7.3	45.2±4.2
DRY WEIGHT (g)	STEM	7.4±1.3	15.7±2.8
	LEAVES	7.5±1.5	15.2±1.9
	ROOT	11.6±3.0	12.3±1.3
LEAF NUMBER		107.7±43.8	285.7±47.2
LEAF AREA (cm^2)		126.3±38.4	293.7±25.2

3A.10 Summary

Relationships between data-logging results for field, tube and glasshouse environments and meteorological data were derived. Strong positive relations were found for shortwave radiation and temperature for each of the environments, and for relative humidity in the field and glasshouse environments. For humidity in the field better correlation was achieved with a combination of humidity and shortwave radiation. Glasshouse humidity was related to humidity at 0900hr, also weakly correlated with shortwave radiation, hours of sun and minimum temperature. In the tube environment humidity was not correlated with any of the meteorological parameters used; the tube and its associated tree may therefore have a greater effect on humidity within the tube than the prevailing weather conditions.

Tube environment was characterised by reduced radiation, increased temperature and increased humidity compared with the field. Radiation level was also reduced in the glasshouse but to a lesser extent than in the tube. There was a tendency for radiation to increase with height above soil level. Temperature in the tube could be similar to or greater than in the glasshouse. The daily range in temperature was greater in the tube, but similar in the field and glasshouse. There was little change in temperature or humidity with height. Humidity could be

similar in the glasshouse and field or it was lower in the glasshouse. Higher humidities in the tube environment may have been one factor affecting leaf temperature which could be even higher than the air temperature in the tube.

The CO_2 level in the tube environment differed from that in the field, it was reduced during the day and raised at night. CO_2 levels were also raised in the glasshouse at night and in the early morning before the vents were opened. Increased concentration of CO_2 in the lower part of the tube (during the day) appeared to be derived from the soil. The size of the tree e.g. height, leaf number, leaf area, within the tube also affects CO_2 levels within the tube, though precise relations were not established.

PART B - EXPERIMENT I

Comparison of the Effects of General Environment, Photoperiod and Hormone Treatment on the Growth of Young Oak Trees.

3B.1 Materials and Methods

The experiment consisted of a factorial combination of field, tube and glasshouse conditions, in natural days or continuous light, with and without gibberellic acid treatment. The experiment extended over two growing seasons from May 1983-October 1984. The twelve treatment combinations are listed in table 3B.1. Factor 1, "environment", will be referred to as FTG-environment. Seedling trees, 120 days old with 15.5 ±5.4 leaves and 21.8 ±8.1cm in height, were divided into 10 blocks of thirteen plants each on the basis of initial size (height) and appearance, judged by eye. Treatments were randomly assigned to the seedlings within each block. One plant of each block was taken at the beginning of the experiment to determine initial dry weight, the remaining 12 plants were allocated to the treatments.

Table 3B.1

Experimental treatments. ND=natural daylength, 24HR=24hour light, $-GA_3$=no gibberellic acid, $+GA_3$=with gibberellic acid (at 50ppm).

FACTOR 1 "ENVIRONMENT"	FACTOR 2 LIGHT	FACTOR 3 HORMONE
FIELD	ND	$-GA_3$
FIELD	ND	$+GA_3$
FIELD	24HR	$-GA_3$
FIELD	24HR	$+GA_3$
TUBE	ND	$-GA_3$
TUBE	ND	$+GA_3$
TUBE	24HR	$-GA_3$
TUBE	24HR	$+GA_3$
GLASSHOUSE	ND	$-GA_3$
GLASSHOUSE	ND	$+GA_3$
GLASSHOUSE	24HR	$-GA_3$
GLASSHOUSE	24HR	$+GA_3$

The experimental plot outdoors was divided into four parts each approximately 3 x 12m, two areas under natural daylength regime, two with 24hour light treatment (fig. 3B.1). Field and tube treatments were divided into two groups of five blocks and seedlings randomly assigned to positions in each area. Thus the seedling trees were blocked according to initial size and appearance, the trees were then planted at random in two rows 1m apart with 1m spacing within rows, but with the restriction that the natural daylength and 24hour light treatments were separated into different areas. In the glasshouse the light treatments had also to be separated, the positions of the trees on the benches was determined using random numbers.

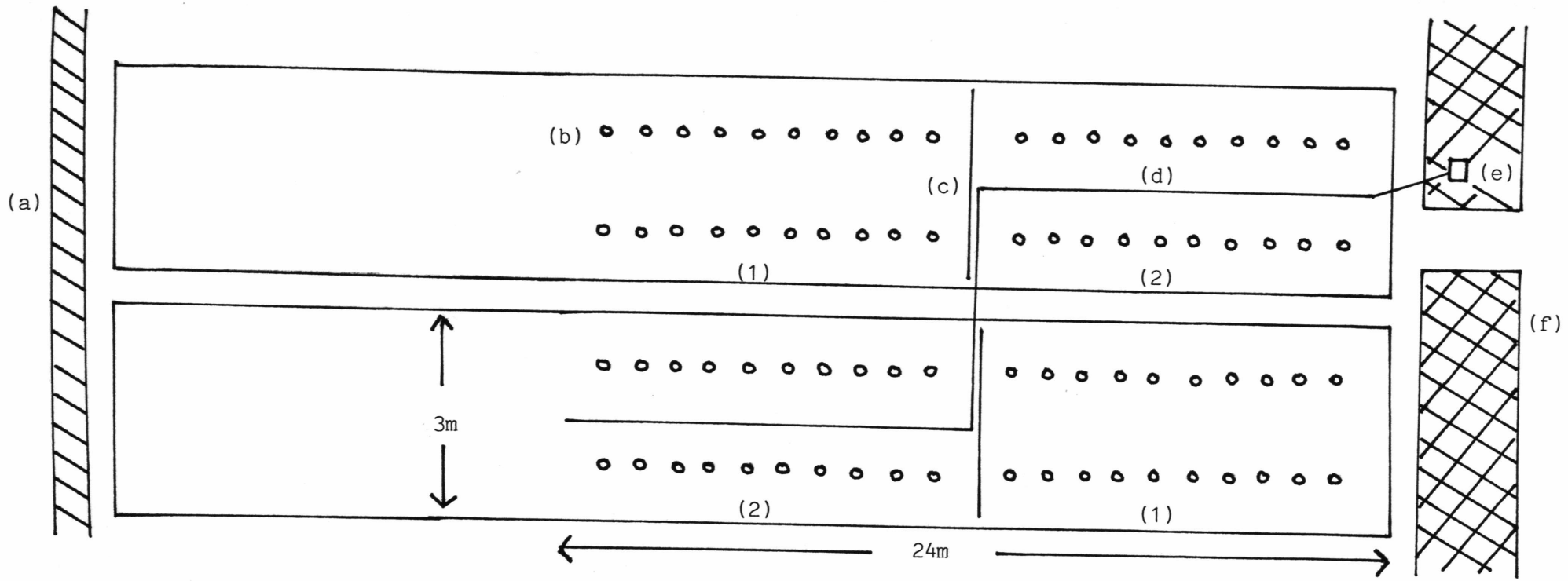
Measurements were taken at the start of the experiment in May 1983 and thereafter in each month throughout the summer i.e. June, July, August and September (n=120), with the final measurements being taken in October when five blocks (n=60) were destructively harvested. Measurements, apart from height, took several days to complete due to the number of trees involved, thus each block of plants i.e. one tree from each treatment, was measured in turn the order in which they were sampled was itself determined by random numbers.

Height measurements were taken at intervals throughout the 1984 season, with the initial height taken on 19/4/84. Other measurements such as numbers of nodes, branches and lengths of stem and its diameter, as well as the number of growth flushes were recorded at the beginning and end of the growing season only. The initial measurements were made prior to bud-burst in field and tube trees and the remaining trees harvested in October 1984.

3B.2 Height Growth in the First Year

Utilising the factorial design of the chief experiment, the data will be presented as main effects and first and second order interactions, where these are statistically significant compared with the error variance.

Two main factors, FTG-environment and hormone, had a significant effect on height growth throughout 1983 (table 3B.2), but light effects did not become significant until September. Prior sorting of the plant material into blocks according to initial height had a significant effect in reducing residual error.



(a) hedge (b) tree (c) mesh screen (d) line of light bulbs (e) time switch (f) glasshouse

Figure 3B.1 Experimental plot showing the positioning of the trees and its division into four areas, (1) two under natural daylength, and (2) two under 24hour light. Not to scale.

Table 3B.2

The effect of main factors FTG-environment, light and hormone on mean height (mm) of seedling oak in 1983.

	MAY	JUNE	JULY	AUG	SEPT	OCT
FIELD	218	236	263	344	422	414
TUBE	214	252	431	708	1107	1298
GLASSHOUSE	220	510	701	984	1173	1324
SIGNIFICANCE	NS	***	***	***	***	***
LSD(P0.05)	12	45	62	85	109	175
NATURAL DAYLENGTH	219	336	454	649	842	903
24HOUR LIGHT	216	329	476	708	960	1121
SIGNIFICANCE	NS	NS	NS	NS	**	**
LSD(P0.05)	10	37	51	69	89	143
-GIBBERELLIC ACID	214	243	360	538	737	861
+GIBBERELLIC ACID	221	422	590	819	1065	1163
SIGNIFICANCE	NS	***	***	***	***	***
LSD(P0.05)	10	37	51	69	89	143
COEFFICIENT OF VARIATION (%)	12.6	30.4	30.2	28.2	27.1	27.1

First-order interactions between FTG-environment and light treatments and hormone and light treatments showed no significant differences however there was a significant interaction between FTG-environment and hormone for the 1983 season from June to October (table 3B.3). Gibberellic acid increased height of trees in the tube and glasshouse environments but not in the field.

The second-order interaction between FTG-environment, light and hormone was significant in July, August and September 1983 and has been represented by Richards' diagrams. In July (fig. 3B.2), two months after application of the treatments, there was no significant effect of gibberellic acid or 24hour light on field trees, in the tube environment however gibberellic acid had increased height both under natural daylength and 24hour light, the latter treatment alone having no significant effect. Glasshouse trees treated with gibberellic acid were significantly taller than trees under other treatments, the

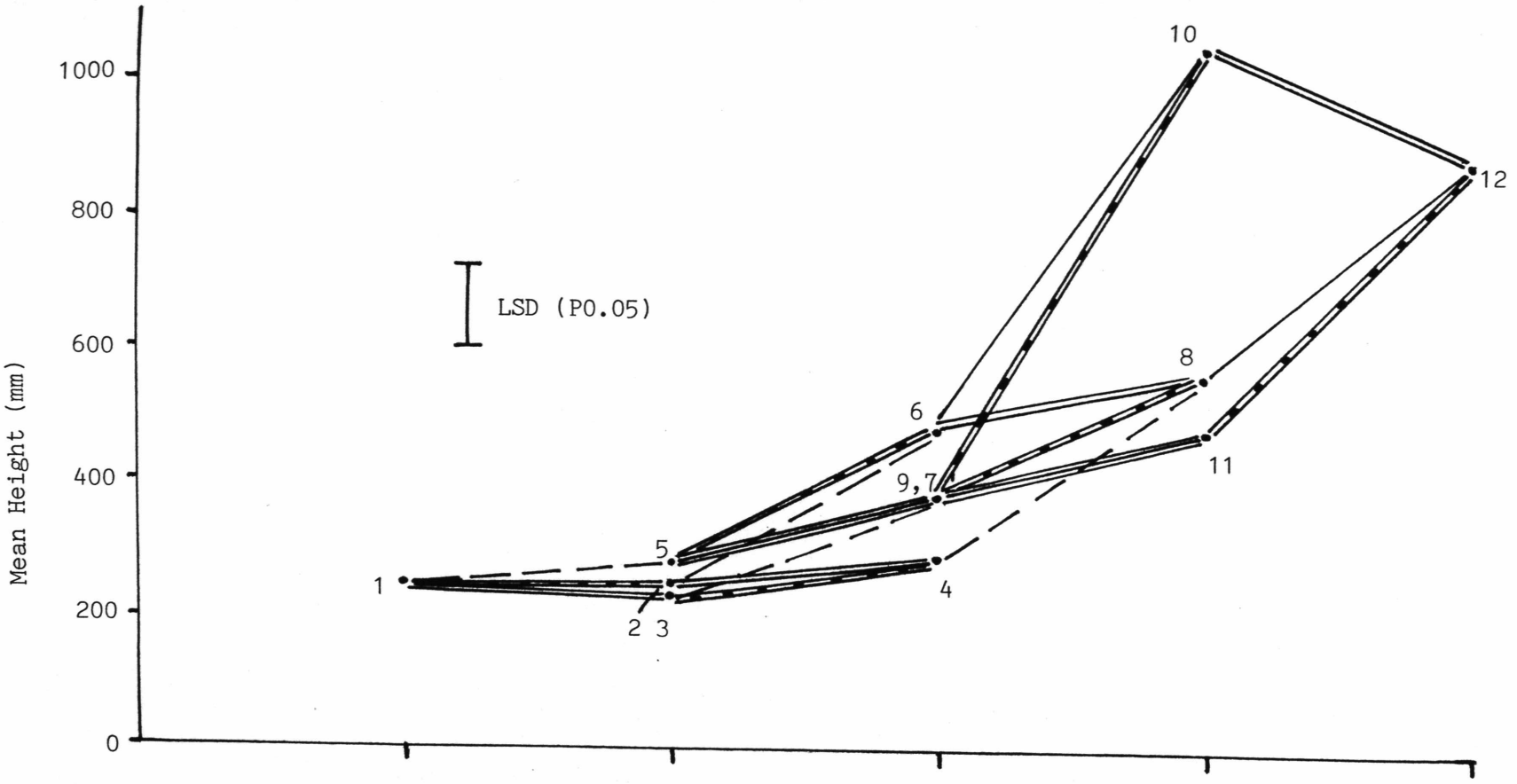


Figure 3B.2 Effect of second-order interaction, FTG-environment x light x hormone, on mean height (mm) in July 1983. For key see Materials and Methods (section 2.14).

greatest height growth being made with gibberellic acid alone and not in combination with 24hour light.

Table 3B.3

Effect of FTG-environment and gibberellic acid on mean height (mm) in 1983.

		MAY	JUNE	JULY	AUG	SEPT	OCT
FIELD	$-GA_3$	221	229	251	326	380	399
FIELD	$+GA_3$	214	242	274	362	464	430
TUBE	$-GA_3$	208	212	336	612	956	1200
TUBE	$+GA_3$	221	282	525	804	1258	1395
GLASSHOUSE	$-GA_3$	213	278	432	677	875	983
GLASSHOUSE	$+GA_3$	228	742	970	1292	1471	1665
SIGNIFICANCE		NS	***	***	***	**	**
LSD(P0.05)		12	64	88	120	154	248

In August (fig. 3B.3) the tube environment had significantly increased height growth compared with trees in the field. The glasshouse environment also increased height growth however there was no significant difference between tube and glasshouse trees grown under natural daylength without hormone treatment.In the field environment there was still no significant effect of gibberellic acid or 24hour light. In the tube and glasshouse environments gibberellic acid increased height growth under both natural daylength and 24hour light, 24hour light alone however had no significant effect in the tube environment but significantly increased the height of glasshouse trees. Gibberellic acid treated trees in the glasshouse continued to be significantly taller than trees under other treatments.

Relations between treatments are most clearly seen in September (fig. 3B.4). In the field environment there was still no significant effect of gibberellic acid or 24hour light. In the tube environment gibberellic acid had significantly increased height growth but 24hour light had no significant effect. Gibberellic acid increased the growth of glasshouse trees, and 24hour light also had a significant effect but there was no further increase in growth with a combination of

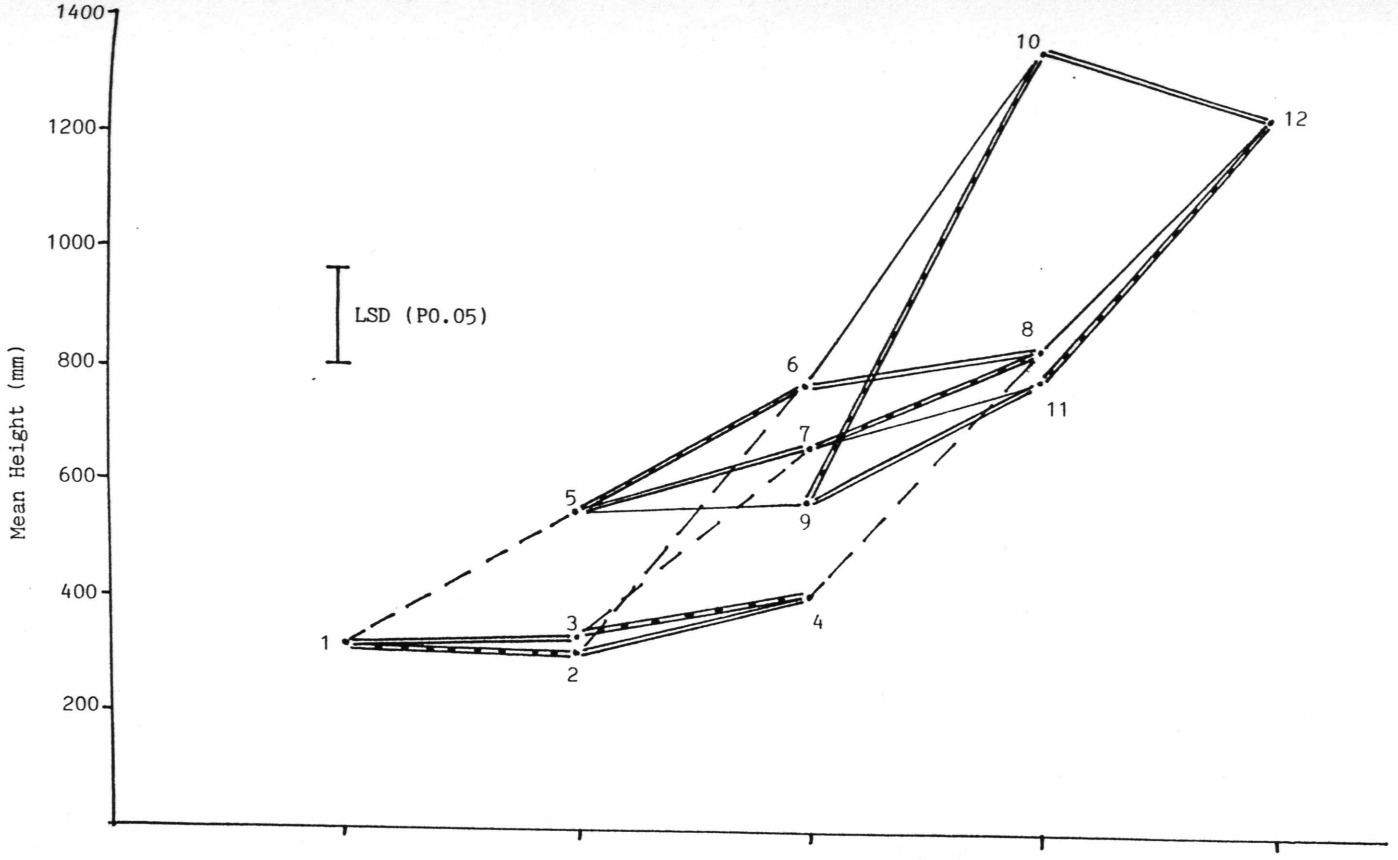


Figure 3B.3 Effect of second - order interaction, FTG-environment x light x hormone, on mean height (mm) in August 1983. For key see Materials and Methods (Section 2.14).

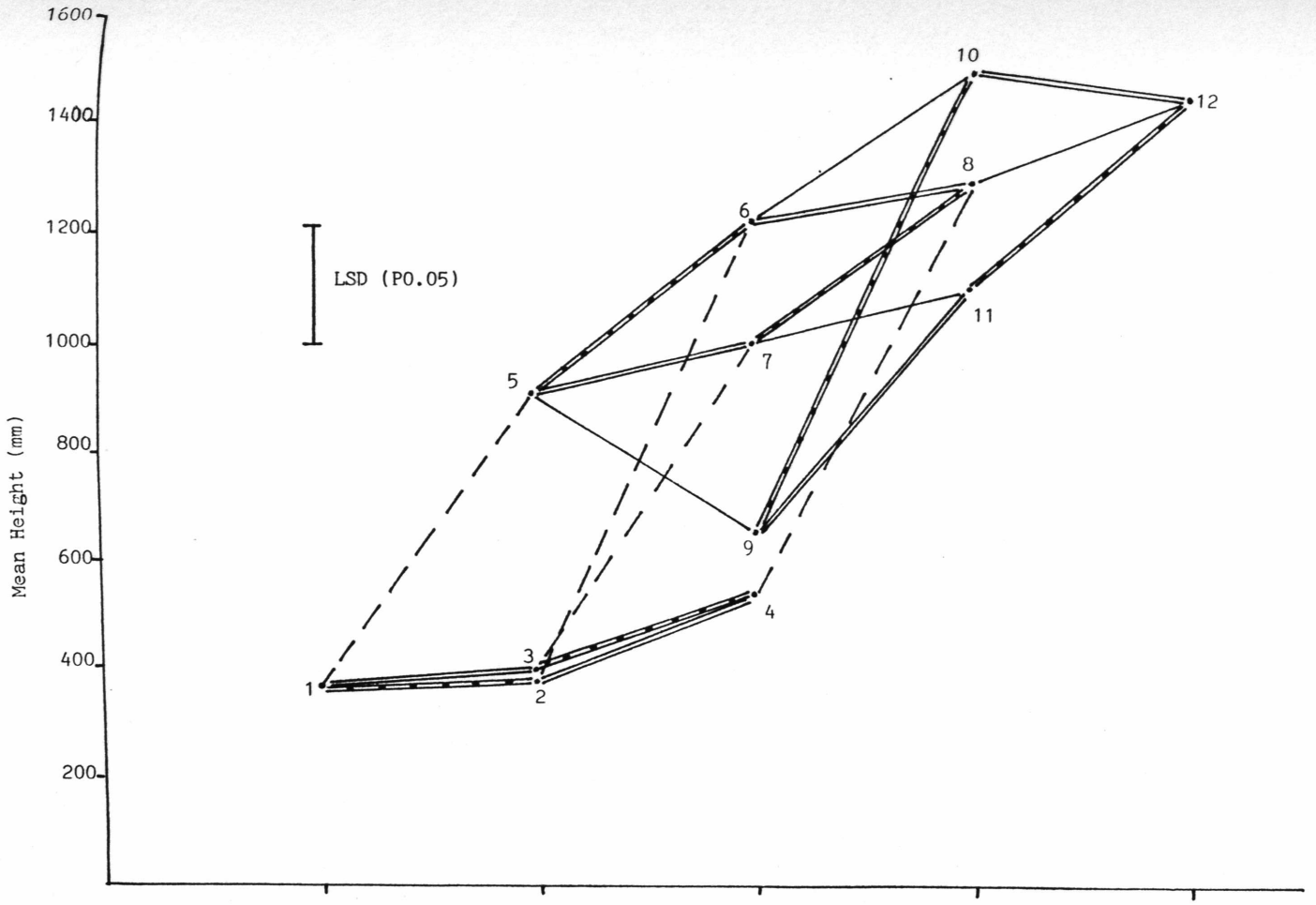


Figure 3B.4 Effect of second - order interaction, FTG-environment x light x hormone, on mean height (mm) in September 1983. For key see Materials and Methods (section 2.14).

gibberellic acid and 24hour light.

Further increases in height growth were seen in the tube environment compared with trees in the field. Trees without hormone treatment under natural daylength in the tube environment achieved greater height growth than those given similar treatment in the glasshouse. Gibberellic acid treated trees in the glasshouse, under both natural daylength and 24hour light, were no longer significantly taller than trees grown with a combination of 24hour light and gibberellic acid in the tube environment.

Gibberellic acid increased height growth, however its effect was only significant in the tube and glasshouse environments. In the tube environment light treatments had no significant affect on the effect of gibberellic acid on growth, however the interaction between glasshouse and gibberellic acid was affected by 24hour light. Growth in the glasshouse environment is compared with that in the tube environment. Under natural daylength the glasshouse environment decreased growth,but a combination of glasshouse +GA_3 gave a greater increase in growth compared with gibberellic acid treatment alone. However under 24hour light the interaction between glasshouse and GA_3 was not significant, a similar increase occurred with gibberellic acid in both tube and glasshouse evironments.

3B.3 Height Growth in the Second Season

After the first growing season tube and glasshouse environments had increased height growth compared with that in the field, with 70% of the tube trees reaching the tops of the tubes. Hormone further increased the growth of tube and glasshouse trees with no significant effect on field trees. The effect of 24hour light increased towards the end of the growing season.

FTG-environment continued to have a strong influence on the growth of oak in the second growing season, 1984, accounting for more than 50% of the variation of height measurements on each occasion. Significant differences were also maintained between light and hormone treatments (table 3B.4).

A significant interaction between FTG-environment and light was apparent through the year (table 3B.5). There was a steady, though non-significant, difference between light treatments in the field, but for tube trees greater height growth was obtained under natural daylength than 24hour light (fig. 3B.5). In the glasshouse, trees under 24hour light were significantly taller than those under a natural daylength

	19/4/84	9/5/84	24/5/84	15/6/84	27/6/84	16/7/84	27/7/84	14/8/84	5/9/84	24/9 84	31/10/84
Field	0.48	0.49	0.53	0.56	0.57	0.68	0.74	0.78	1.00	1.06	1.12
Tube	1.18	1.19	1.22	1.25	1.32	1.46	1.54	1.68	1.85	1.89	1.90
Glasshouse	1.51	1.59	1.71	1.78	1.79	1.86	1.90	2.06	2.17	2.29	2.34
Significance	***	***	***	***	***	***	***	***	***	***	***
LSD(P0.05)	0.16	0.16	0.17	0.17	0.17	0.17	0.16	0.16	0.19	0.21	0.22
Natural daylength	0.93	0.97	1.03	1.06	1.10	1.22	1.29	1.39	1.54	1.60	1.63
24hour light	1.18	1.22	1.27	1.34	1.36	1.44	1.50	1.63	1.80	1.90	1.94
Significance	***	***	**	***	***	**	**	***	**	**	**
LSD(P0.05)	0.13	0.13	0.14	0.14	0.14	0.14	0.13	0.13	0.15	0.17	0.18
-Gibberellic acid	0.92	0.95	1.00	1.03	1.07	1.18	1.25	1.39	1.55	1.65	1.69
+Gibberellic acid	1.18	1.22	1.30	1.36	1.38	1.48	1.54	1.62	1.80	1.85	1.88
Significance	***	***	***	***	***	***	***	**	**	*	*
LSD(P0.05)	0.13	0.13	0.14	0.14	0.14	0.14	0.13	0.13	0.15	0.17	0.18
Blocks	NS	NS	NS	NS	NS	NS	NS	NS	*	*	*
Coefficient of variation (%)	23.2	22.7	23.2	22.1	21.6	19.6	18.6	16.9	17.8	18.7	19.1

Table 3B.4 The effect of significant main factors on the mean height (m): FTG-environment, light and hormone during 1984.

	Field ND	Field 24HR	Tube ND	Tube 24HR	Glasshouse ND	Glasshouse 24HR	Significance	$LSD_{(P0.05)}$
19/4/84	0.40	0.55	1.13	1.22	1.24	1.78	*	0.22
9/5/84	0.42	0.56	1.15	1.23	1.32	1.86	*	0.22
24/5/84	0.46	0.59	1.19	1.25	1.45	1.97	*	0.24
15/6/84	0.49	0.64	1.24	1.27	1.45	2.11	**	0.24
27/6/84	0.50	0.64	1.34	1.29	1.45	2.13	***	0.24
16/7/84	0.61	0.74	1.51	1.41	1.55	2.16	***	0.23
27/7/84	0.66	0.83	1.61	1.46	1.59	2.20	***	0.23
14/8/84	0.69	0.88	1.74	1.62	1.73	2.38	***	0.23
5/9/84	0.91	1.09	1.94	1.77	1.79	2.55	***	0.27
24/9/84	0.96	1.16	1.97	1.80	1.87	2.72	***	0.29
31/10/84	1.02	1.21	1.98	1.82	1.88	2.80	***	0.31

Table 3B.5 Interaction of FTG-environment and light treatments (ND = natural daylength, 24HR = 24hour light) on mean height (m) during 1984.

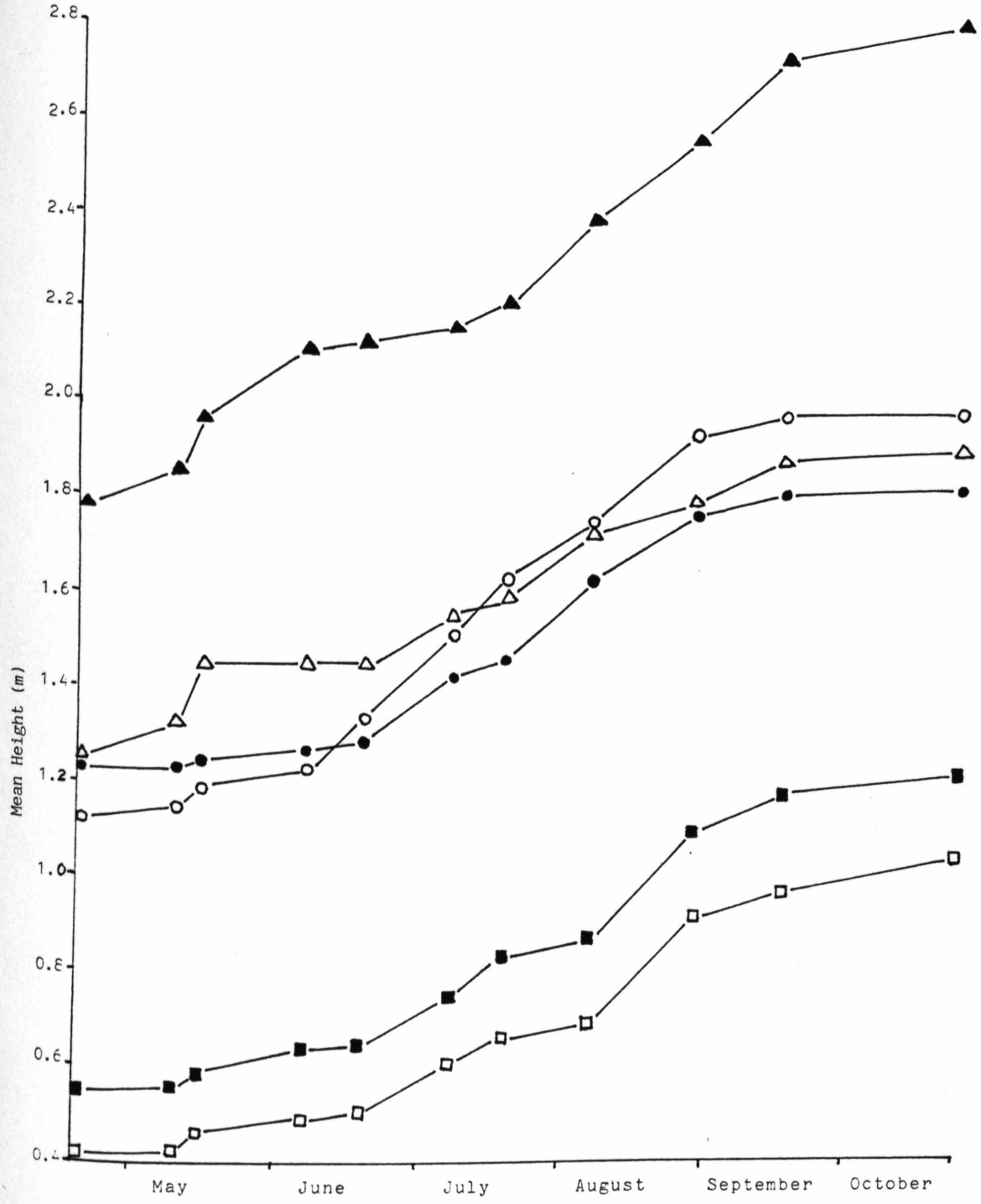


Figure 3B.5 Mean height (m) of oak in field (□), tube (○) and glasshouse (△) under natural daylength (open symbols) and 24hour light (shaded symbols) during 1984 growing season (interaction: FTG-environment and light).

regime, the difference between them increasing from September. Trees in the field and tube and those under natural daylength in the glasshouse lost their leaves and entered a period of dormancy over the winter months, however glasshouse trees under continuous illumination retained their leaves and continued to grow throughout this period.

No gibberellic acid was applied to the trees in the second year and the difference between non-hormone and hormone-treated trees decreased throughout the year (fig. 3B.6).

Second-order interaction, FTG-environment x light x hormone, was significant on four occasions in 1984. For each occasion, 19/4/84, 27/7/84, 14/8/84 and 31/10/84 this interaction has been represented by a Richards' diagram, figures 3B.7, 3B.8, 3B.9 and 3B.10 respectively.

In the field the effect of gibberellic acid and 24hour light treatments did not change through the year, there was some increase with a combination of gibberellic acid and 24hour light but this was not significant. In the tube environment GA_3-treated trees were taller than non-hormone treated trees on 19/4/84 and 27/7/84, with no significant effect of 24hour light on height growth.On 14/8/84 and 31/10/84 there was no significant effect of either gibberellic acid or 24hour light treatments.

The interaction between GA_3 and 24hour light in the glasshouse was similar on 19/4/84, 27/7/84 and 14/8/84. On these occasions there was an increase in height with gibberellic acid and 24hour light but no further increase with both treatments combined. However at the end of the year, 31/10/84, the effect of GA_3 on the growth of trees was affected by the light treatment under which they were grown. There was a significant increase with 24hour light and with gibberellic acid under natural daylength. A combination of 24hour light and GA_3 gave a significant increase in growth compared with hormone treatment alone, but did not increase growth compared with 24hour light alone.

Tube environment gave a significant increase in height over field grown trees. The greatest height growth was achieved in the glasshouse environment under 24hour light, either with or without hormone treatment in the first year. The glasshouse environment alone i.e. trees grown under natural daylength without hormone treatment, however gave no advantage in height growth over the tube environment. 24hour light significantly increased height growth only in the glasshouse environment. Hormone treatment continued to show an effect on the growth of trees in the glasshouse through the second growing season. This was not seen in the tube environment where gibberellic acid did have an effect

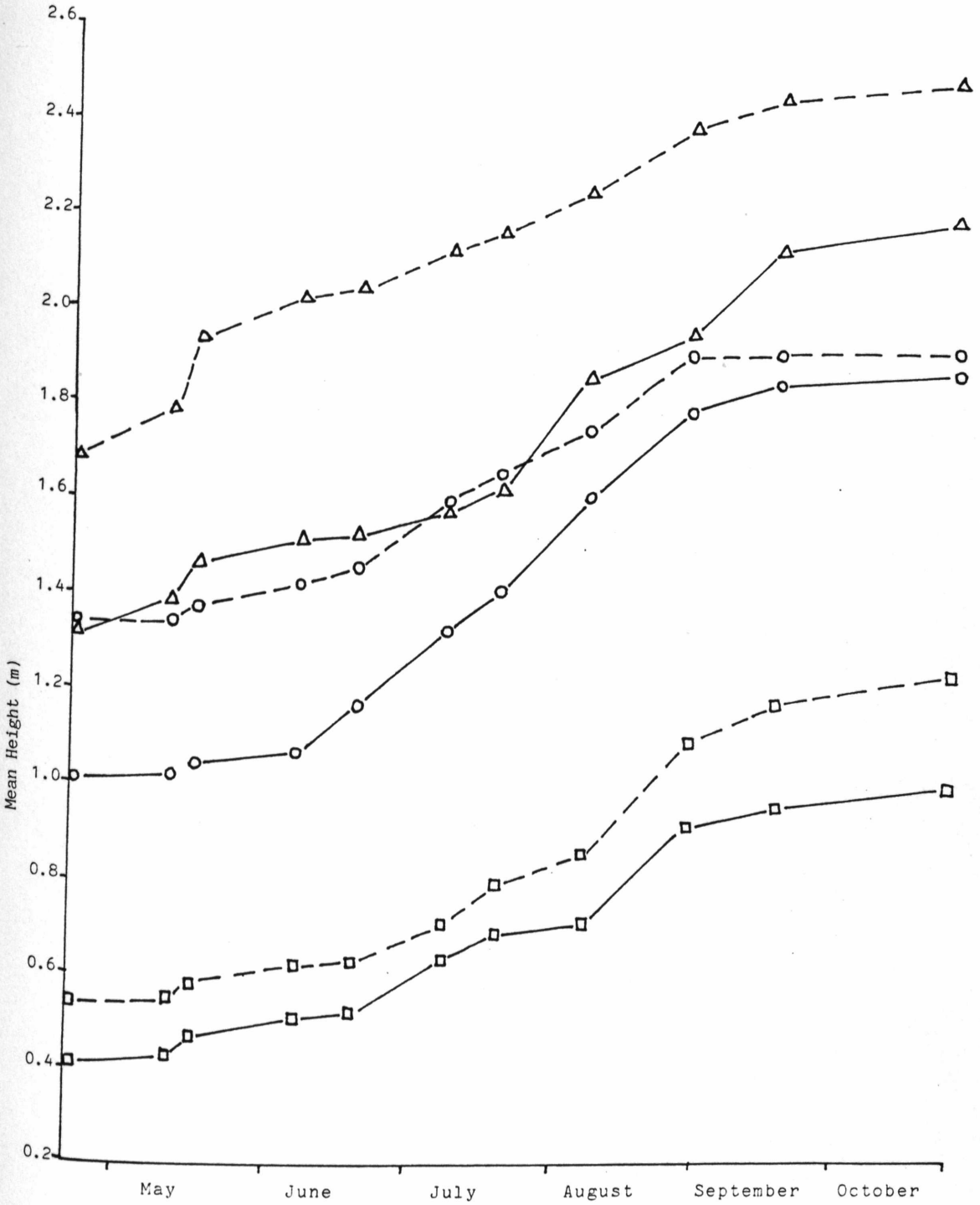


Figure 3B.6 Mean height (m) of oak in field (□), tube (○) and glasshouse (△) with (- - -) and without (———) gibberellic acid during 1984 growing season (interaction: FTG-environment and GA_3 treatment).

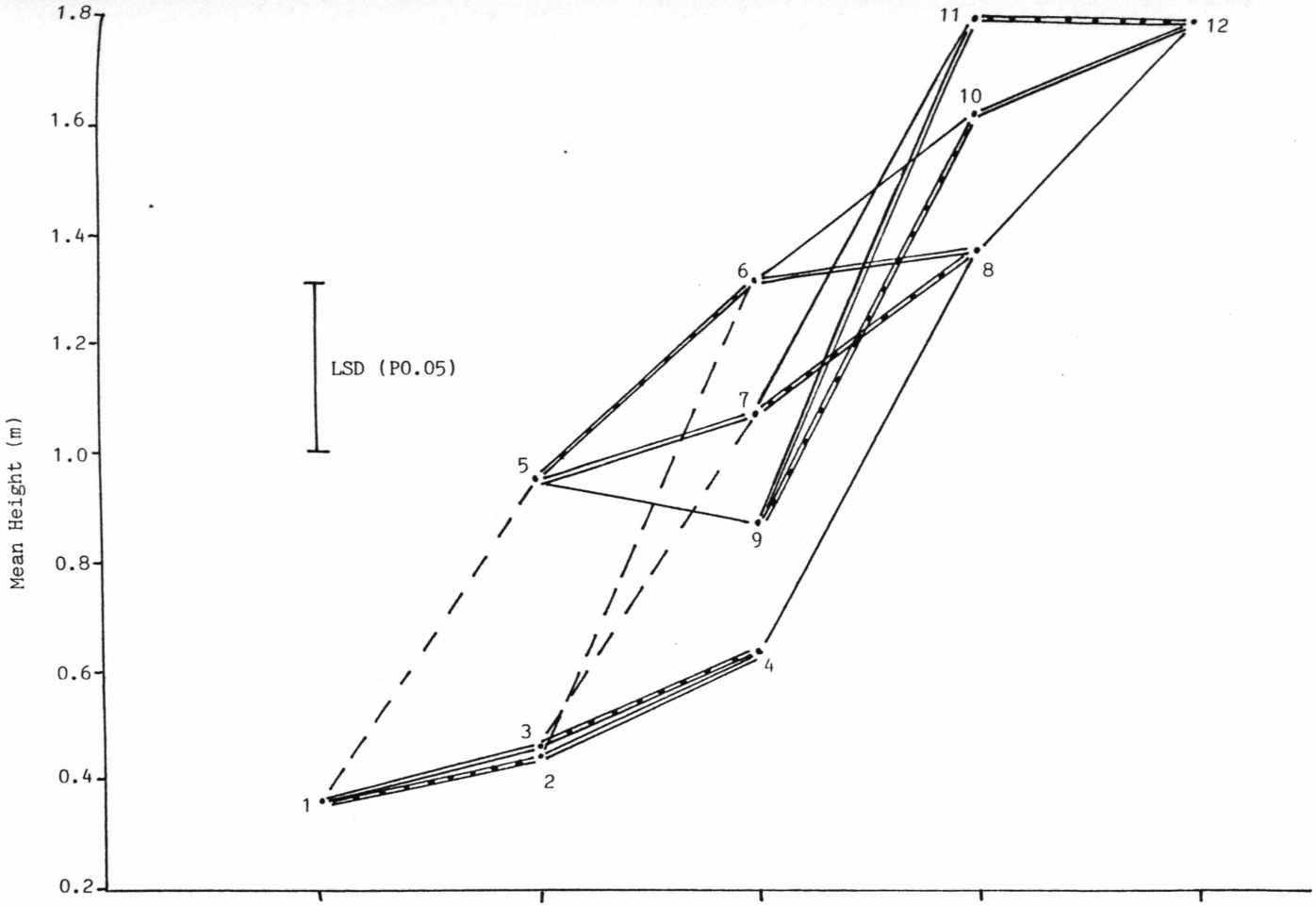


Figure 3B.7 Effect of second - order interaction, FTG-environment x light x hormone, on mean height (m), 19/4/84. For key see Materials and Methods (section 2.14).

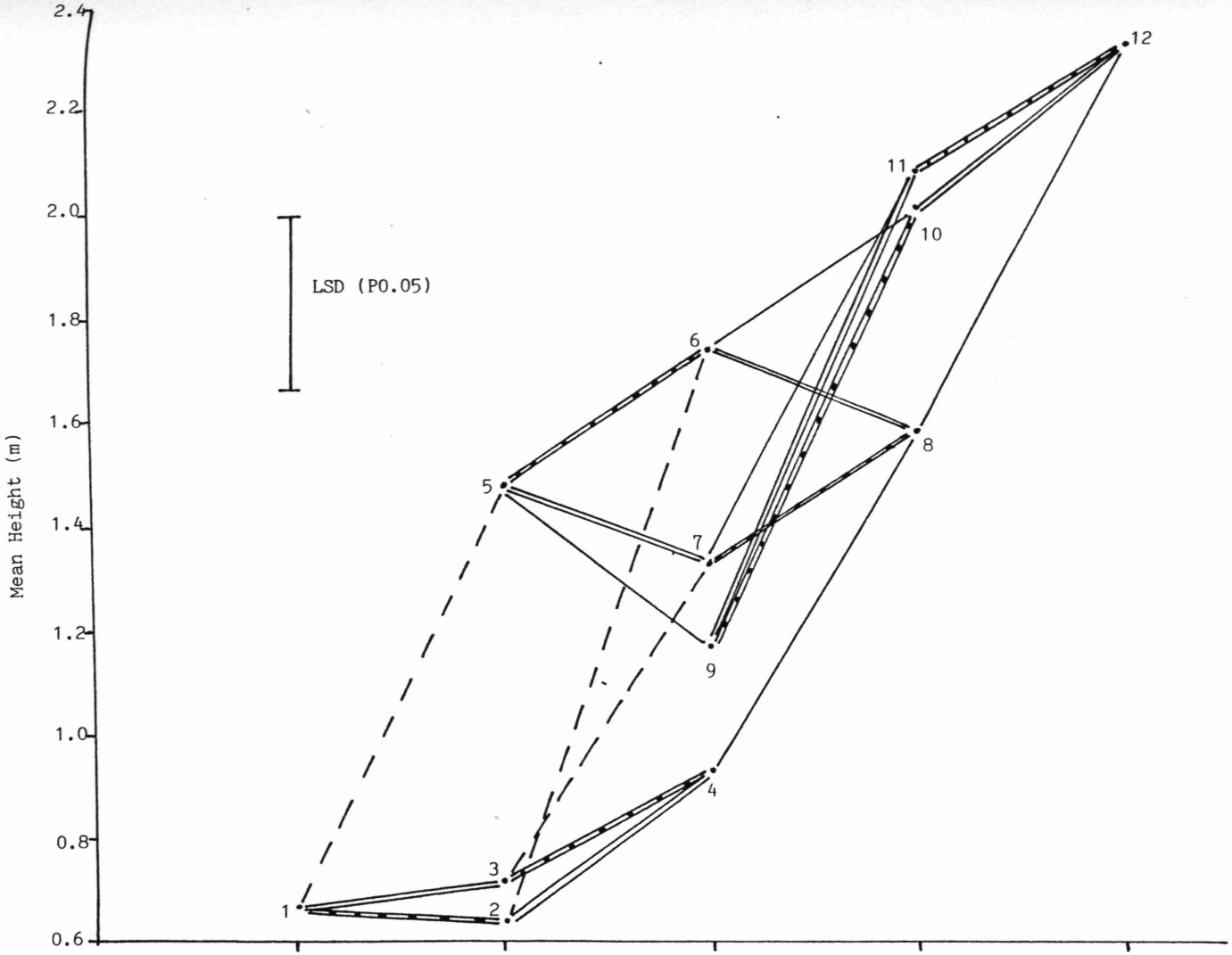


Figure 3B.8 Effect of second - order interaction, FTG-environment x light x hormone, on mean height (m), 27/7/84. For key see Materials and Methods (section 2.14).

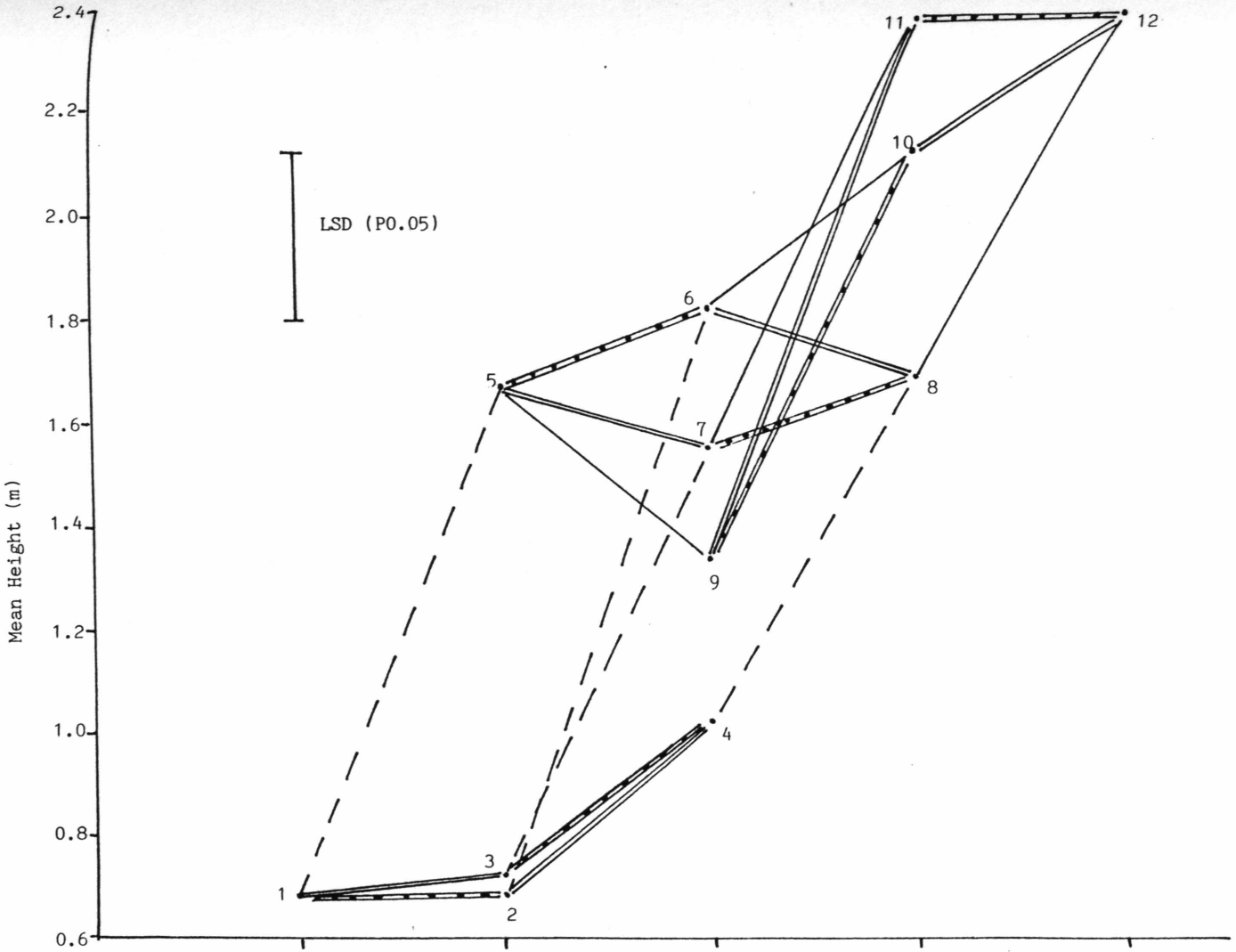


Figure 3B.9 Effect of second - order interaction, FTG-environment x light x hormone, on mean height (m), 14/8/84. For key see Materials and Methods (section 2.14).

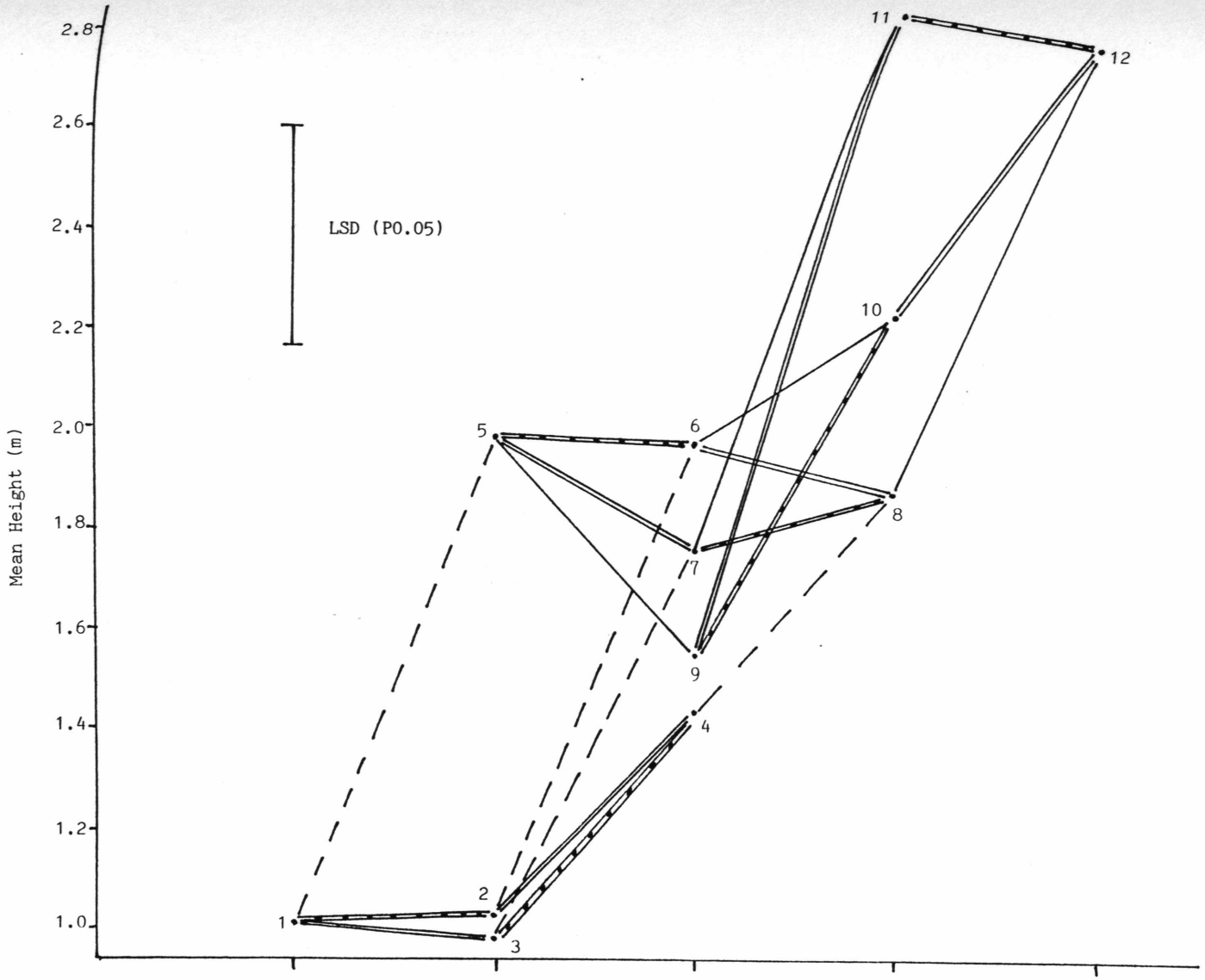


Figure 3B.10 Effect of second - order interaction, FTG-environment x light x hormone, on mean height (m), 31/10/84. For key see Materials and Methods (section 2.14).

on growth in the first year.

3B.4 Date of Bud Break

The date when the first buds had opened was noted and using Kruskal-Wallis one-way analysis of variance by rank (Cohen and Holliday 1982) it was shown that there was no significant difference between the eight treatments in the field and tube environments. It was noted that buds within the tube expanded before those above the top of the tube (fig. 3B.11).

3B.5 Number of Growth Flushes

Table 3B.6

The effect of main factors FTG-environment, light and hormone on the mean number of growth flushes completed.

	MAY 1983	OCTOBER 1983	MARCH 1984	OCTOBER 1984
FIELD	1.8	3.8	4.3	7.0
TUBE	1.8	5.4	5.2	7.7
GLASSHOUSE	2.1	5.1	5.3	8.1
SIGNIFICANCE	**	***	***	**
LSD (P0.05)	0.2	0.4	0.6	0.6
NATURAL DAYLENGTH	2.0	4.5	4.6	7.3
24HOUR LIGHT	1.8	4.9	5.3	7.9
SIGNIFICANCE	*	**	**	*
LSD (P0.05)	0.2	0.3	0.5	0.5
-GIBBERELLIC ACID	1.8	5.1	4.9	7.7
+GIBBERELLIC ACID	1.9	4.4	4.9	7.5
SIGNIFICANCE	NS	***	NS	NS
LSD (P0.05)	0.2	0.3	0.5	0.5
COEFFICIENT OF VARIATION (%)	16.8	12.6	17.9	13.6

FTG-environment, light and hormone had a highly significant effect on the number of flushes completed by the trees assessed in October 1983 (table 3B.6). Tube and glasshouse trees were not significantly different but both had undergone more growth flushes than field trees.



Figure 3B.11 Bud break on a tube grown tree, Spring 1984.

This difference between FTG-environments continued throughout the second growing season. There was an increase under 24hour light and a slight decrease with gibberellic acid by October 1983. Trees under 24hour light continued to show a greater number of flushes than those under natural daylength in 1984. Gibberellic acid had no significant effect on the number of flushes in the second growing season. The interactions between FTG-environment and light, and between FTG-environment and GA_3 treatment were not significant.

There were significant differences between FTG-environments at the start of the experiment. The effect of these differences was studied by analysing the number of flushes completed by October 1983 and October 1984 taking the number of flushes completed at the start of both seasons, May 1983 and March 1984 respectively, as covariate (table 3B.7)

Table 3B.7

The effect of the main factors, FTG-environment, light and hormone on mean number of growth flushes undergone by October 1983 and October 1984. Means adjusted for covariate.

	OCTOBER 1983	OCTOBER 1984
FIELD	3.9	7.5
TUBE	5.5	7.4
GLASSHOUSE	4.9	7.8
SIGNIFICANCE	***	NS
LSD (P0.05)	0.4	0.5
NATURAL DAYLENGTH	4.5	7.6
24HOUR LIGHT	5.0	7.6
SIGNIFICANCE	***	NS
LSD (P0.05)	0.3	0.4
-GIBBERELLIC ACID	5.1	7.7
+GIBBERELLIC ACID	4.4	7.5
SIGNIFICANCE	***	NS
LSD (P0.05)	0.3	0.4
COVARIATE	**	***
COEFFICIENT OF VARIATION (%)	11.5	9.7

By October 1983 tube trees had undergone on average half a flush more than glasshouse trees, and field trees had undergone on average one fewer flushes than in glasshouse trees. The effects of 24hour light (increasing the number of flushes) and gibberellic acid (decreasing the number of flushes) by October 1983 were still apparent. The interactions, however were not significant i.e. the effects of 24hour light and gibberellic acid were manifest in each of the FTG-environments.

When the number of flushes which had occurred by March 1984 were taken as covariate in the analysis of the number of flushes completed by the end of the experiment no significant differences were apparent between FTG-environment, light and hormone treatments. This indicates that trees in the field, tube and glasshouse had produced a similar number of flushes in the second growing season.

The effect of main factors, FTG-environment, light and hormone on the mean length of new stem produced per flush is given in table 3B.8. The results have been divided into pre- and post- treatment after the second flush. The mean length of new growth was increased by the tube and glasshouse environments. Gibberellic acid also increased the mean length of growth flushes, however there is no clear effect of 24hour light particularly for the 3rd, 4th and 5th flushes.

3B.6 Number of Nodes on the Main Axis and Internode Length

Significant differences in the total number of nodes per plant between treatments at the start of the experiment meant that the results for October 1983 had to be analysed taking the number present in May 1983 as covariate. Figures for October 1983 and October 1984 represent the total number of nodes produced during the 1983 and 1984 growing seasons respectively. Figures for May 1983 and March 1984 represent the total number of nodes per plant at the beginning of each growing season. Significant differences were shown between main factors FTG-environment and hormone, but there was no significant effect of light treatments (table 3B.9).

The total number of nodes produced in 1983 was significantly increased by tube and glasshouse environments. By March 1984 the total number of nodes per plant was increased by the tube compared with the field environment, but the largest number of nodes was produced by glasshouse trees. During the 1984 season field and tube trees produced a similar number of nodes, but significantly fewer than the glasshouse trees. Gibberellic acid had a significant effect increasing the total number of nodes produced during both 1983 and 1984 growing seasons.

	Pre - Treatment		Post - Treatment			
	1st Flush	2nd Flush	3rd Flush	4th Flush	5th Flush	6th Flush
Field	136.2 (20)	124.2 (20)	68.2 (20)	109.2 (13)	142.5 (2)	
Tube	118.5 (20)	120.0 (20)	98.8 (20)	396.0 (20)	451.9 (18)	316.0 (10)
Glasshouse	117.1 (19)	149.5 (19)	368.4 (19)	377.1 (19)	315.4 (14)	373.9 (9)
Natural daylength	123.4 (29)	133.9 (29)	154.1 (29)	319.6 (24)	384.4 (16)	190.0 (3)
24 Hour light	124.7 (30)	128.0 (30)	195.7 (30)	315.5 (28)	371.4 (18)	362.7 (13)
-Gibberellic acid	120.8 (29)	125.0 (29)	63.8 (29)	213.7 (28)	334.5 (19)	310.4 (12)
+Gibberellic acid	127.2 (30)	136.7 (30)	283.0 (30)	438.3 (24)	432.0 (15)	390.0 (4)

Table 3B.8 The effect of FTG-environment, light and hormone on the mean length (mm) of new stem per flush, measured in October 1983, number of trees given in brackets.

At the beginning of 1984 gibberellic acid treated trees had a greater number of nodes than non-hormone treated trees.

Table 3B.9

Effect of main factors on the total number of nodes present on the main axis at the beginning and produced during the 1983 and 1984 growing seasons. October 1983 results analysed taking May 1983 as covariate.

	MAY 1983	OCTOBER 1983	MARCH 1984	OCTOBER 1984
FIELD	18.2	15.5	48.6	48.0
TUBE	15.8	60.1	78.6	51.1
GLASSHOUSE	19.9	62.1	112.4	64.3
SIGNIFICANCE	**	***	***	*
LSD (P0.05)	0.6	11.3	11.4	11.7
NATURAL DAYLENGTH	19.0	41.6	75.8	53.5
24HOUR LIGHT	17.0	50.2	84.0	55.4
SIGNIFICANCE	NS	NS	NS	NS
LSD (P0.05)	2.0	9.1	9.3	9.5
-GIBBERELLIC ACID	16.8	37.6	71.9	56.4
+GIBBERELLIC ACID	19.2	54.2	87.9	52.5
SIGNIFICANCE	*	***	**	NS
LSD (P0.05)	2.0	9.3	9.3	9.5
COEFFICIENT OF VARIATION (%)	21.3	36.3	22.5	33.7

Interactions between FTG-environment and light were not significant, neither were the interactions between FTG-environment and hormone except in October 1983. The number of nodes produced during the 1983 season was increased by GA_3 in the tube environment but only significantly increased in the glasshouse environment (fig. 3B.12).

The effect of the main factors FTG-environment, light and hormone on mean internode length of growth produced during the first (1983) and second (1984) growing seasons and for the entire plant at the beginning of each season, May 1983 and March 1984 respectively, are given in table 3B.10. Interactions between FTG-environment and light and FTG-environment and hormone were not significant.

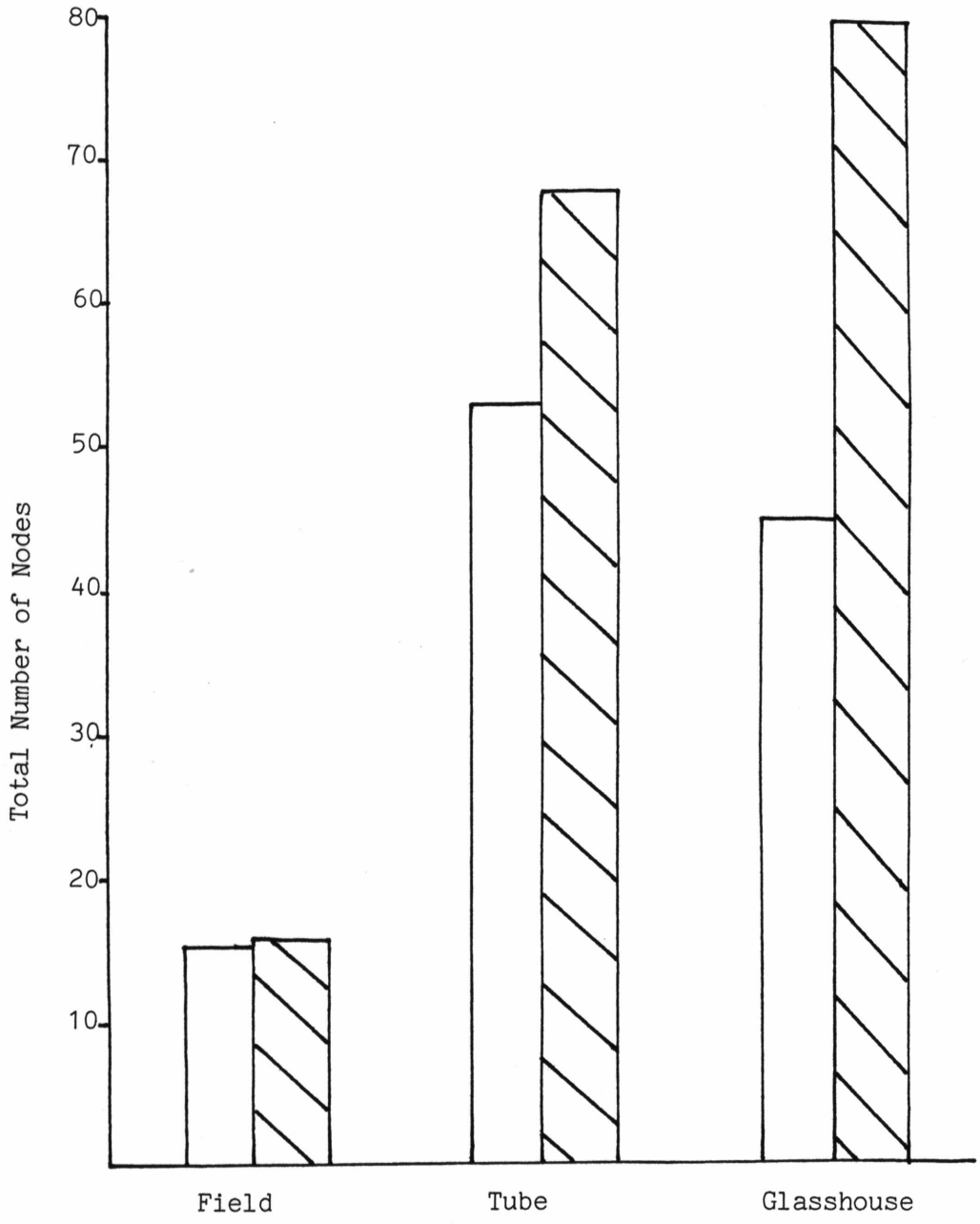


Figure 3B.12 The effect of FTG-envrionment and gibberellic acid (shaded columns) on the total number of nodes produced on the main axis during 1983 growing season, taking May 1983 as covariate LSD (P0.05) 15.7.

The mean internode lengths (for growth produced during 1983) of tube and glasshouse trees were significantly greater than those of field trees. Gibberellic acid also increased mean internode length but there was no significant effect of 24hour light. At the beginning of the second season the difference between field trees and those grown in the tube and glasshouse had been maintained. There was no significant difference between hormone and non-hormone treated trees, but 24hour light significantly increased mean internode length. Growth produced during the second season showed no significant differences between internode lengths.

Table 3B.10

The effect of the main factors on mean internode length (mm of growth made) during the 1983 and 1984 seasons and for the entire plant at the beginning of each season.

	MAY 1983	OCTOBER 1983	MARCH 1984	OCTOBER 1984
FIELD	12.1	7.4	9.9	12.7
TUBE	12.2	14.9	14.9	14.2
GLASSHOUSE	12.0	13.9	13.5	14.3
SIGNIFICANCE	NS	***	***	NS
LSD (P0.05)	1.5	2.1	1.7	2.5
NATURAL DAYLENGTH	12.3	11.3	11.8	13.4
24HOUR LIGHT	11.9	12.8	13.8	14.0
SIGNIFICANCE	NS	NS	**	NS
LSD (P0.05)	1.2	1.7	1.4	2.1
-GIBBERELLIC ACID	12.2	11.2	12.4	14.1
+GIBBERELLIC ACID	12.0	13.0	13.2	13.4
SIGNIFICANCE	NS	*	NS	NS
LSD (P0.05)	1.2	1.7	1.4	2.1
COEFFICIENT OF VARIATION (%)	19.0	27.8	20.9	29.1

3B.7 Branching

At the start of the experiment the majority of seedlings had no branches at all, with the exception of those placed in Block I which had up to 5 small branches. The total number and length of the primary branches was measured on two occasions only, in July and October 1983. The effect of significant main factors, FTG-environment, light and hormone are given in table 3B.11, there were no significant interactions.

In July the total number of primary branches and number of branches per 10cm stem were greatest in the field grown trees and least in the glasshouse, however the mean length of branches was smallest in field trees. Gibberellic acid had reduced the number of branches per 10cm stem in each environment under both light treatments (fig. 3B.13).

By October the branch number per 10cm stem was again greater in the field, however the total number of branches had risen in the tube environment, and the mean length had further increased in the glasshouse. Only 4 trees had secondary branches by October 1983.

The final number of primary branches and number per 10cm stem length in October 1984 were further analysed statistically taking the initial measurements (March 1984) as covariate. The total number of primary branches was not significantly different between the three FTG-environments, however the branch number per 10cm stem was lower in glasshouse grown trees (table 3B.12). The mean length of primary branches was increased by the glasshouse environment. The number of secondary branches was significantly increased on field trees, but the difference between tube and glasshouse trees was not significant. Gibberellic acid increased the number of primary branches in the field, tube and glasshouse under both light treatments.

3B.8 Basal Stem Diameter

After two months growth in 1983 the basal diameter was significantly greater in field trees than in tube or glasshouse grown plants; no significant effects of light and hormone treatments were found (table 3B.13).In October (1983) the basal diameter was not significantly different between the three environments, though the tube trees were some 10% thinner than the field trees. However by March 1984 this effect had become highly significant, tube trees being some 20-24% thinner than the field and glasshouse trees respectively. In both March and October 1984 there was also a significant interaction between environment and light treatments, this was largely due to there being a significant

	Number of Primary Branches		Number of Branches per 10cm Stem Length		Mean Length (mm) of Primary Branches	
	July	October	July	October	July	October
Field	10.7	13.7	4.3	3.5	82.6	128.1
Tube	8.8	20.4	2.1	1.6	113.4	141.9
Glasshouse	6.9	12.3	1.4	1.1	133.2	213.0
Significance	**	**	***	***	***	***
LSD(P0.05)	2.0	4.5	0.7	0.7	26.8	37.5
Natural daylength	8.1	13.4	2.5	1.9	114.0	169.2
24 hour light	9.6	17.5	2.6	2.2	117.4	152.7
Significance	NS	*	NS	NS	NS	NS
LSD(P0.05)	1.6	3.7	0.6	0.6	21.9	30.6
-Gibberellic acid	10.2	17.2	3.3	2.5	122.7	167.5
+Gibberellic acid	7.4	13.7	1.9	1.6	108.7	154.5
Significance	**	NS	***	*	NS	NS
LSD(P0.05)	1.6	3.7	0.6	0.6	21.9	30.6
Coefficient of Variation (%)	51.1	45.8	59.9	53.4	52.1	36.5

Table 3B.11 The effect of main factors, FTG-environment, light and hormone on the mean number and length (mm) of lateral branches, 1983.

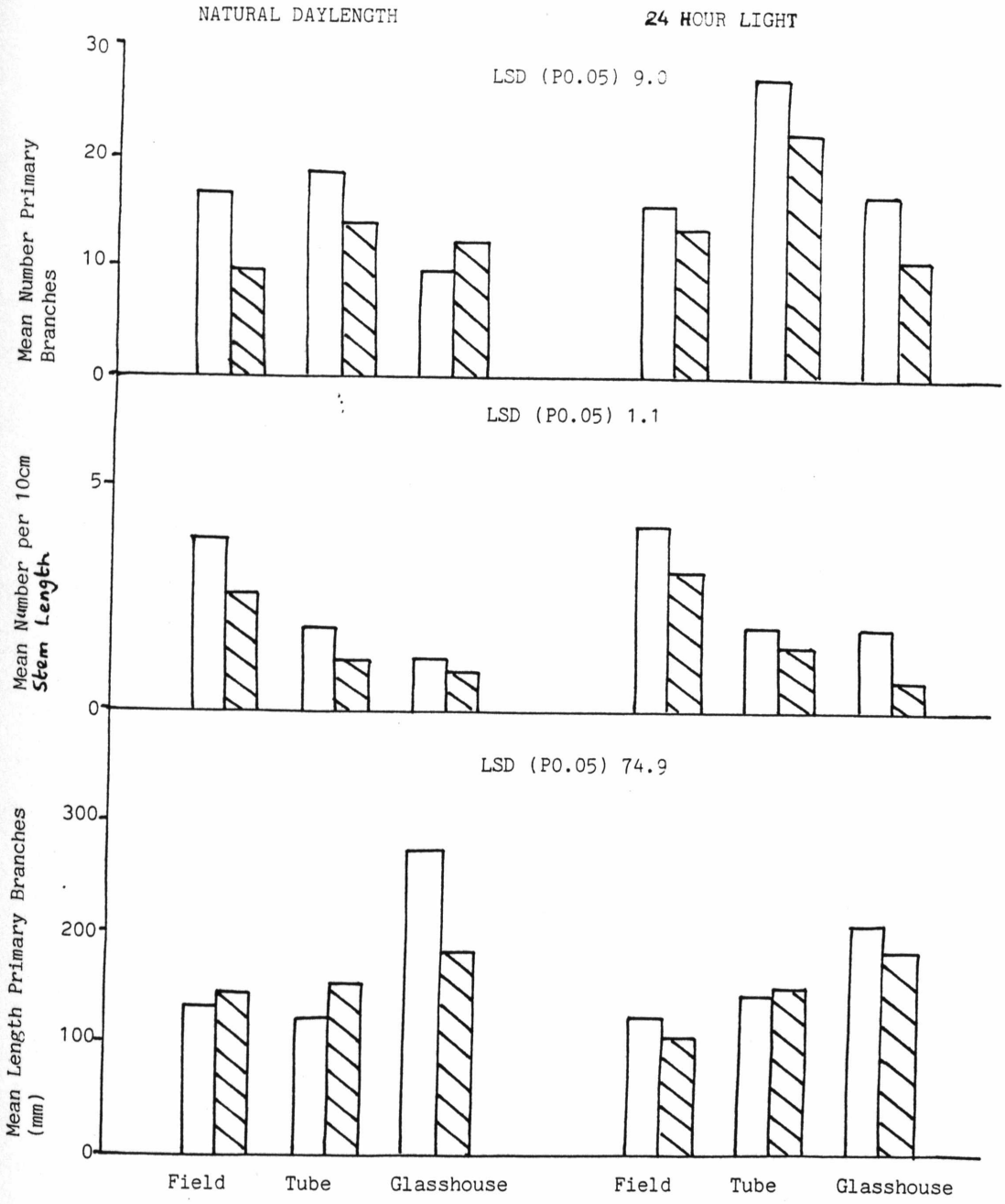


Figure 3B.13 The effect of light treatment and hormone (+GA_3 shaded columns) on the mean number and length of branches of oak in field, tube and glasshouse after one season, 1983.

	Number of Primary Branches		Number of Branches per 10cm Stem Length		No: Secondary Branches	Mean Length (mm) of Primary Branches	
	March	October	March	October	October	March	October
Field	12.4	32.1	2.9	2.6	89.6	155.0	185.0
Tube	14.7	37.4	1.2	2.2	43.8	177.0	181.0
Glasshouse	11.0	29.5	0.7	1.5	25.7	214.0	287.0
Significance	NS	NS	***	*	***	NS	***
LSD(P0.05)	4.8	6.8	0.6	0.7	23.6	64.1	51.7
Natural daylength	10.8	31.8	1.6	2.1	46.0	192.0	204.0
24 hour light	14.6	34.2	1.6	2.2	60.1	172.0	238.0
Significance	NS	NS	NS	NS	NS	NS	NS
LSD(P0.05)	3.9	5.7	0.5	0.4	19.3	52.3	42.2
-Gibberellic acid	13.3	29.0	1.8	1.9	48.0	180.0	224.0
+Gibberellic acid	12.2	37.0	1.4	2.3	58.1	184.0	218.0
Significnace	NS	**	NS	NS	NS	NS	NS
LSD(P0.05)	3.9	5.5	0.5	0.5	19.3	52.3	42.2
Covariate		***		*			
Coefficient of variation (%)	59.9	31.8	62.6	40.8	69.7	55.1	36.6

Table 3B.12 The effect of main factors FTG-environment, light and hormone, on the mean number of primary and secondary branches and mean length (mm) of primary branches at the beginning and end of the second growing season, 1984.

increase in basal diameter of glasshouse trees under 24hour light (fig. 3B.14). The apparent decrease in basal diameter of tube trees between October 1983 and March 1984 was due to sampling error.

Table 3B.13

The effect of main factors FTG-environment,light and hormone on the mean basal diameter (mm) on five sampling occasions.

	1983			1984	
	MAY	JULY	OCTOBER	MARCH	OCTOBER
FIELD	6.5	12.2	18.3	18.6	28.1
TUBE	6.8	10.8	16.5	14.9	20.6
GLASSHOUSE	7.0	11.0	17.8	19.6	26.0
SIGNIFICANCE	NS	*	NS	***	***
LSD (P0.05)	0.5	0.9	1.8	2.1	2.9
NATURAL DAYLENGTH	6.7	11.4	17.7	17.1	24.0
24HOUR LIGHT	6.9	11.2	17.4	18.4	25.9
SIGNIFICANCE	NS	NS	NS	NS	NS
LSD (P0.05)	0.4	0.8	1.5	1.7	2.3
-GIBBERELLIC ACID	6.6	11.2	17.8	17.7	24.6
+GIBBERELLIC ACID	6.9	11.4	17.3	17.8	25.3
SIGNIFICANCE	NS	NS	NS	NS	NS
LSD (P0.05)	15.4	19.1	16.5	18.4	2.3
COEFFICIENT VARIATION (%)	15.4	19.1	16.5	18.4	18.2

3B.9 Stem Diameter at 5cm Above Soil Level

Prior to the application of gibberellic acid to trees in May 1983 there was a slight (0.2mm) but just significant difference between the diameters (at 5cm above soil level) of seedlings assigned to hormone and non-hormone treatments i.e. due to random selection. By July 1983 this difference between GA_3 and control treatments had increased but from the end of the season (October 1983) this difference declined somewhat and was no longer significant, as the error variance increased (coefficient of variation rose from 19.6 to 25.3%) (table 3B.14). After one growing season the diameter at 5cm was significantly greater in

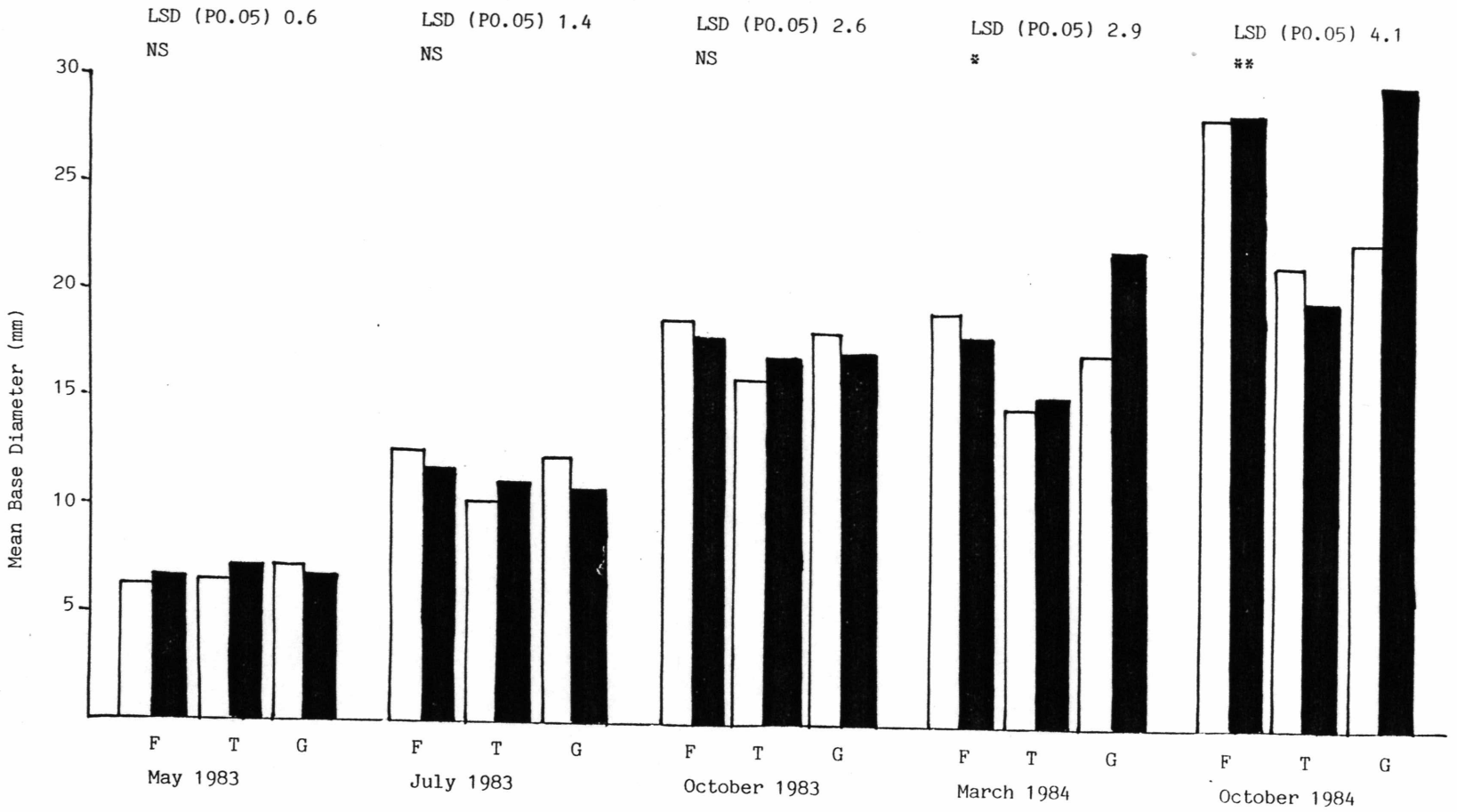


Figure 3B.14 The effect of natural daylength and 24hour light (shaded columns) on the mean basal diameter (mm) of oak in field (F), tube (T) and glasshouse (G).

glasshouse trees, but the difference between field and tube trees was not significant. By October 1984 glasshouse and field trees were no longer significantly different, but in both the diameter at this height was greater than that of tube trees. As with the basal diameter, in October 1984 there was a significant interaction between FTG-environment and light (P0.05). 24hour light had no significant effect on the diameter at 5cm of field and tube trees but increased that of glasshouse trees (fig. 3B.15).

Table 3B.14

The effect of main factors, FTG-environment, light and hormone on the mean stem diameter (mm) at 5cm above soil level on five sampling occasions.

	1983			1984	
	MAY	JULY	OCTOBER	MARCH	OCTOBER
FIELD	4.1	6.5	9.7	11.5	20.9
TUBE	4.3	6.8	10.8	10.8	17.0
GLASSHOUSE	4.2	7.7	12.3	13.8	20.4
SIGNIFICANCE	NS	***	**	**	*
LSD (P0.05)	0.3	0.6	1.4	1.9	2.9
NATURAL DAYLENGTH	4.3	6.9	10.8	11.3	19.1
24HOUR LIGHT	4.2	7.1	11.1	12.7	19.8
SIGNIFICANCE	NS	NS	NS	NS	NS
LSD (P0.05)	0.2	0.5	1.1	1.6	2.4
-GIBBERELLIC ACID	4.1	7.6	10.6	11.7	18.9
+GIBBERELLIC ACID	4.3	7.6	11.3	12.3	19.9
SIGNIFICANCE	*	***	NS	NS	NS
LSD (P0.05)	0.2	0.5	1.1	1.6	2.4
COEFFICIENT OF VARIATION (%)	14.0	19.6	20.6	25.3	23.4

3B.10 Stem Volume

Volume (cm^3) of the stem was calculated assuming the stem to be a series of cylinders each 10cm in height. The diameter of each successive cylinder was taken at its mid point i.e. the stem diameter at 5cm, 15cm, 25cm etc. above soil level. The sum of the volumes of

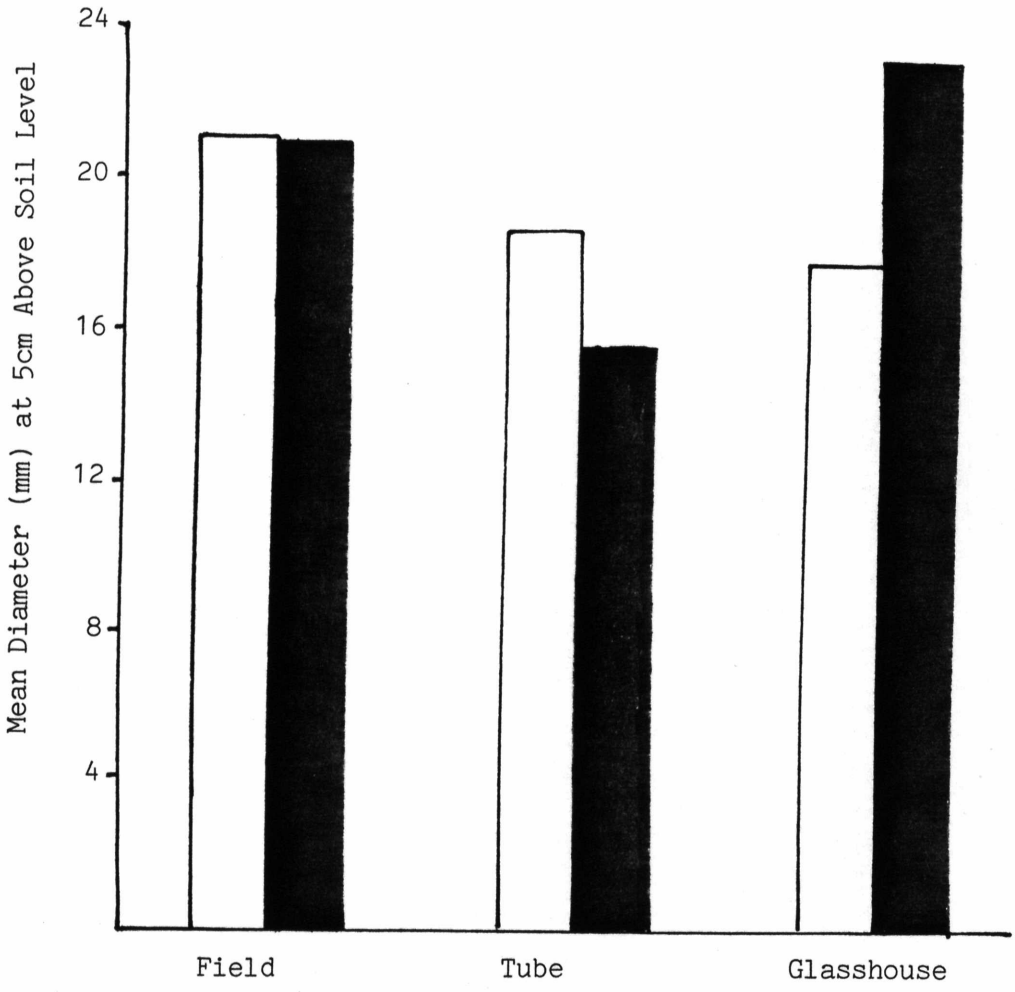


Figure 3B.15 The effect of environment and daylength, natural daylength and 24hour light (shaded columns) on the mean diameter (mm) at 5cm above soil level in October 1984, LSD (P0.05) 4.1.

cylinders was taken as an estimate of stem volume.

Table 3B.15

The effect of main factors, FTG-environment, light and gibberellic acid on an estimate of stem volume (cm^3).

	MAY 1983	JULY 1983	OCTOBER 1983	MARCH 1984	OCTOBER 1984
FIELD	2.45	5.55	14.7	19.2	100.0
TUBE	2.50	8.92	55.8	47.3	186.0
GLASSHOUSE	2.62	15.70	59.1	75.2	250.0
SIGNIFICANCE	NS	***	***	***	***
LSD (P0.05)	0.64	3.05	15.64	16.52	52.4
NATURAL DAYLENGTH	2.61	8.75	36.3	37.4	149.0
24HOUR LIGHT	2.44	11.37	50.2	57.0	208.0
SIGNIFICANCE	NS	*	*	*	**
LSD (P0.05)	0.52	2.49	12.77	13.50	42.7
-GIBBERELLIC ACID	2.31	6.68	35.3	39.5	163.0
+GIBBERELLIC ACID	2.74	13.43	51.1	55.0	195.0
SIGNIFICANCE	NS	***	*	*	NS
LSD (P0.05)	0.52	2.49	12.77	13.5	42.7

Volume was significantly affected by FTG-environment, light and hormone treatments (table 3B.15). After two months growth, in July 1983, the glasshouse environment had significantly increased stem volume compared with the tube and field environments, there was also some increase in the tube environment compared with field grown trees. This trend was also seen at the end of the first growing season and for the two estimates made during the 1984 growing season i.e. the tube and glasshouse environments had significantly increased stem volumes compared with field grown trees. The final mean stem volume of glasshouse trees was 2.5 times that of field trees. 24hour light and gibberellic acid significantly increased volume also.

The interaction between FTG-environment and light was not significant in the 1983 growing season but was significant in March and October 1984. The interaction between FTG-environment and hormone was significant in July and October 1983, but not significant for subsequent occasions. The significant effect of 24hour light was limited to the

glasshouse environment (fig. 3B.16). Gibberellic acid had significantly increased stem volume of tube and glasshouse trees by July 1983, but in October the increase with GA_3 was seen only in glasshouse trees (fig. 3B.17).

Figure 3B.18 shows the shape of the stem in October 1983 as affected by the field, tube and glasshouse environments, averaged over light and hormone treatments. Tube and glasshouse trees had similar stem shape both showing less taper than field trees.

3B.11 Density

Table 3B.16

Effect of main factors, FTG-environment, light and hormone on stem density (g/cm^3).

	OCTOBER 1983	OCTOBER 1984
FIELD	0.697	0.755
TUBE	0.491	0.598
GLASSHOUSE	0.549	0.635
SIGNIFICANCE	***	***
LSD (P0.05)	0.060	0.053
NATURAL DAYLENGTH	0.597	0.683
24HOUR LIGHT	0.561	0.643
SIGNIFICANCE	NS	NS
LSD (P0.05)	0.048	0.043
-GIBBERELLEC ACID	0.590	0.662
+GIBBERELLIC ACID	0.568	0.664
SIGNIFICANCE	NS	NS
LSD (P0.05)	0.048	0.043
COEFFICIENT OF VARIATION (%)	16.1	12.5

Density (g/cm^3) of the stem was calculated by dividing the dry weight of the stem by the estimated stem volume. FTG-environment had a significant effect on density (table 3B.16). In October 1983 field grown trees had the greatest stem density, the glasshouse and tube

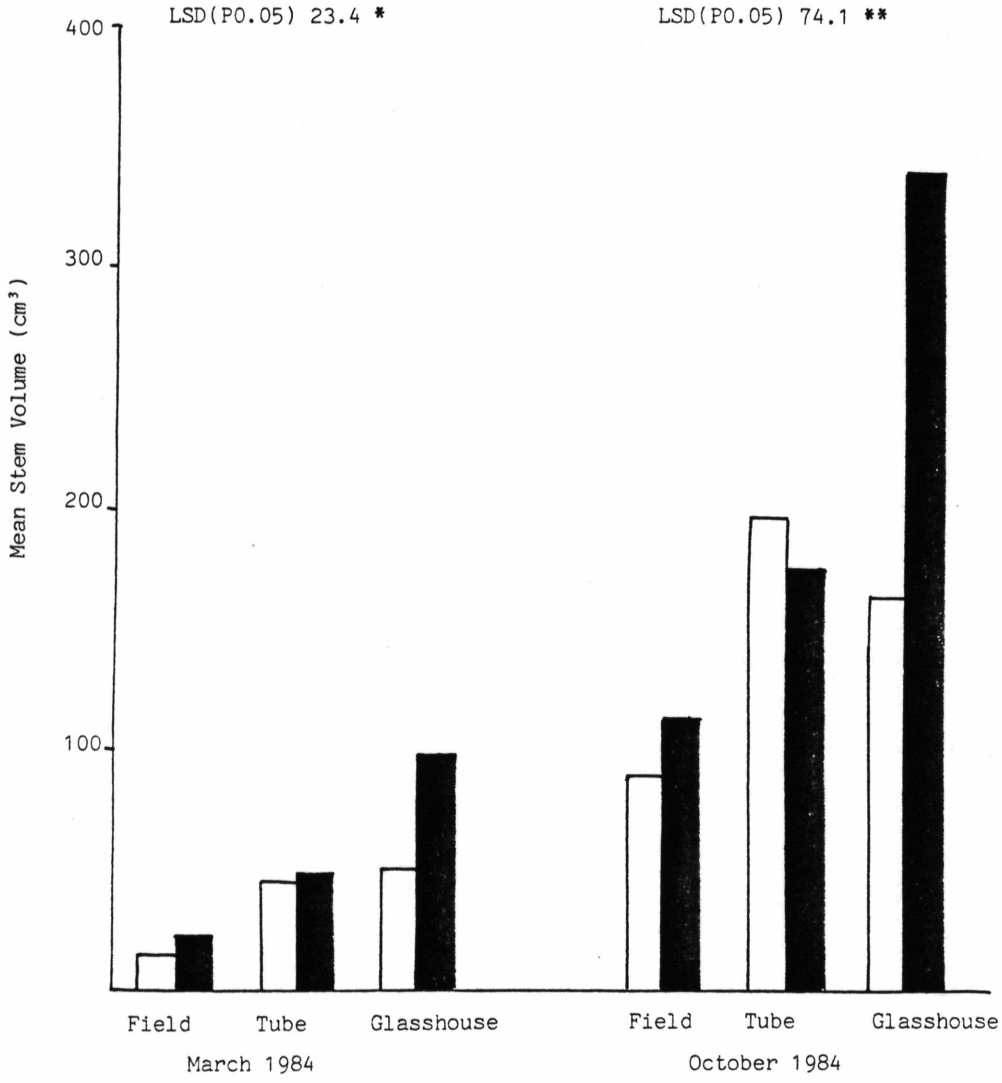


Figure 3B.16 Effect of natural daylength and 24hour light (shaded columns) on mean stem volume (cm^3) in field, tube and glasshouse environments.

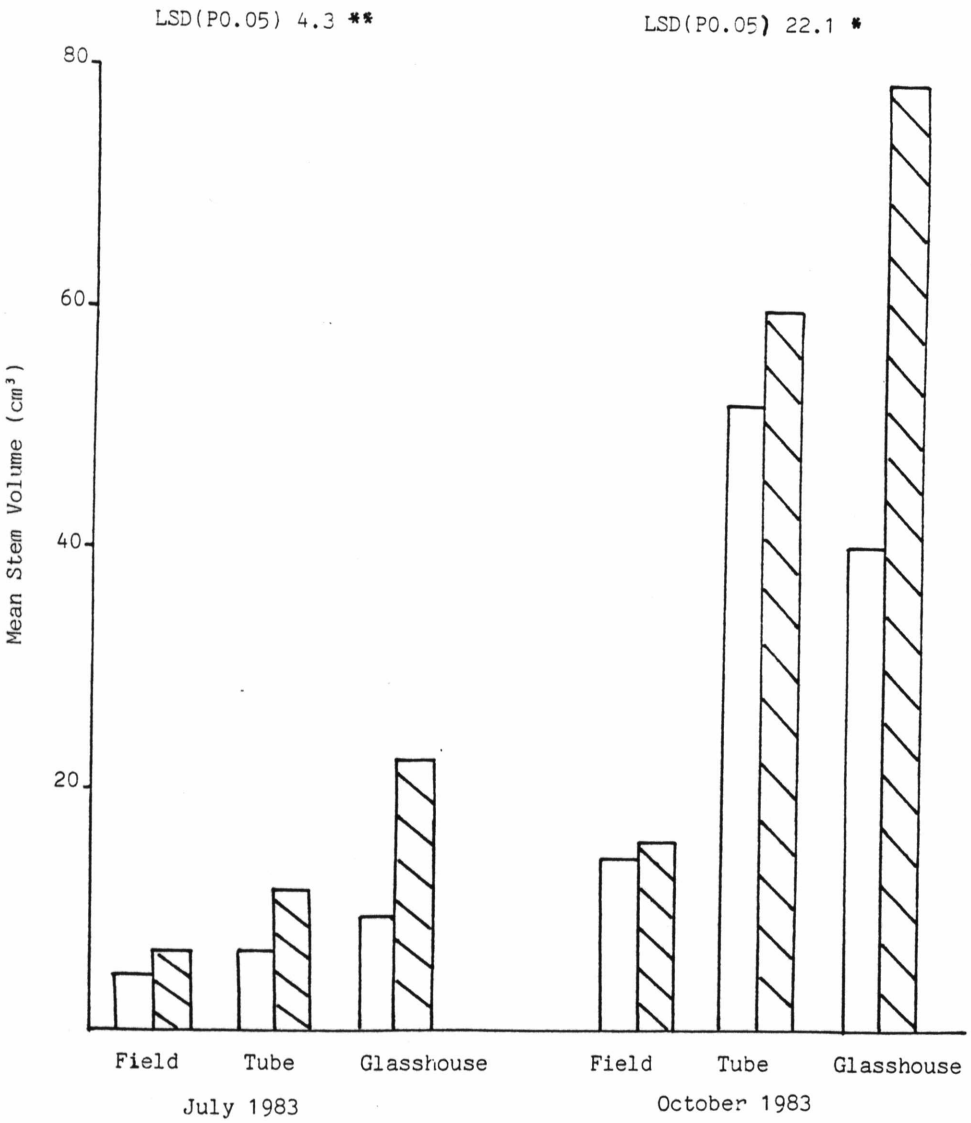


Figure 3B.17 Effect of gibberellic acid (shaded columns) on the mean stem volume (cm^3) of field, tube and glasshouse trees.

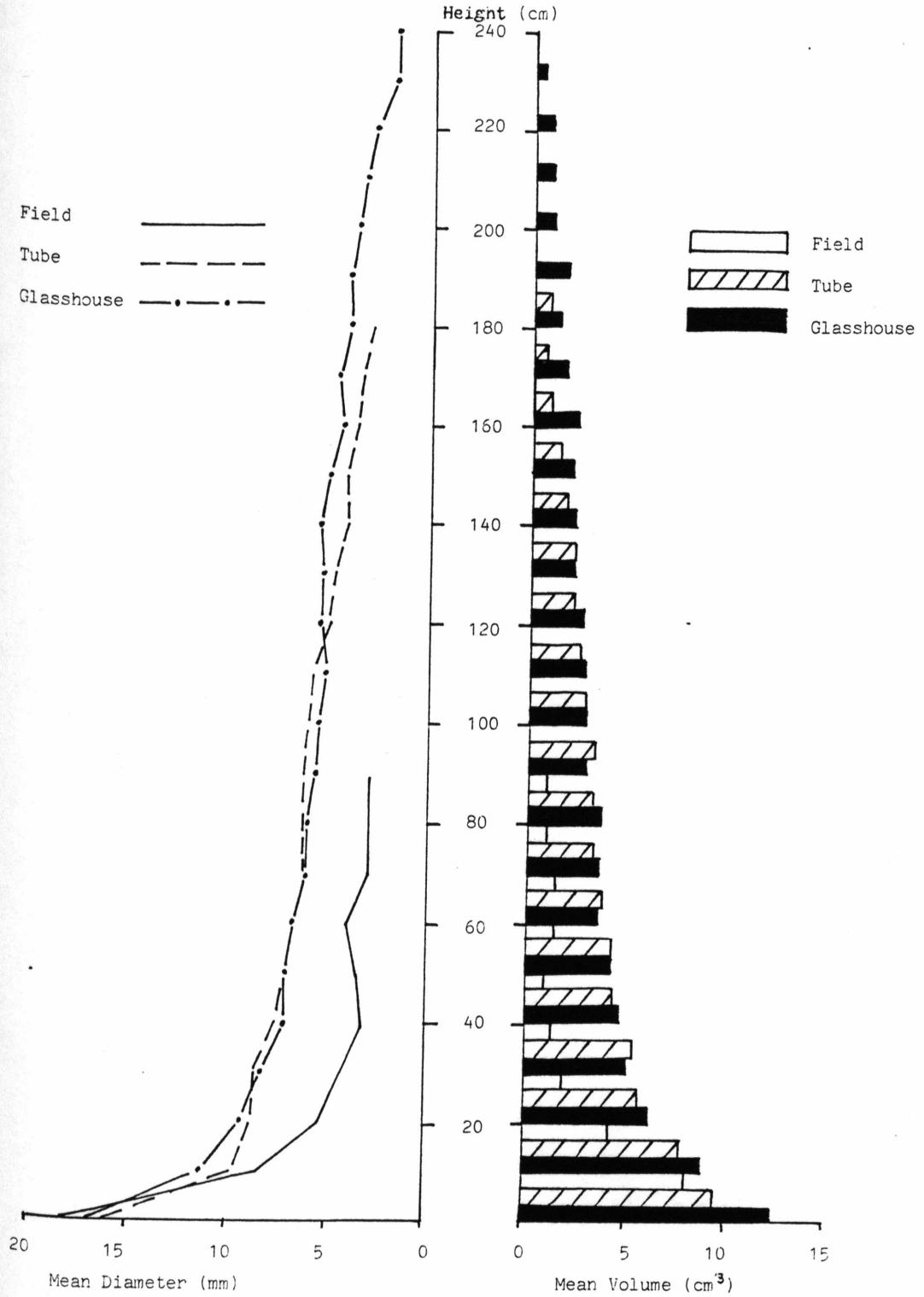


Figure 3B.18 Mean stem diameter (mm) and volume (cm^3) of field, tube and glasshouse trees in October 1983.

environments had a lower density with tube trees having the least dense stems, though the difference between these two environments was not significant. Similar results were obtained at the end of the second growing season. Gibberellic acid and 24hour light had no significant effect on density. Also interactions between FTG-environment, light and hormone were not significant.

3B.12 Wood Anatomy

Table 3B.17

Effect of main factors, FTG-environment, light and hormone on the number of vessels/mm² for transverse stem sections taken in October 1983 and 1984.

	BASE-SECTION 1983	MID-SECTION 1983	BASE-SECTION 1984 1st yr.	BASE-SECTION 1984 2nd yr.	TOP-SECTION 1984
FIELD	69.5	88.4	72.0	28.7	79.9
TUBE	68.7	49.8	82.2	53.1	64.9
GLASSHOUSE	89.2	71.8	66.6	55.9	89.8
SIGNIFICANCE	***	***	***	***	***
LSD (P0.05)	3.8	3.4	2.7	7.3	6.5
NATURAL DAYLENGTH	79.7	73.9	78.8	46.2	82.3
24HOUR LIGHT	71.9	66.1	68.3	45.6	74.1
SIGNIFICANCE	***	***	***	NS	***
LSD (P0.05)	3.1	2.8	3.3	5.9	5.3
-GIBBERELLIC ACID	74.6	76.1	76.9	47.3	72.0
+GIBBERELLIC ACID	77.0	64.0	70.3	44.3	84.4
SIGNIFICANCE	NS	***	***	NS	***
LSD (P0.05)	3.5	2.8	3.3	5.9	5.3

Table 3B.17 gives the effects of main factors, FTG-environment, light and hormone on the mean number of vessels/mm² for transverse sections taken in October 1983 and 1984, results for base sections (1984) have been divided to show differences between the first and second year's growth. There was no consistent relation between the field, tube and glasshouse environments, only one tree was examined

for each treatment, a larger sample may have helped to unravel these puzzling results. Both 24hour light and gibberallic acid appeared to decrease the number of vessels/mm². The number of vessels/mm² for field trees under natural daylength was estimated at 73.5/mm², sections for this treatment were unfortunately lost. Figure 3B.19 shows the number of vessels/mm² for each of the twelve treatments. Vessels are not evenly distributed across the width of the stem since oak had a ring porous structure (fig. 3B.20).

The effect of environment on the size of vessels varied according to the position of the sections and the time they were taken (table 3B.18). In 1983 vessel size was increased in the tube and glasshouse with largest vessels occurring in the tube trees. Field trees had the largest vessels in the 2nd year's growth and glasshouse the narrowest. In the top sections, which for tube trees were taken above the level of the tube (120cm), the tube vessels were again the largest and glasshouse the narrowest. 24hour light and gibberellic acid increased vessel size, though this effect of GA_3 was not seen in the top sections 1984. Frequency disturbution of vessel sizes for base sections (1984) for each of the 12 treatments is given in figure 3B.21.

3B.13 Comparison Between Methods to Assess Leaf Area

The leaf area of ten seedlings (May 1983) was assessed using five different methods, details are given in Materials and Methods. The first two methods were non-destructive (i) conversion of leaf length to leaf area using the relationship Area = 0.2198 Length $^{2.0859}$ and (ii) comparison with leaf shapes of known area. The other three methods were based on measuring the area of the leaves having traced their outlines on paper: (iii) by counting the number of 1mm² squares covered by the leaves, (iv) by weighing the paper and finally (v) using the automatic area measurement system. The total and mean leaf areas for each seedling obtained using these different methods were not significantly different (table 3B.19).

3B.14 Leaf Length - Leaf Area Relations

Leaf area in 1983 was assessed in May, June (n=120), September (n=60) and October (n=48). For measurements up to the final assessment, the leaf lengths of all leaves on each tree were measured and converted into area. In May and June the general relationship
Area = 0.2198 Length $^{2.0859}$ was used, for September leaf area was estimated from leaf length using relationships derived for individual

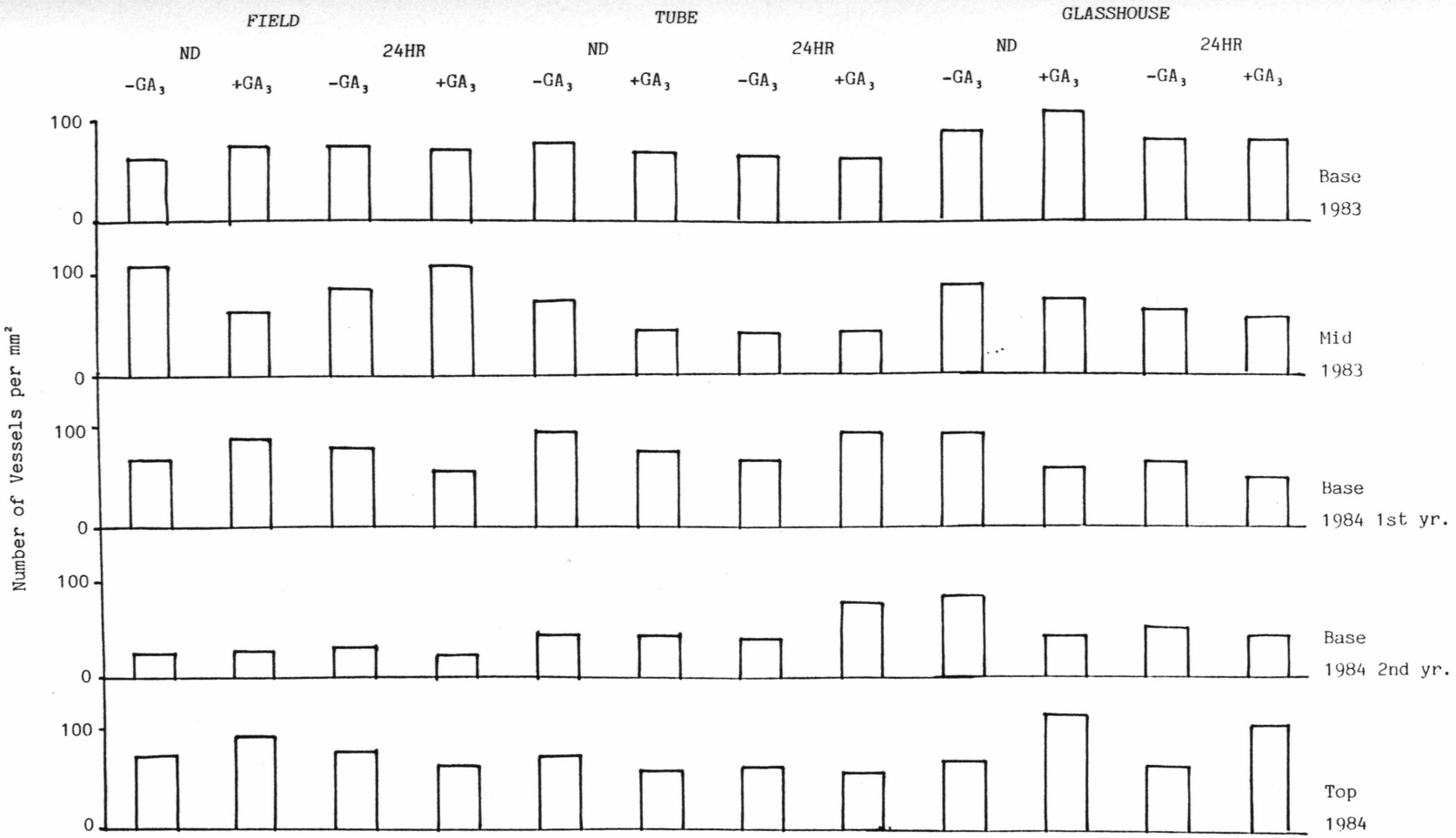
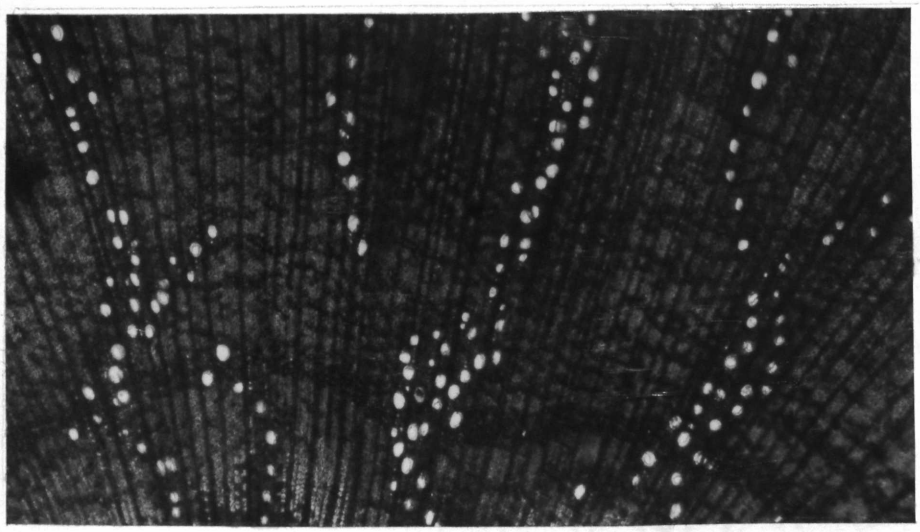
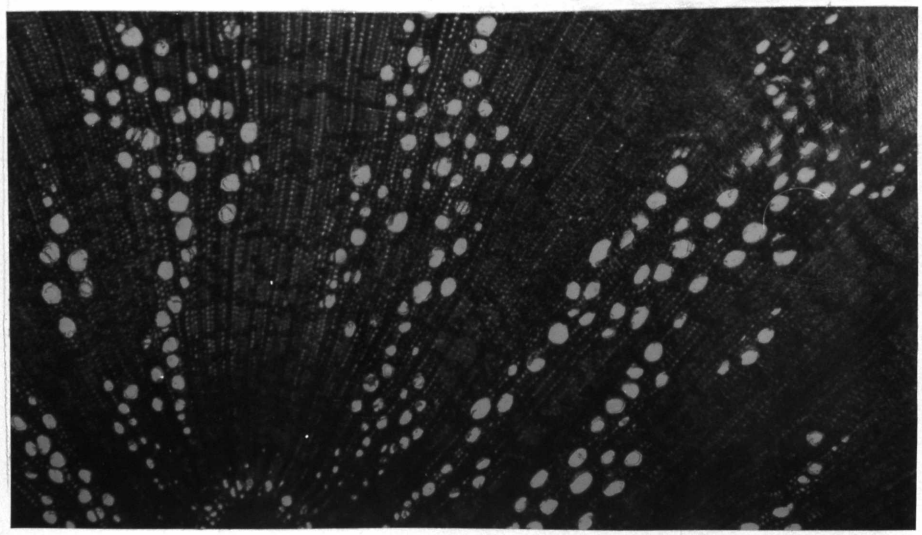


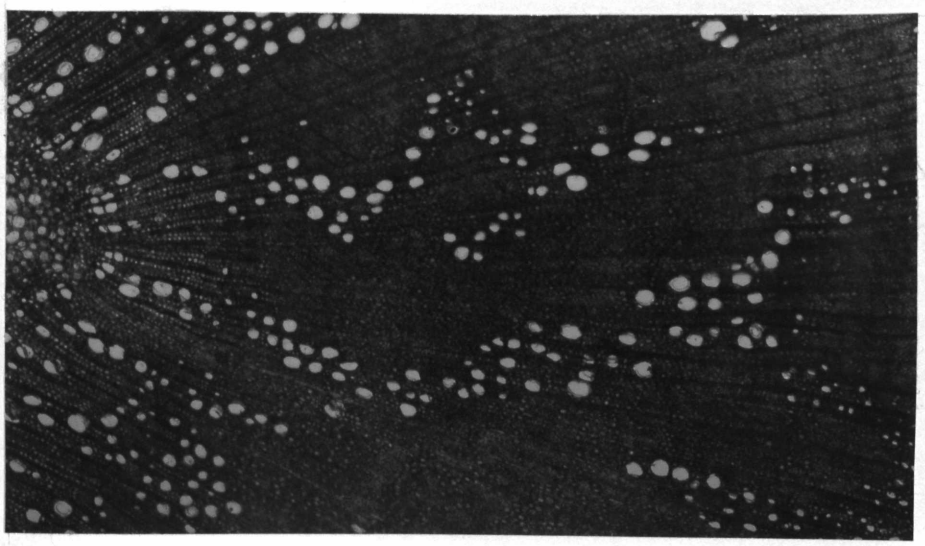
Figure 3B.19 Mean number vessels/mm² for transverse stem sections.



Field



Tube



Glasshouse

Figure 3B.20 Transverse stem sections, 1983. (x32)

	Base-Section 1983	Mid-Section 1983	Base-Section 1984 1st yr.	Base-Section 1984 2nd yr.	Top-Section 1984
Field	2.62 (891)	2.68 (851)	2.65 (1076)	3.98 (1111)	3.33 (948)
Tube	3.85 (975)	4.51 (886)	2.46 (1210)	3.62 (1058)	3.89 (952)
Glasshouse	2.91 (1142)	2.89 (935)	2.55 (1372)	2.52 (1387)	2.83 (1030)
Significance	***	***	*	***	***
$LSD_{max(P0.05)}$	0.13	0.16	0.10	0.15	0.18
Natural daylength	2.98 (1292)	3.20 (1327)	2.42 (1696)	3.24 (1744)	3.16 (1447)
24 Hour light	3.25 (1716)	3.52 (1345)	2.66 (1962)	3.36 (1812)	3.50 (1483)
Significance	***	***	***	NS	***
$LSD_{max(P0.05)}$	0.11	0.14	0.08	0.13	0.15
-Gibberellic acid	2.93 (1694)	3.29 (1315)	2.36 (1730)	3.07 (1818)	3.65 (1457)
+Gibberellic acid	3.39 (1314)	3.43 (1357)	2.72 (1928)	3.54 (1738)	3.02 (1473)
Significance	***	NS	***	***	***
$LSD_{max(P0.05)}$	0.11	0.14	0.08	0.13	0.15

Table 3B.18 Effect of main factors, FTG-environment, light and hormone, on the mean vessel size (mm x 10^{-2}). Number of vessels counted is given in brackets.

$$LSD_{max(P0.05)} = t_{res;P0.05} \cdot s^2 \sqrt{\left(\frac{1}{n_{max}} + \frac{1}{n_{min}}\right)}$$

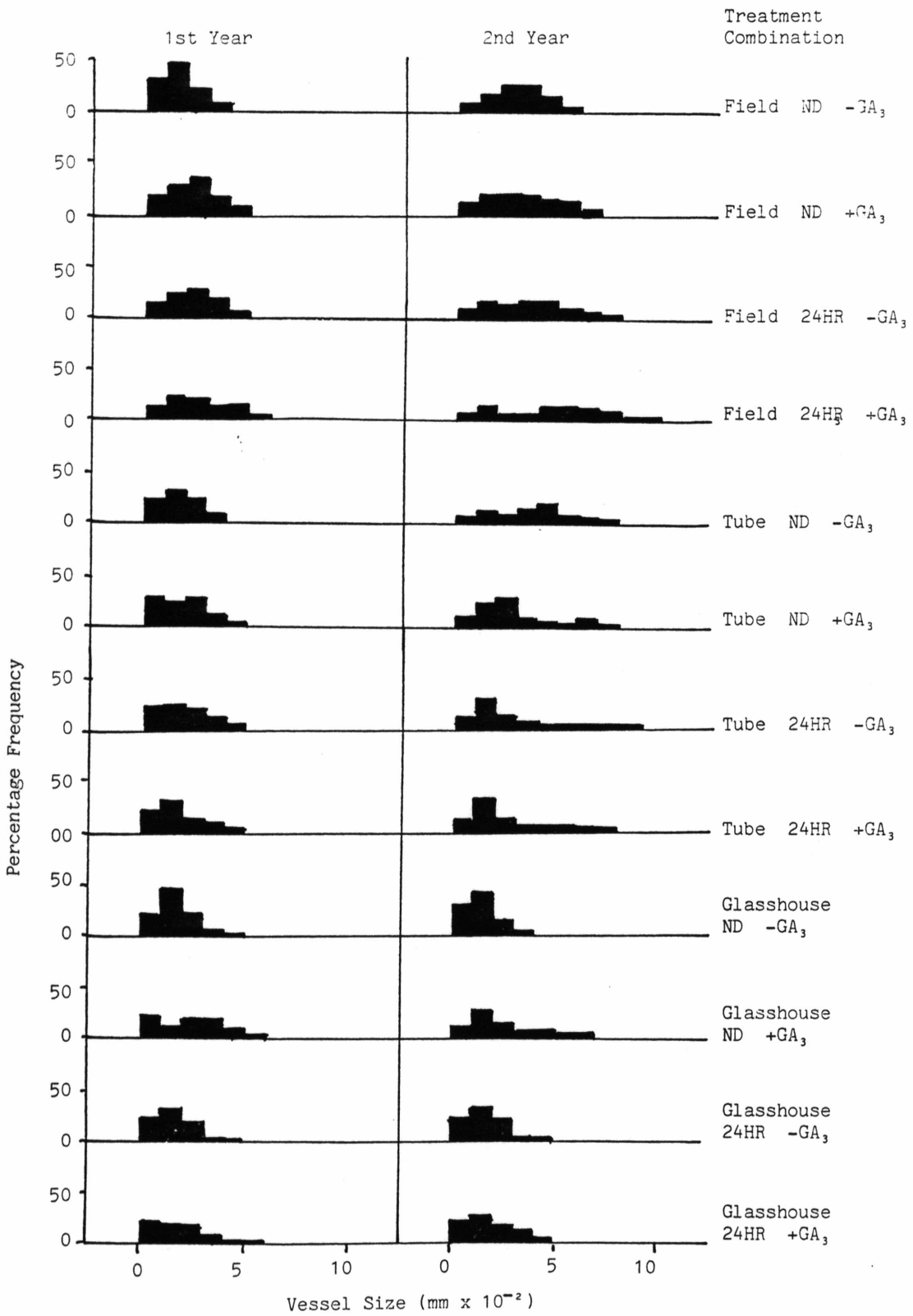


Figure 3B.21 Distribution of mean vessel sizes (mm x 10^{-2}) taken from transverse sections at the base of the stem, October 1984.

	Total Leaf Area (cm^2)					Mean Leaf Area per Leaf (cm^2)				
Tree	(i)	(ii)	(iii)	(iv)	(v)	(i)	(ii)	(iii)	(iv)	(v)
I	417.8	332.7	358.7	373.7	376.2	15.5	12.3	13.3	13.9	13.9
II	64.5	59.1	68.8	67.8	69.4	5.9	5.4	6.3	6.1	6.3
III	344.6	293.5	328.9	335.5	338.3	31.3	26.7	29.9	30.5	30.8
IV	328.6	351.9	398.5	405.9	418.7	20.5	22.0	24.9	25.4	26.2
V	352.5	309.5	353.1	363.2	369.5	27.1	23.8	27.2	27.9	28.4
VI	91.7	93.8	94.6	110.5	111.3	15.3	15.6	15.8	18.4	18.6
VII	419.4	426.9	426.8	441.8	453.4	24.7	21.1	25.1	26.0	26.7
VIII	413.0	418.3	402.0	422.6	431.6	19.7	19.9	19.1	20.1	20.6
IX	410.6	391.1	394.1	418.0	427.3	25.7	24.4	24.6	26.4	26.7
X	165.5	172.7	164.9	176.7	180.1	10.4	10.8	10.3	11.0	11.3
Mean	310.0	286.0	299.0	312.0	318.0	19.6	18.6	19.6	20.5	20.9

Table 3B.19 Leaf area of ten seedling oaks, using 5 different methods of assessment. (i) Conversion of leaf length to leaf area (ii) comparison with leaf shapes of known area (iii) counting $1mm^2$ covered by leaves when traced onto graph paper (iv) weight of paper tracings of leaves and (v) using automatic area measurement system. Details of all methods given in Materials and Methods (Section 2.6f).

treatments to obviate the possibility of systematic errors associated with one or more individual treatments. The final leaf areas, October 1983, were obtained by the weight of paper tracings of the leaves. Then for each treatment the areas of 200 of these 'paper leaves', picked at random, were measured using the automatic area measurement system. These data were used to relate leaf length to leaf area for each treatment using linear regression analysis. Table 3B.20 gives the exponential relationship for each treatment. Regression slopes, b, for the logarithmic relationships between leaf length and leaf area (log y = log a + b log x) for each treatment were compared with the relationship for control trees i.e. in the field under natural daylength without hormone treatment (table 3B.21). Other field treatments were not significantly different from the control trees, however the leaves of the trees of tube and glasshouse treatments showed significant shape differences from the field trees.

3B.15 Leaf Number, Area and Weight

Tube and glasshouse environments had a significant effect on the number of leaves formed after one month's growth, with the largest number of leaves occurring on glasshouse trees (table 3B.22). Later in the year this difference in number of leaves between environments was no longer apparent. 24hour light substantially increased the number of leaves present in September and October. In September also the interaction between FTG - environment and light was significant ($P<0.05$). 24hour light increased the number of leaves of tube and glasshouse trees but not of field trees, increases under 24hour light occurred in all environments in October (fig. 3B.22). Gibberellic acid treatment gave a significant decrease in the number of leaves in October and this occurred in all environments (fig. 3B.23).

Total leaf area was significantly increased in the glasshouse environment by June and in both tube and glasshouse from September. 24hour light had no significant effect on the total leaf area. As with total number of leaves gibberellic acid caused a decrease in total leaf area in October in each environment, some decrease with GA_3 was seen in field and glasshouse trees in September (fig. 3B.24).

Mean leaf area per leaf was significantly greater in the tube and glasshouse environments from September, with the largest leaves occurring on glasshouse trees. The mean leaf area of field and tube trees decreased throughout the year. 24hour light also significantly decreased mean leaf area in September, this effect occurring to some extent in

Treatment			Equation	Variance accounted for (%)	
Field	ND	$-GA_3$	$A=0.8857\ L^{1.7363}$	89.7	***
		$+GA_3$	$A=1.2056\ L^{1.6781}$	95.1	***
	24HR	$-GA_3$	$A=1.4336\ L^{1.6316}$	88.1	***
		$+GA_3$	$A=0.8831\ L^{1.7394}$	89.0	***
Tube	ND	$-GA_3$	$A=0.3986\ L^{1.9333}$	94.1	***
		$+GA_3$	$A=0.4619\ L^{1.9029}$	94.3	***
	24HR	$-GA_3$	$A=0.4900\ L^{1.8811}$	92.0	***
		$+GA_3$	$A=0.2306\ L^{2.0515}$	94.3	***
Glasshouse	ND	$-GA_3$	$A=0.3398\ L^{1.9762}$	96.3	***
		$+GA_3$	$A=0.2459\ L^{2.0154}$	94.5	***
	24HR	$-GA_3$	$A=0.3399\ L^{1.9460}$	94.9	***
		$+GA_3$	$A=0.2804\ L^{1.9973}$	94.1	***

Table 3B.20 Regression analysis of relationship between leaf length (L) and leaf area (A) for oak in the field, tube and glasshouse, under natural daylength (ND) and 24 hour light (24HR), with and without treatment with gibberellic acid (GA_3).

Treatment			Slope b	RMS s^2	r	var(x)	Pooled variance s^2	t_{398}	
Field	ND	$-GA_3$	1.736	0.043	0.947	0.126			
		$+GA_3$	1.678	0.023	0.975	0.160	0.033	1.196	NS
	24HR	$-GA_3$	1.631	0.041	0.939	0.115	0.042	1.767	NS
		$+GA_3$	1.739	0.034	0.943	0.092	0.039	0.054	NS
Tube	ND	$-GA_3$	1.933	0.038	0.971	0.161	0.041	3.672	***
		$+GA_3$	1.903	0.024	0.971	0.113	0.034	3.124	**
	24HR	$-GA_3$	1.881	0.043	0.959	0.139	0.043	2.539	*
		$+GA_3$	2.051	0.041	0.971	0.159	0.042	5.755	***
Glasshouse	ND	$-GA_3$	1.976	0.020	0.981	0.133	0.032	4.850	***
		$+GA_3$	2.015	0.035	0.972	0.149	0.039	5.211	***
	24HR	$-GA_3$	1.946	0.032	0.974	0.156	0.038	4.013	***
		$+GA_3$	1.997	0.446	0.970	0.179	0.044	4.784	***

Table 3B.21 Comparison of regression slopes,b, logarithmic relationships between leaf length and leaf area for each treatment with the field trees without hormone treatment under natural daylength.

$$t_{(n_1+n_2-2)} = \frac{t_1 - b_2}{\sqrt{s^2\left(\frac{1}{S_{xx_1}} + \frac{1}{S_{xx_2}}\right)}}$$

$$S_{xx} = (n-1).var(x)$$

	Total Number of Leaves in First Year				Mean Total Leaf Area (cm^2)				Mean Leaf Area per Leaf (cm^2)			
	May	June	Sept	Oct	May	June	Sept	Oct	May	June	Sept	Oct
Field	15.9	16.0	235	240	292	275	2344	2013	17.6	17.2	9.8	8.7
Tube	15.5	26.4	282	286	283	323	3334	2860	18.0	14.7	12.7	10.9
Glasshouse	15 2	64.2	251	258	264	871	3969	3681	17.2	14.6	16.9	15.1
Significance	NS	***	NS	NS	NS	***	***	***	NS	NS	***	***
LSD(P0.05)	1.6	8.8	55	81	321	93	771	748	2.0	2.5	2.6	2.3
Natural daylength	15.9	35.0	226	219	286	481	3071	2599	17.6	15.4	14.4	12.5
24 hour light	15.2	36.0	286	305	273	498	3361	3104	17.7	15.6	11.9	10.6
Significance	NS	NS	**	*	NS	NS	NS	NS	NS	NS	*	NS
LSD(P0.05)	1.3	7.2	45	66	26	75	629	611	1.6	2.0	2.1	1.9
-Gibberellic acid	15.3	32.8	277	307	267	441	3480	3332	17.3	15.8	12.5	11.5
+Gibberellic acid	15.7	38.2	235	217	292	539	2951	2371	17.9	15.2	13.7	11.6
Significance	NS	NS	NS	*	NS	NS	NS	**	NS	NS	NS	NS
LSD(P0.05)	1.3	7.2	45	66	26	76	629	611	1.6	2.0	2.1	1.9
Number of Blocks	10	10	5	4	10	10	5	4	10	10	5	4
Coefficient of variation (%)	23.1	55.7	34.0	43.0	25.8	42.5	37.6	36.4	25.4	35.7	31.3	28.2

Table 3B.22 The effect of main factors, FTG-environment, light and hormone on mean number of leaves and mean leaf area of oak during 1983.

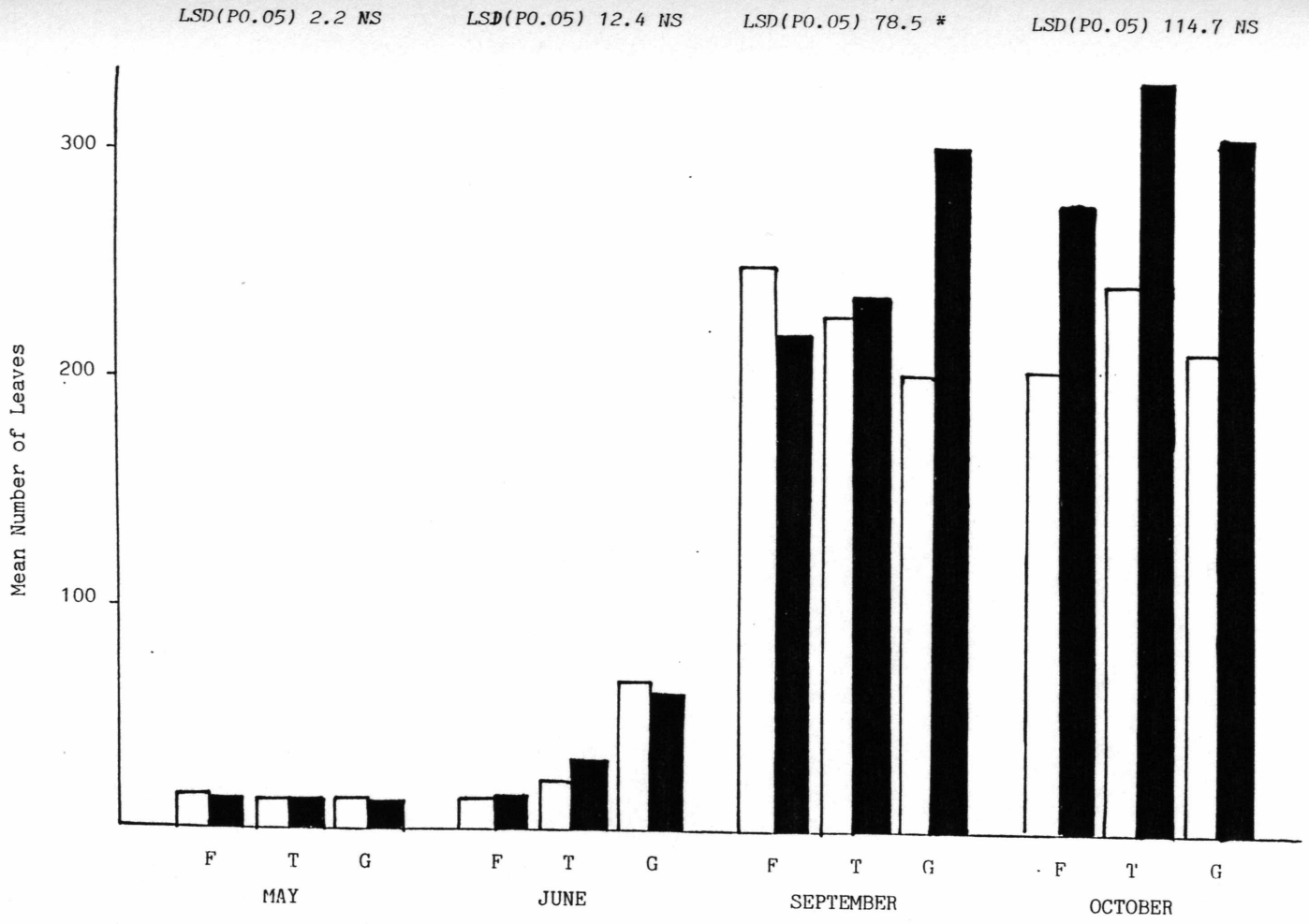


Figure 3B.22 The effect of natural daylength and 24hour light (shaded columns) on the mean number of leaves in field (F), tube (T) and glasshouse (G) in 1983.

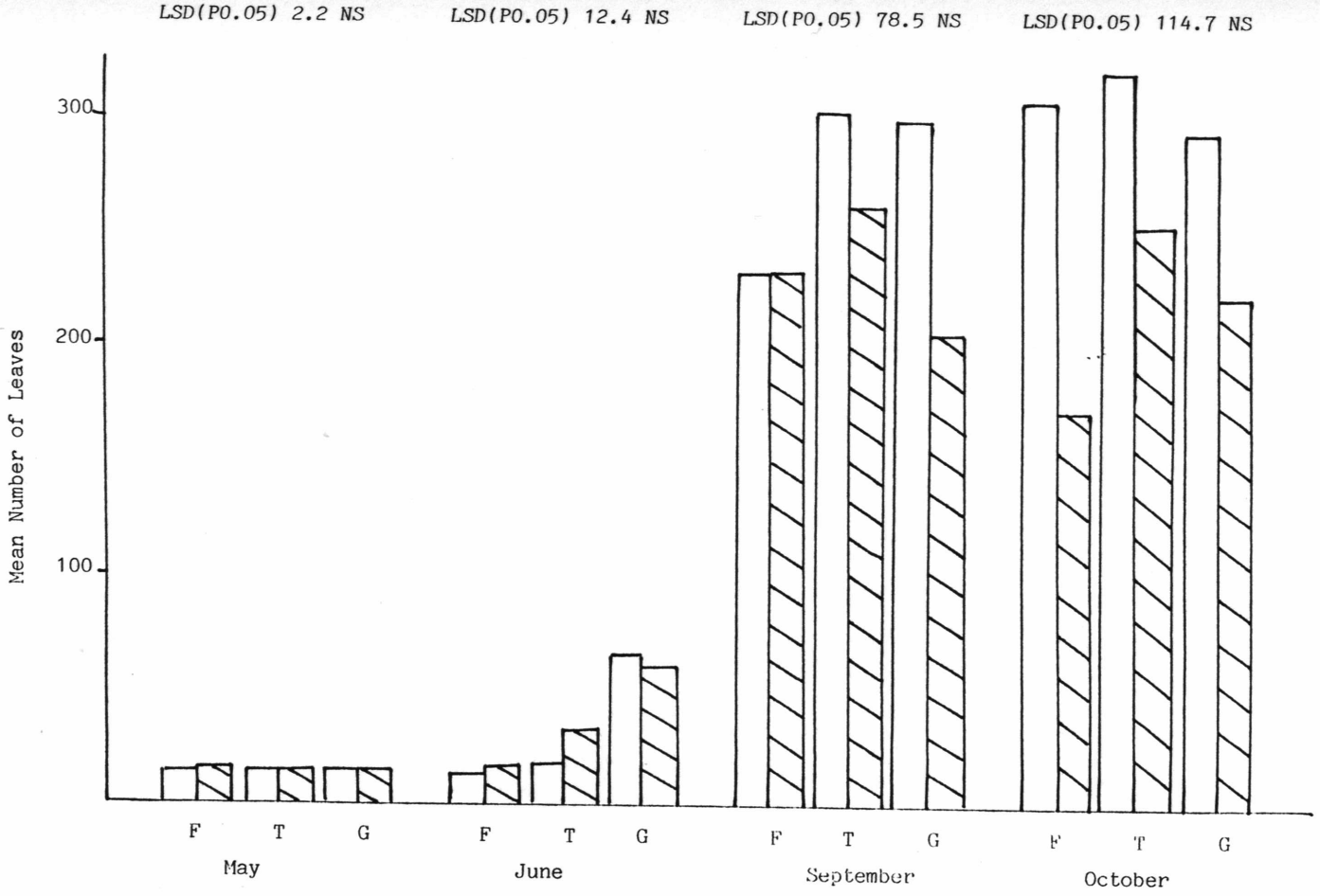


Figure 3B.23 The effect of gibberellic acid application (shaded columns) on the mean number of leaves in field (F), tube (T) and glasshouse (G) during 1983.

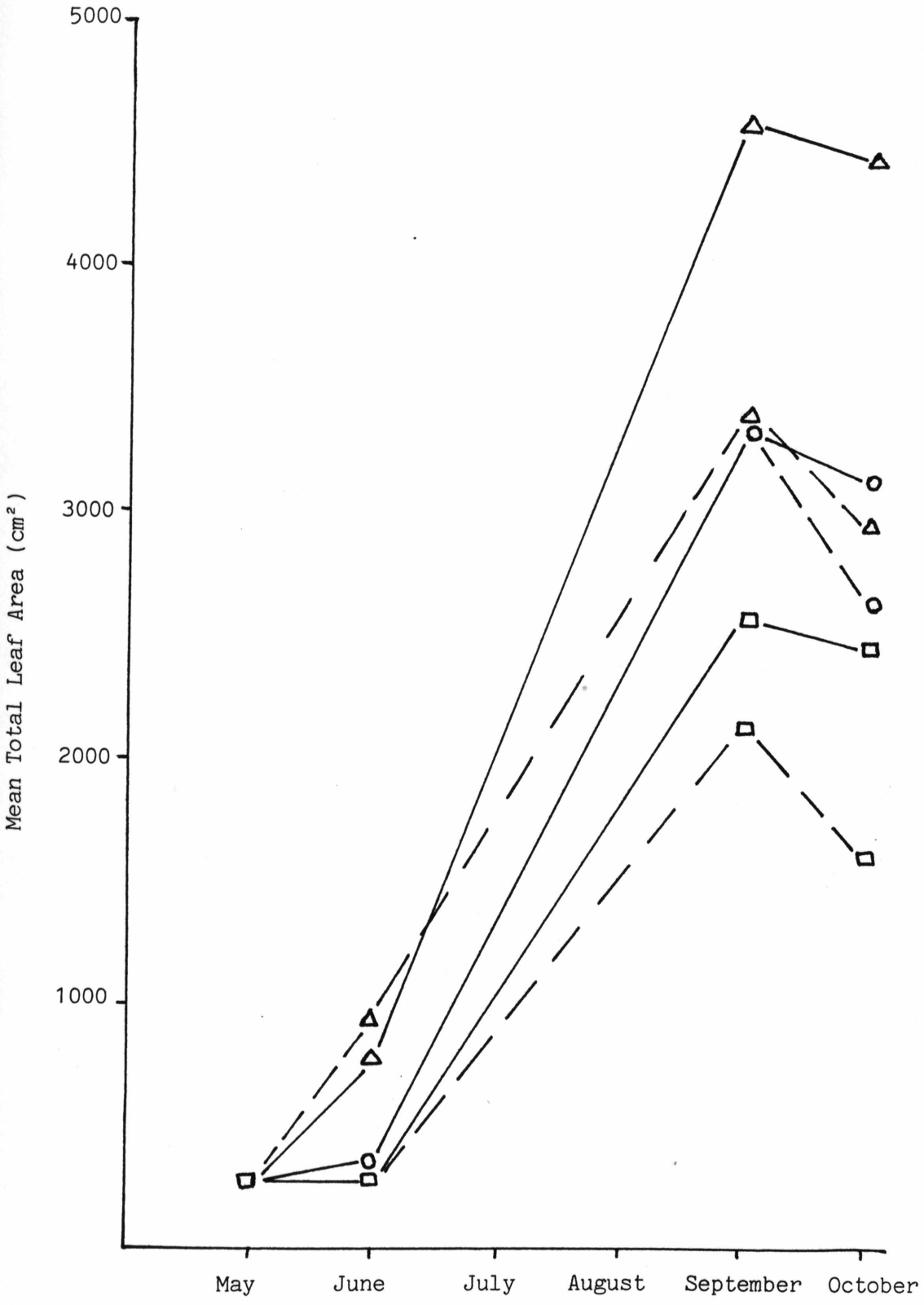


Figure 3B.24 The effect of gibberellic acid (— —) on the mean total leaf area (cm²) in field (□), tube (○) and glasshouse (△) during 1983.

each environment (fig. 3B.25). Gibberellic acid had no significant effect on mean leaf area.

For the second growing season leaf area could only be assessed in October 1984 due to the large number of leaves involved. A sample of 200 leaves was taken from each tree picked from several branches at random and parts of the main stem working from the base to the top of the tree. The remaining leaves were also picked from the tree, counted and dried. Unless stated otherwise the results for 1984 refer to the sample of leaves, an estimate of total leaf area was obtained by multiplying the mean leaf area of the sample by the total number of leaves.

The mean leaf area of glasshouse trees in October 1984 was again much larger (more than 50%) than that of field and tube trees (table 3B.23). There was no significant effect of daylength and GA_3 treatments. Strikingly, the total number of leaves on field trees was over twice that on either tube and glasshouse trees. 24hour light increased the total number of leaves but gibberellic acid had no significant effect. The estimated total leaf area was also significantly increased by 24 hour light reflecting the increase in leaf number, and reduced in the tube environment (fig. 3B.26)

Mean dry weight per leaf was significantly increased by the glasshouse environment at the end of both growing seasons, but there was no significant effect of either light or gibberellic acid treatments (table 3B.24). There were no significant differences in specific leaf area between the FTG-environments in 1983 but there was an increase in the glasshouse environment in October 1984. Light and gibberellic acid treatments again had no significant effect, also there were no significant interactions between FTG-environment, light and hormone for either dry weight per leaf or specific leaf area.

3B.16 Stomata

The number of stomata/mm² on the abaxial leaf surface was greatest in field trees, with no significant difference between tube and glasshouse trees. Light and hormone treatments had no significant effect on number stomata/mm² or stomatal index ($\frac{\text{no: stomata}}{\text{no: stomata + no: epidermal cells}} \times 100$) (table 3B.25).

Field, tube and glasshouse environments also had no significant effect on stomatal index. However the interaction between FTG-environment and hormone was significant ($P<0.05$) i.e. gibberellic acid significantly increased the stomatal index of field trees but had no significant effect on either tube or glasshouse trees (fig. 3B.27). Figure

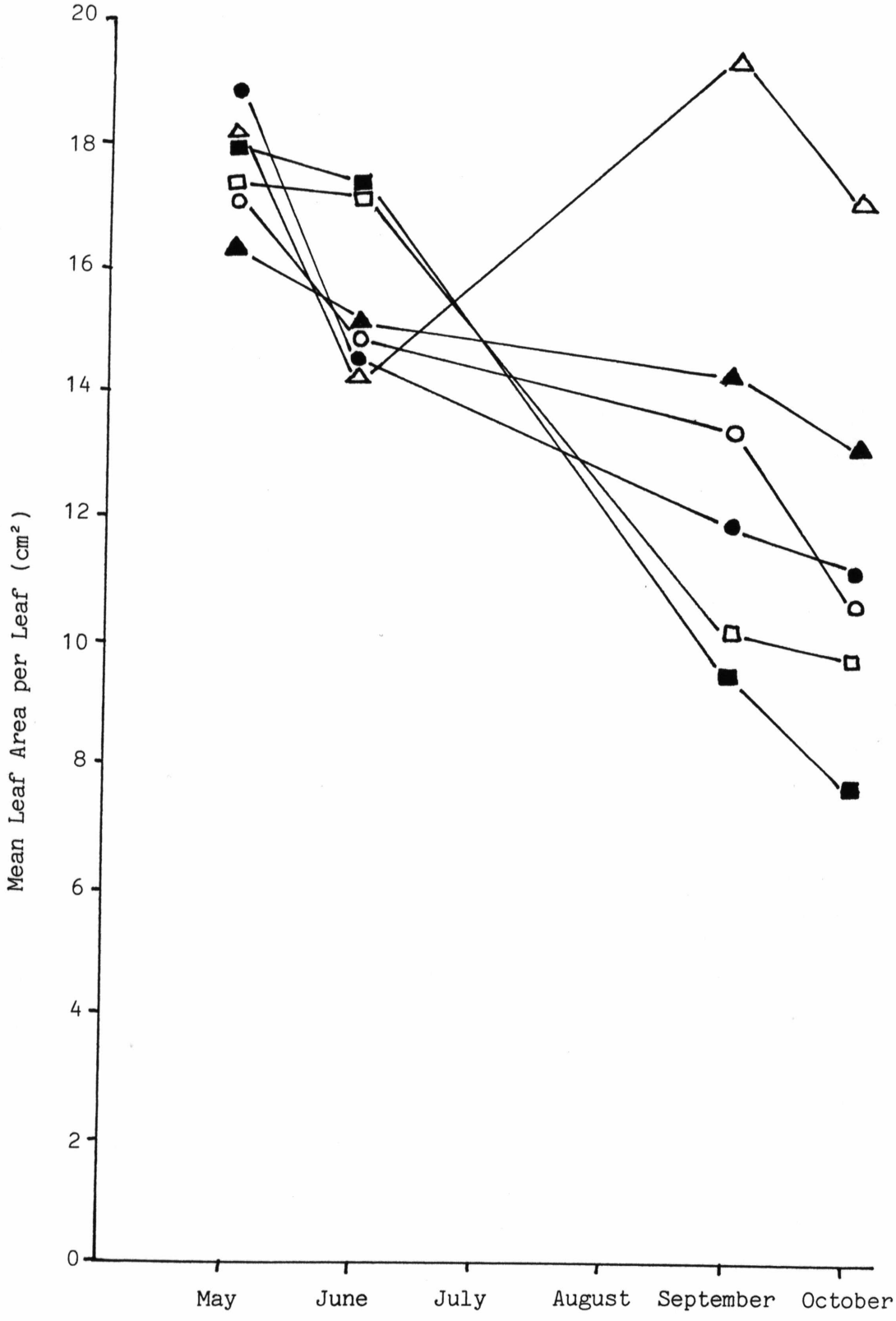


Figure 3B.25 The effect of natural daylength (open symbols) and 24hour light (shaded symbols) on the mean leaf area per leaf (cm^2) in field (□), tube (○) and glasshouse (△) during 1983.

	Total Area (cm^2) Sample n=200 leaves	Mean Leaf Area (cm^2) Sample n=200 leaves	Total Number of Leaves	Estimated Total Leaf Area (cm^2)
Field	1784	8.9	1813	17015
Tube	2026	10.1	870	8520
Glasshouse	3570	17.8	800	13721
Significance	***	***	***	**
LSD(P0.05)	430	2.1	351	4683
Natural daylength	2462	12.3	978	10115
24 hour light	2459	12.3	1344	16055
Significance	NS	NS	*	**
LSD(P0.05)	351	1.8	287	3823
-Gibberellic acid	2627	13.1	1066	12823
+Gibberellic acid	2293	11.5	1256	13347
Significance	NS	NS	NS	NS
LSD(P0.05)	351	1.8	287	3823
Coefficient of Variation (%)	27.4	27.4	47.4	56.1

Table 3B.23 The effect of the main factors, FTG-environment, light and hormone on mean leaf area and number of leaves, October 1984.

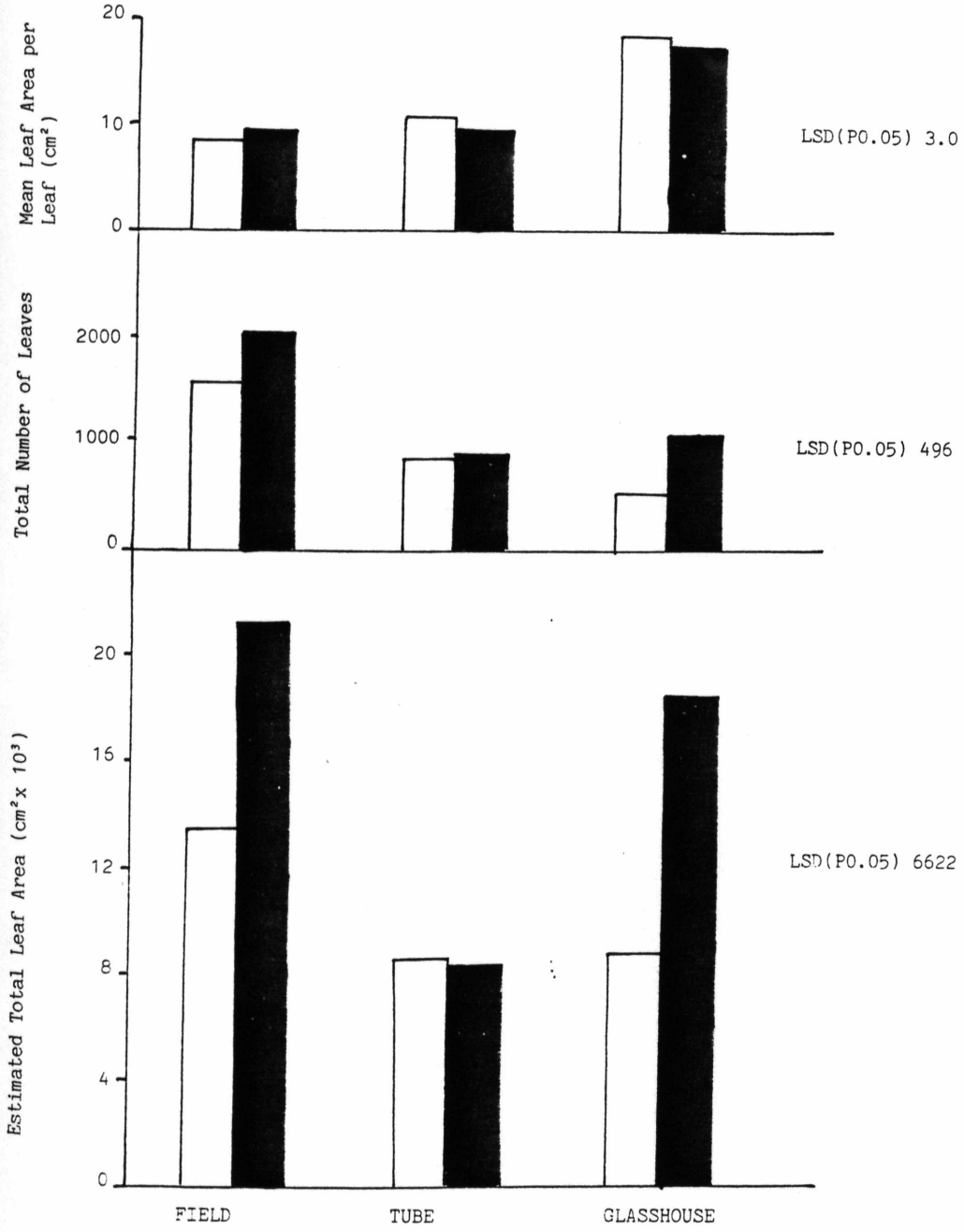


Figure 3B.26 The effect of natural daylength and 24hour light (shaded columns) on the mean leaf area per leaf (n=200), total number of leaves and estimated total leaf area in field, tube and glasshouse, October 1984.

	Mean Weight per Leaf (g) 1983	Specific Leaf Area (cm^2/g) 1983	Mean Weight per Leaf (g) 1984	Specific Leaf Area (cm^2/g) 1984
Field	0.055	175.1	0.073	123.2
Tube	0.065	172.6	0.086	122.8
Glasshouse	0.096	165.0	0.128	140.9
Significance	***	NS	***	***
LSD(P0.05)	0.019	35.1	0.018	9.6
Natural daylength	0.080	161.8	0.097	126.5
24 hour light	0.064	180.8	0.094	131.4
Significance	NS	NS	NS	NS
LSD(P0.05)	0.016	28.6	0.015	7.9
-Gibberellic acid	0.067	184.7	0.100	130.7
+Gibberellic acid	0.077	157.1	0.091	127.2
Significance	NS	NS	NS	NS
LSD(P0.05)	0.016	28.6	0.015	7.9
Coefficient of variation (%)	37.1	28.5	29.9	11.7

Table 3B.24 The effect of main factors, FTG-environment, light and hormone, on mean weight per leaf (g) and specific leaf area (cm^2/g dry wt). 1984 results are for a sample of n=200 leaves.

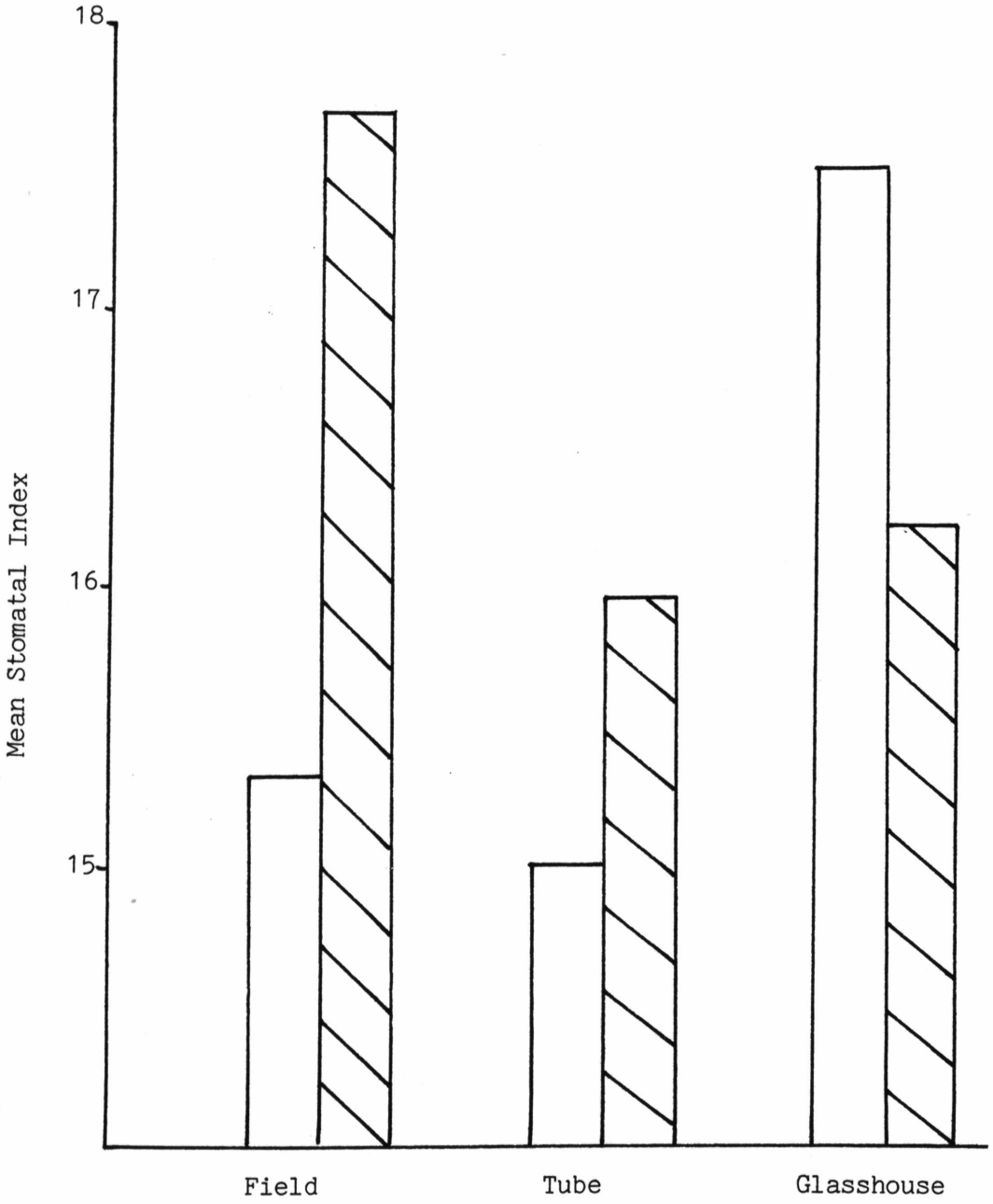


Figure 3B.27 Effect of FTG-environment and gibberellic acid (shaded columns) on mean stomatal index, LSD(P0.05) 1.88.

$$\text{Stomatal index} = \frac{\text{no: stomata}}{\text{no: stomata + no: epidermal cells}} \times 100$$

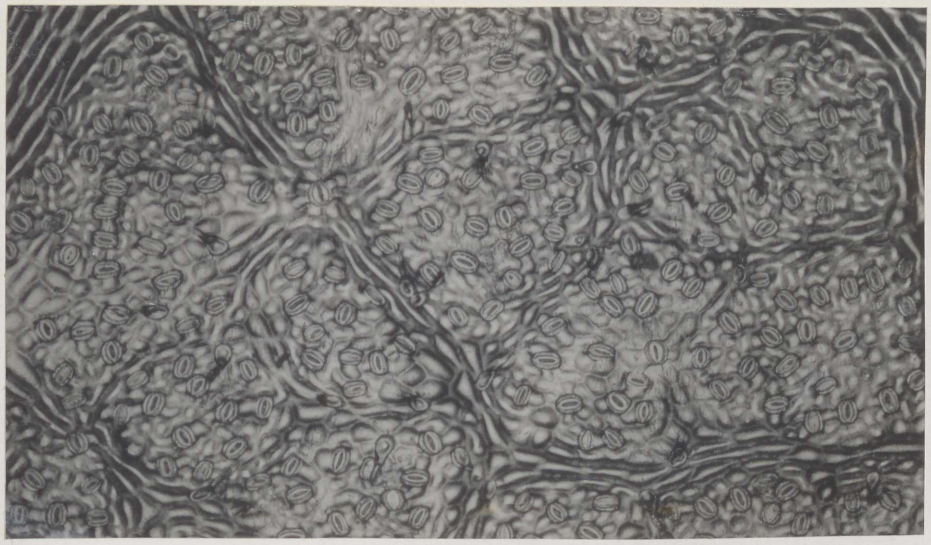
3B.28 gives examples of the appearance of the abaxial leaf surface of field, tube and glasshouse trees.

Table 3B.25

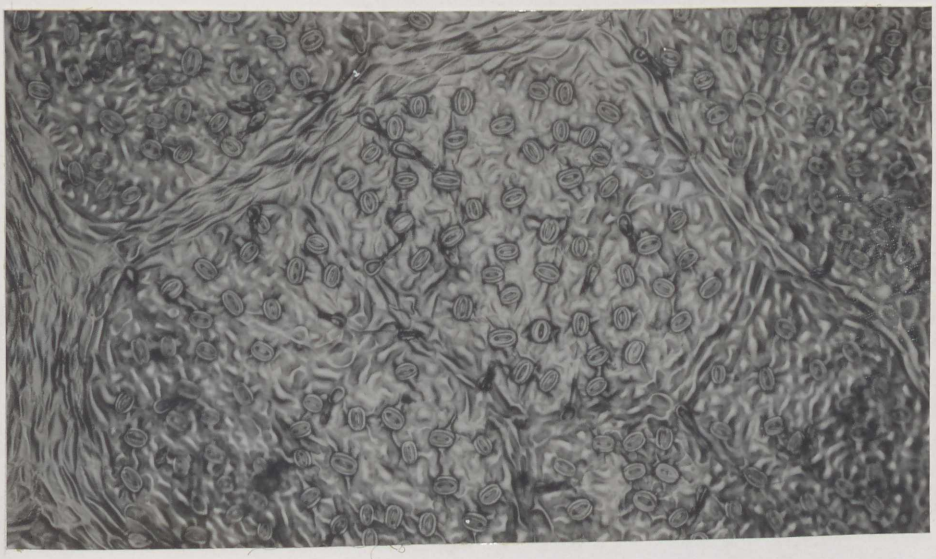
The effect of main factors FTG-environment, light and hormone on the number stomata/mm² and stomatal index (no: stomata / no: stomata + no: epidermal cells x 100) of abaxial leaf surface.

	NO: STOMATA/MM²	STOMATAL INDEX
FIELD	386.6	16.50
TUBE	342.7	15.47
GLASSHOUSE	342.0	16.86
SIGNIFICANCE	*	NS
LSD (P0.05)	34.5	1.33
NATURAL DAYLENGTH	355.2	16.12
24HOUR LIGHT	359.0	16.44
SIGNIFICANCE	NS	NS
LSD (P0.05)	28.2	1.08
-GIBBERELLIC ACID	351.8	15.94
+GIBBERELLIC ACID	362.4	16.62
SIGNIFICANCE	NS	NS
LSD (P0.05)	28.2	1.08
COEFFICIENT OF VARIATION (%)	13.5	11.4

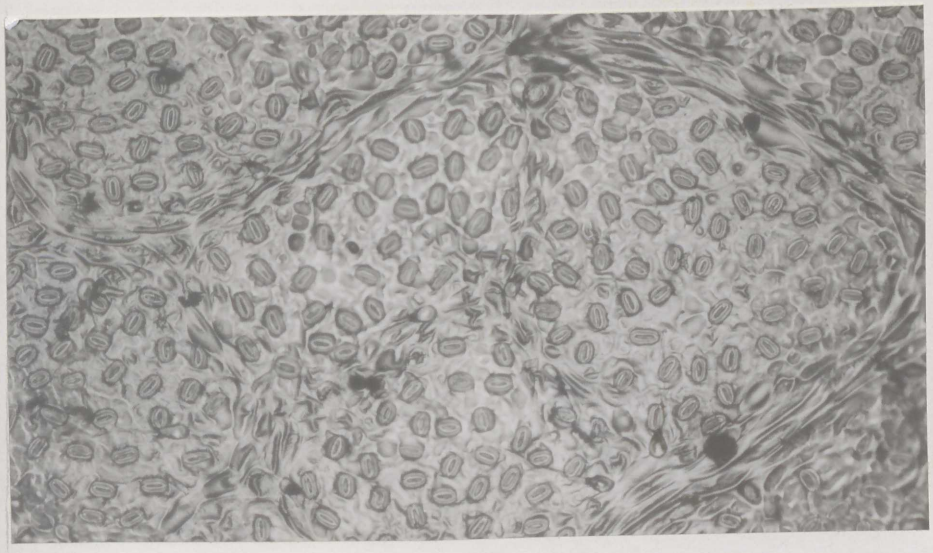
The effect of the main factors FTG-environment, light and hormone on the mean length and width of guard cells (measurements made as shown in materials and methods) are given in table 3B.26. Due to differences in the number of measurements made the maximum least significant differene, LSD_{max}, is used to compare treatment means where more than two treatments are involved. ($LSD_{max} = t_{res;P0.05} \times \sqrt{s^2 (1/n_{max} + 1/n_{min})}$). Both length and width were increased by 24 hour light and gibberellic acid. The length and width of guard cells of glasshouse trees were reduced compared with those of field and tube trees. For tube trees length was increased but width reduced compared with field trees.



Field



Tube



Glasshouse

Figure 3B.28 Examples of the appearance of the abaxial leaf surface of field, tube and glasshouse trees. (x 32)

Table 3B.26

The effect of main factors FTG-environment, light and hormone on the mean length ($mmx10^{-2}$) and width ($mmx10^{-2}$) of guard cells.

	LENGTH $mmx10^{-2}$	n	WIDTH $mmx10^{-2}$	n
FIELD	2.493	512	1.978	559
TUBE	2.559	502	1.875	565
GLASSHOUSE	2.394	472	1.824	504
SIGNIFICANCE	***		***	
LSD_{max} (P0.05)	0.038		0.030	
NATURAL DAYLENGTH	2.456	725	1.878	805
24HOUR LIGHT	2.510	763	1.911	823
SIGNIFICANCE	***		**	
LSD_{max} (P0.05)	0.031		0.024	
-GIBBERELLIC ACID	2.445	747	1.881	816
+GIBBERELLIC ACID	2.522	741	1.908	812
SIGNIFICANCE	***		*	
LSD_{max} (P0.05)	0.031		0.024	

First-order interactions between FTG-environment and light (fig. 3B.29), and FTG-environment and hormone (fig. 3B.30) were significant. 24hour light increased the length of guard cells of glasshouse trees with no significant effect on field and tube trees. The width of guard cells was increased by 24hour light in field and glasshouse environments but decreased in tube trees. Gibberellic acid had no significant effect on length in field and glasshouse environments, however there was a decrease in width with gibberellic acid in these two environments but an increase in the tube environment.

The frequency distributions of guard cell lengths and widths are given in figure 3B.31. The second order interaction between FTG-environment, light and hormone was significant. Richards' diagrams have been used to represent this interaction for length (fig. 3B.32) and width (fig. 3B.33) measurements. The effect of 24hour light and gibberellic acid varied according to the environment in which they were applied. In the field environment there was no significant effect of gibberellic acid or 24hour light on mean length of guard cells. Both treatments when applied separately decreased the mean width of guard cells, but 24hour

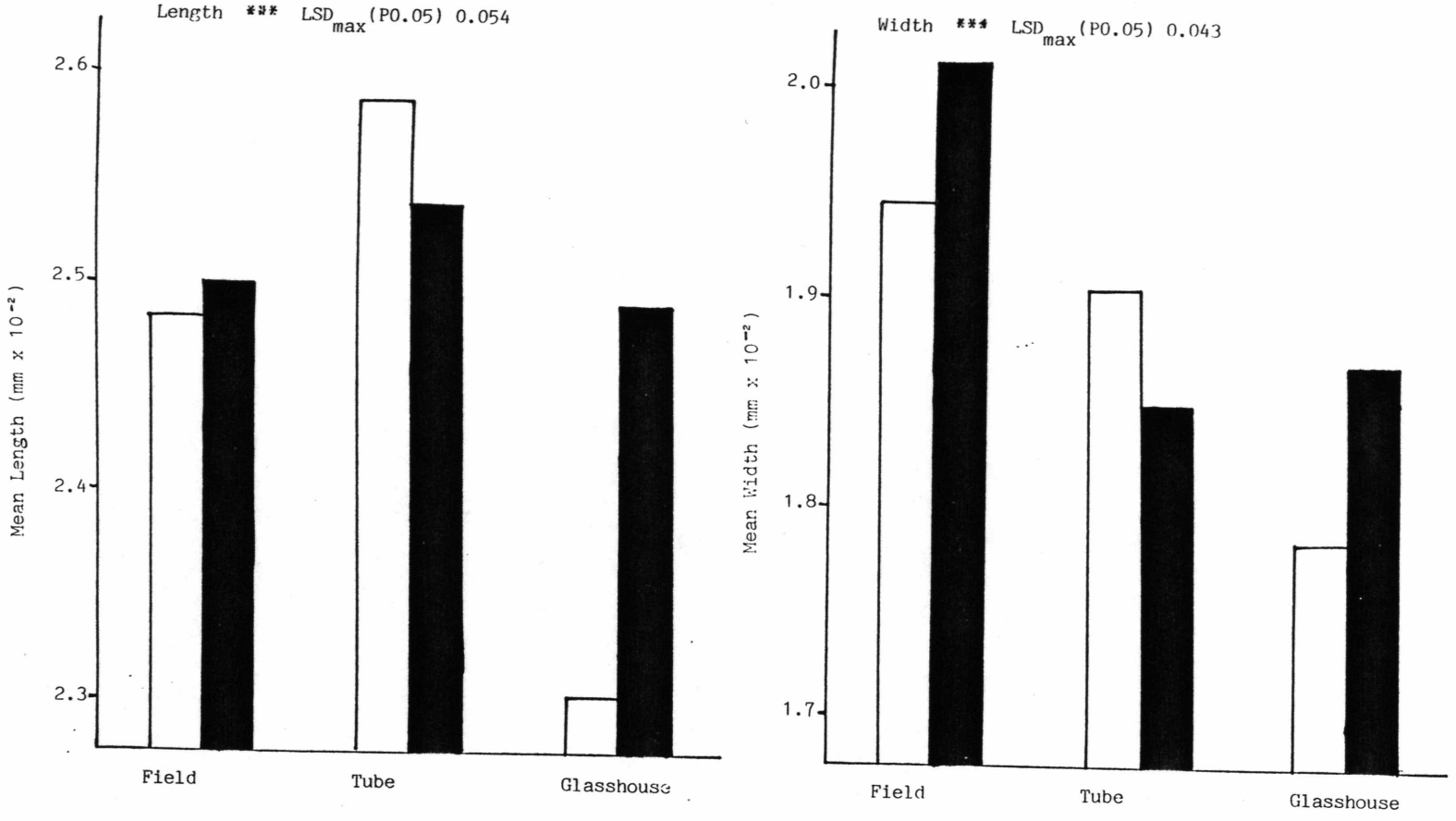


Figure 3B.29 The effect of natural daylength and 24hour light (shaded columns) on the mean length and width of guard cells of field, tube and glasshouse trees.

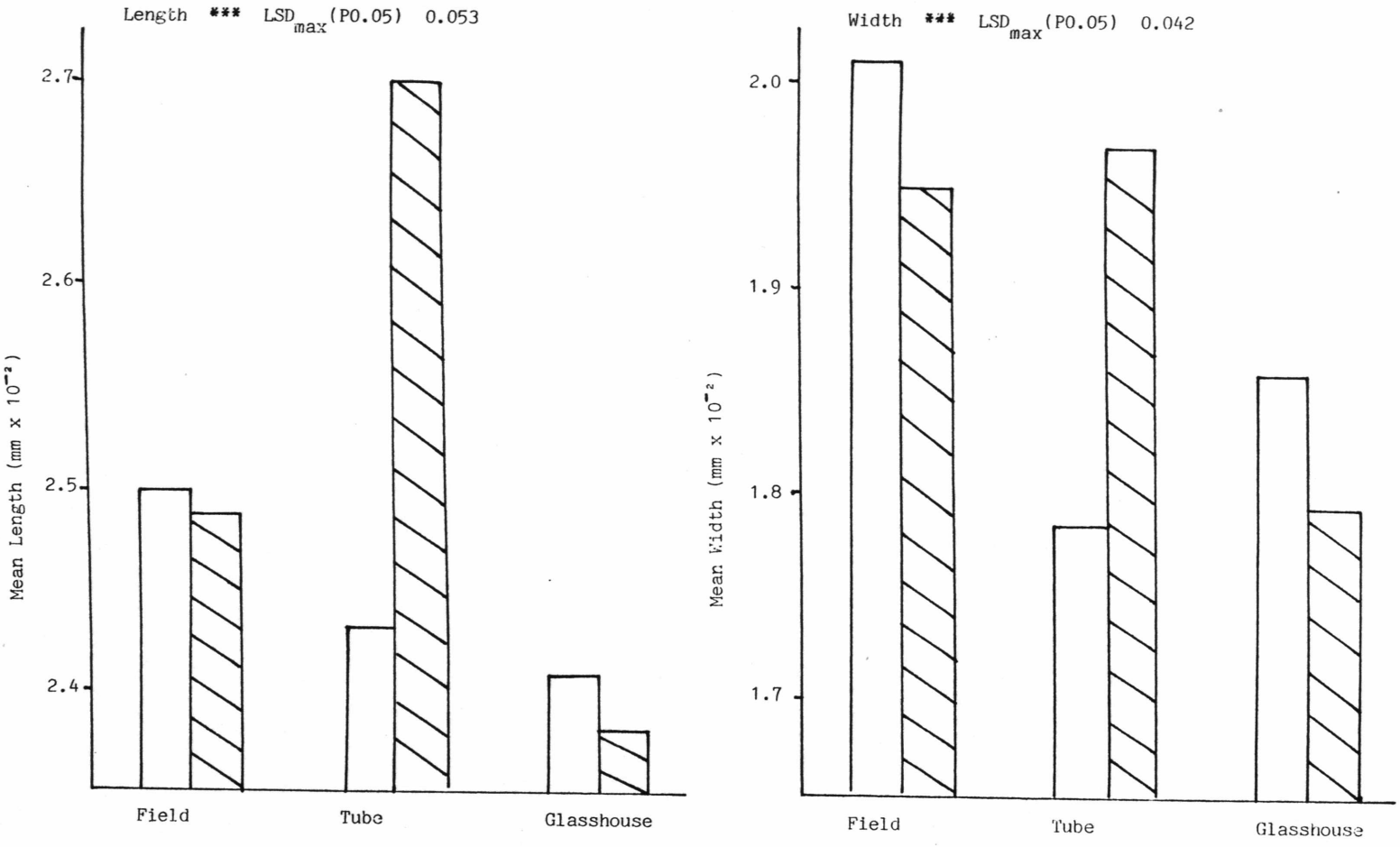


Figure 3B.30 The effect of gibberellic acid (shaded columns) on the mean length and width of guard cells of field, tube and glasshouse trees.

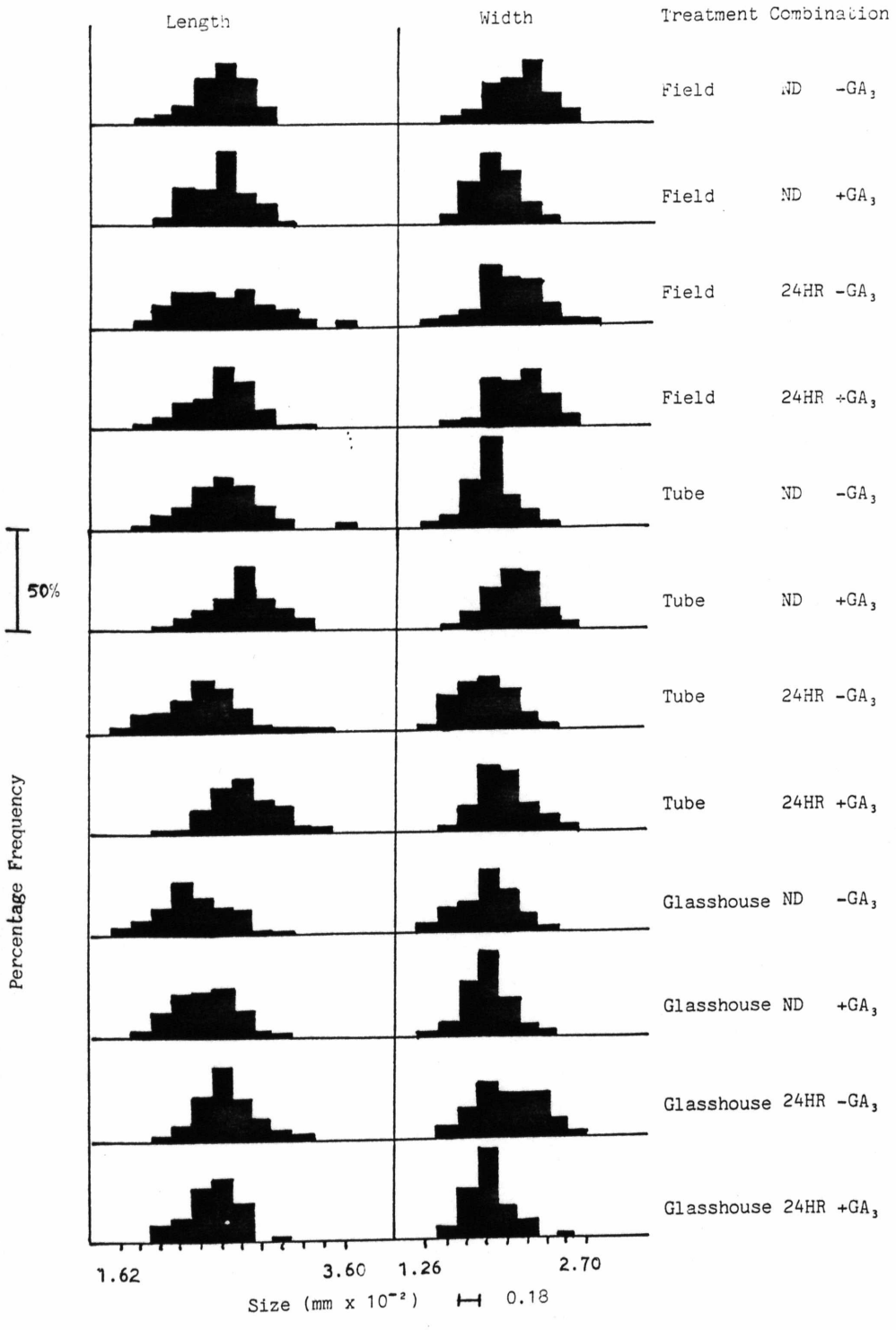


Figure 3B.31 Distribution (% frequency) of guard cell length and width.

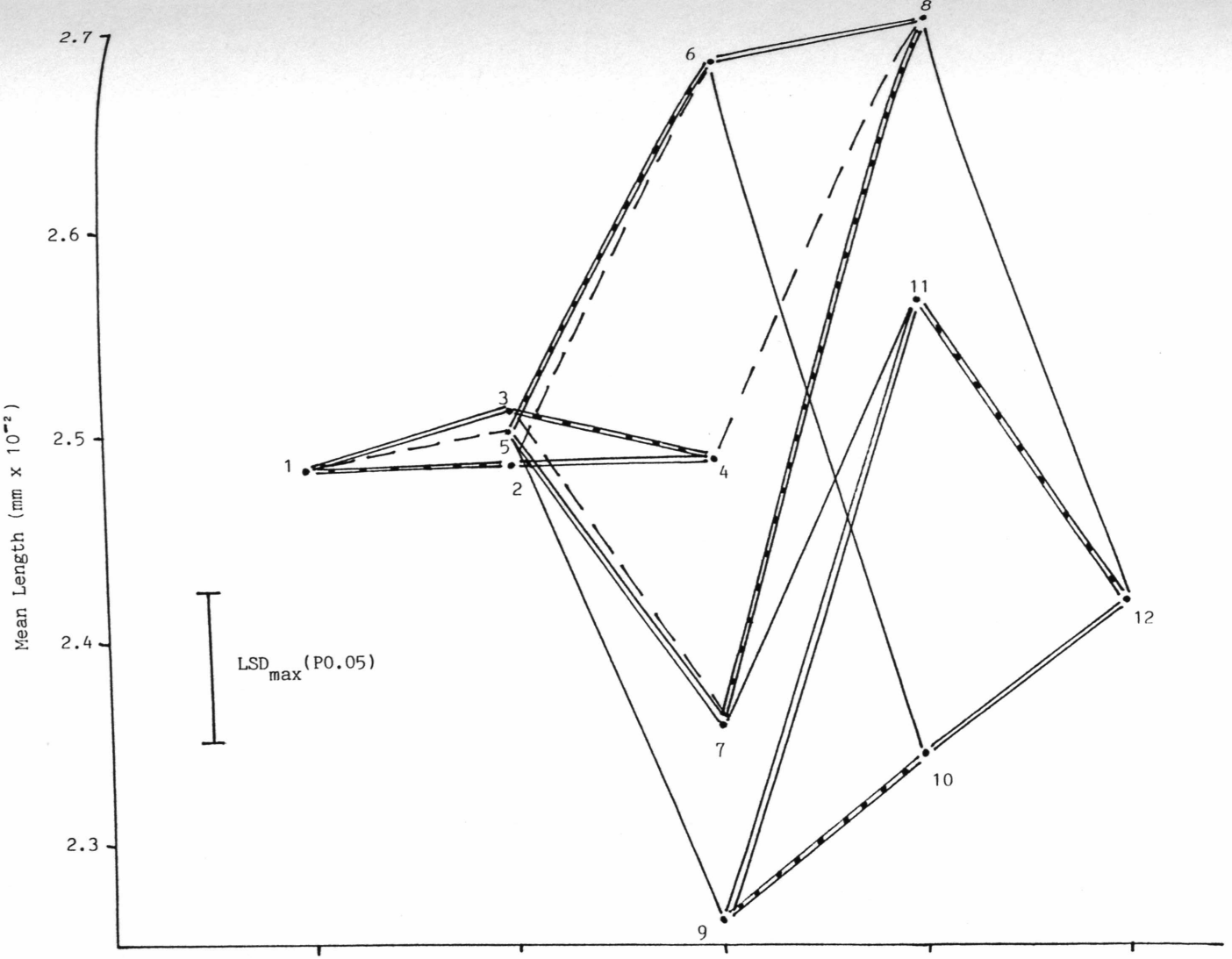


Figure 3B.32 Mean length (mm x 10^{-2}) of guard cells: interaction between FTG-environment, light and hormone. For key see Materials and Methods (Section 2.14).

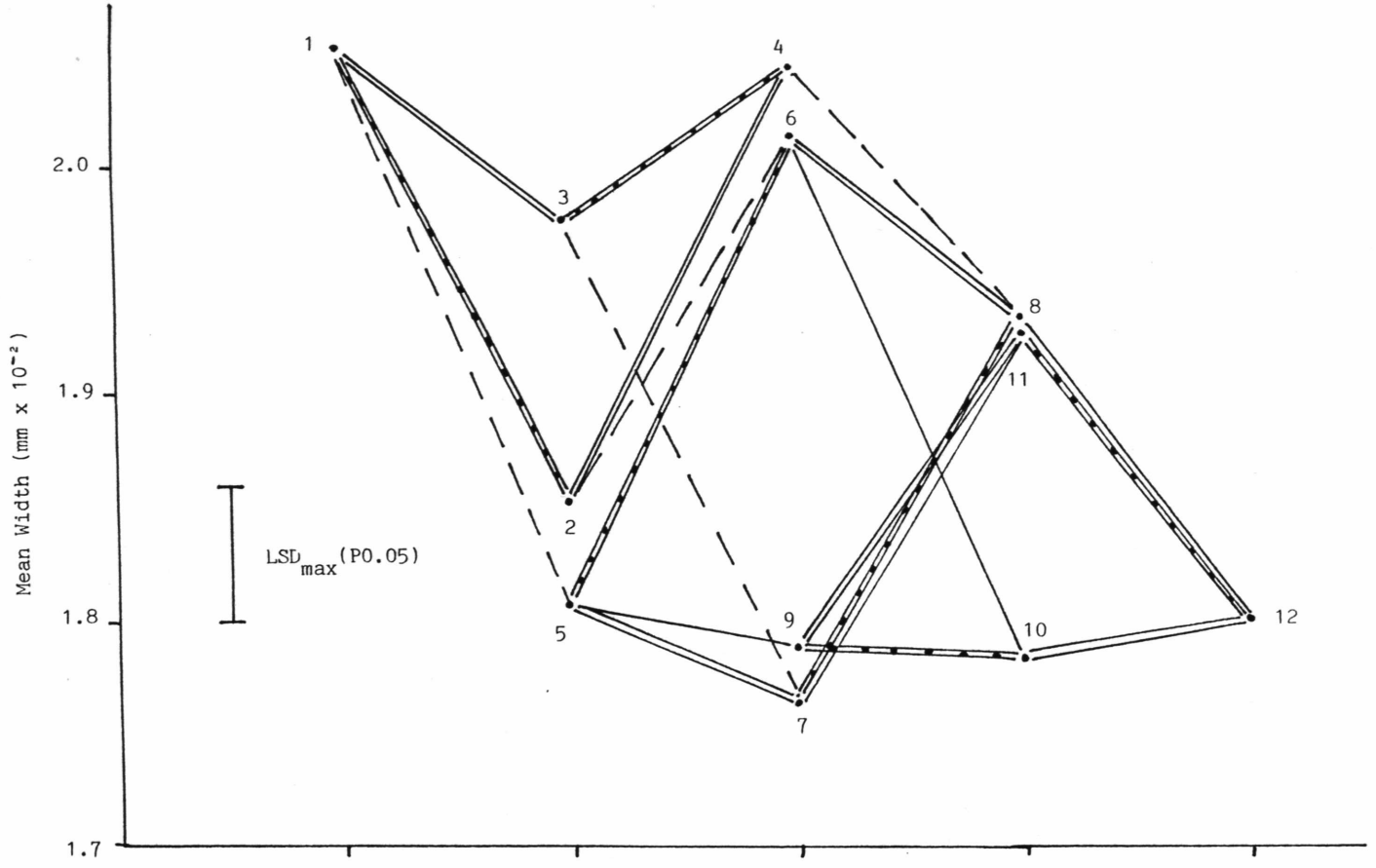


Figure 3B.33 Mean width (mm x 10^{-2}) of guard cells; interaction between FTG-environment, light and hormone. For key see Materials and Methods (Section 2.14).

light + GA_3 had no significant effect. In the tube environment mean length and width were increased by gibberellic acid alone and in combination with 24hour light. 24hour light alone decreased mean length but had no significant effect on the mean width of guard cells. Mean length of guard cells of trees grown in the glasshouse was increased by 24hour light and gibberellic acid treatments when applied separately or combined. 24hour light increased mean width but treatment with gibberellic acid and 24hour light + GA_3 had no significant effect.

There was no significant difference between the mean length of guard cells in the field and tube environments, but tube significantly decreased mean width. Tube + gibberellic acid increased the mean length of guard cells but had no significant effect on width under both light treatments. The interaction between tube and 24hour light was affected by gibberellic acid. Mean length and width were decreased by tube + 24hour light in the absence of gibberellic acid but in the presence of GA_3 both length and width were increased by tube + 24hour light. Combination of tube, 24hour light and gibberellic acid increased mean length but decreased mean width.

Glasshouse environment decreased the mean length of guard cells compared with those of trees in the field and tube environments, mean width was decreased compared with field grown trees but not significantly different from tube trees. Compared with trees grown in the tube environment glasshouse + gibberellic acid decreased mean length in natural daylength but had no significant effect under 24hour light. Glasshouse + GA_3 had no significant effect on mean width under both light treatments. Glasshouse + 24hour light had no significant effect on length but increased mean width in the absence of GA_3. In the presence of GA_3 glasshouse + 24hour light decreased both mean length and width of guard cells. Combination of the glasshouse environment, 24hour light and gibberellic acid decreased mean length but had no significant effect on mean width of guard cells.

3B.17 Dry Weight

Total dry weight of glasshouse trees was significantly greater (almost 40%) than in the field trees and also greater (34%) than trees in the tube environment at the end of the first growing season (table 3B.27), the effect also persisted through the second year. 24hour light grown trees had a significantly increased total dry weight by the end of 1984, however this effect was seen in glasshouse trees only (fig. 3B.34). Hormone had no significant effect on total dry weight.

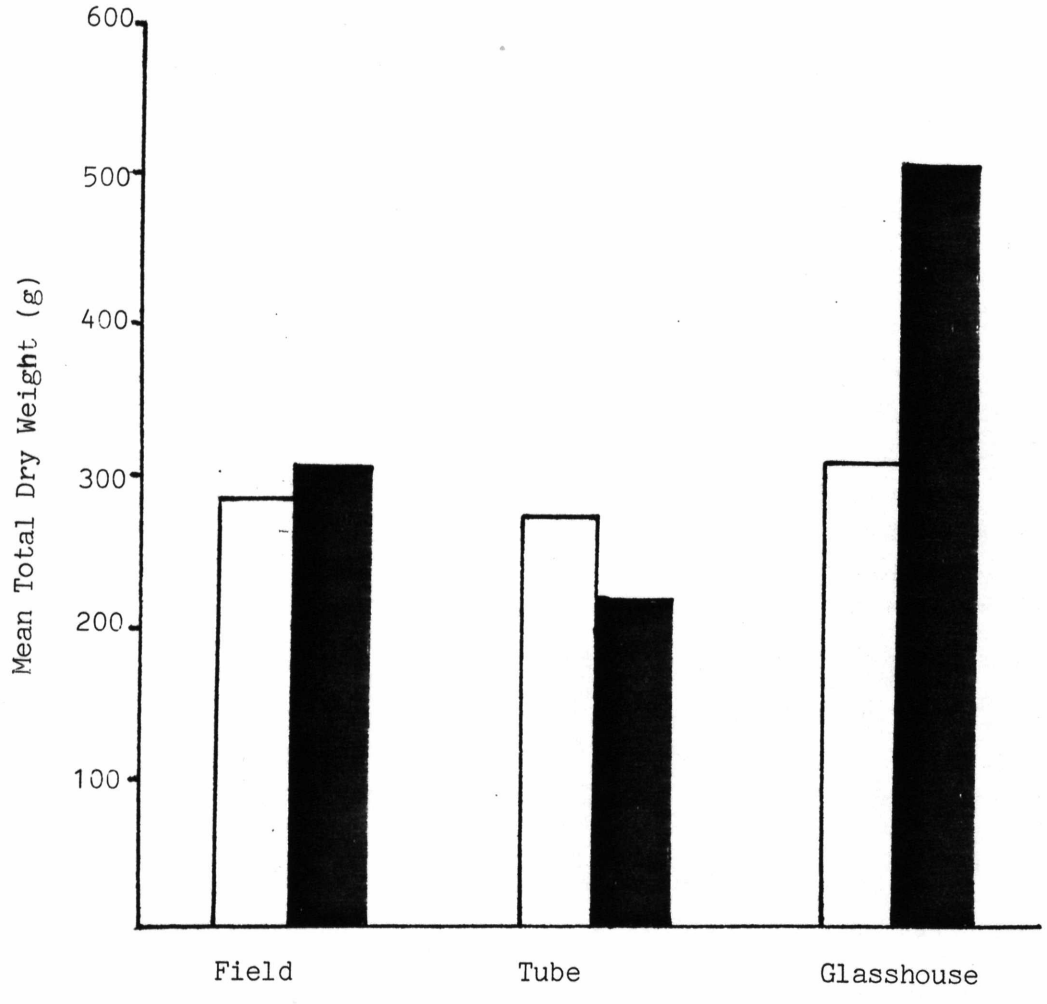


Figure 3B.34 Mean total dry weight (g) per tree in October 1984, interaction between FTG-environment and light. (Natural daylength □ , 24hour light ■) LSD(P0.05) 95.4.

Table 3B.27

The effect of the main factors, FTG-environment, light and hormone on mean total dry weight (g) after one (1983) and two (1984) growing seasons.

	1983	1984
FIELD	69.8	295.0
TUBE	72.4	245.0
GLASSHOUSE	97.2	408.0
SIGNIFICANCE	**	***
LSD (P0.05)	18.5	67.7
NATURAL DAYLENGTH	78.4	288.0
24HOUR LIGHT	81.2	344.0
SIGNIFICANCE	NS	*
LSD (P0.05)	15.1	55.1
-GIBBERELLIC ACID	79.4	310.0
+GIBBERELLIC ACID	80.2	323.0
SIGNIFICANCE	NS	NS
LSD (P0.05)	15.1	55.1
COEFFICIENT OF VARIATION (%)	36.2	33.5

3B.18 Distribution of Dry Matter

The distribution of dry matter between stem, branch, leaves and root is expressed as percentage of the total dry weight. At the end of the first year there were significant differences between FTG-environments and gibberellin treatments (table 3B.28). The proportion of stem and leaves were increased in the glasshouse and tube environments and roots decreased compared with the field trees, in which roots represented over 50% of the total dry weight of the tree. Continuous illumination had no significant effect on the distribution of dry weight, but gibberellic acid increased the proportion of stem particularly of glasshouse trees (fig. 3B.35).

Significant differences between field, tube and glasshouse environments, also daylength and gibberellic acid treatments were still

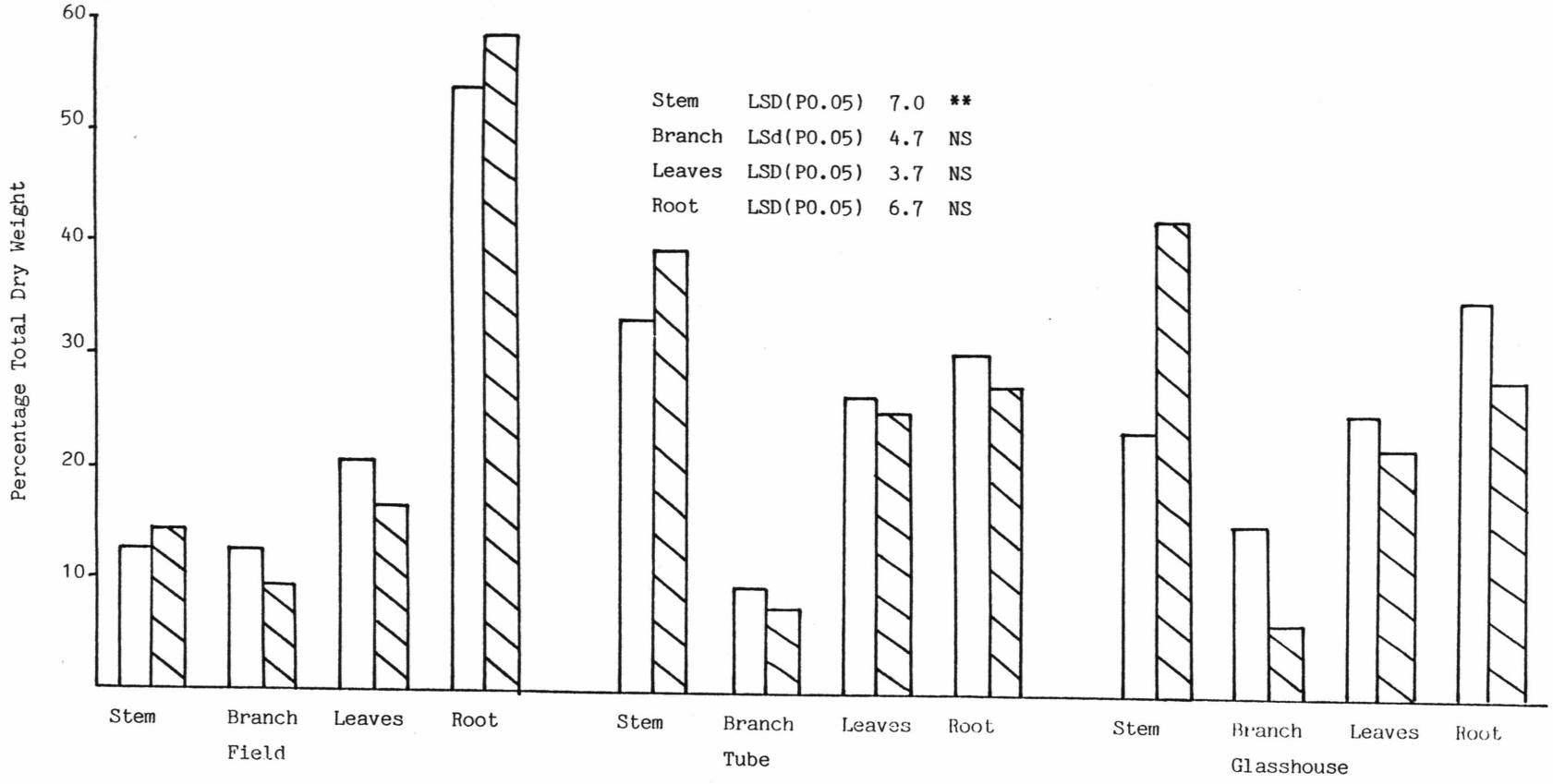


Figure 3B.35 The effect of FTG-environment and gibberellic acid (shaded columns) on the distribution of dry matter after one growing season (October 1983).

present after the second year's growth (table 3B.29). The proportion of stem was increased and root decreased in both tube and glasshouse environments, the dry matter used for branch formation was greatest in field trees. 24hour light significantly increased the percentage of stem and reduced the percentage of roots, the percentage of leaves was also reduced by 24hour light, but in the glasshouse only (fig. 3B.36). Treatment with gibberellic acid increased the percentage of stem and decreased percentage of leaves with no significant effect on percentage of branches and roots (fig. 3B.37).

Table 3B.28

The effect of main factors, FTG-environment, light and hormone on the distribution of dry matter, expressed as mean percentage of total dry weight after one growing season, October 1983.

	% STEM	% BRANCH	% LEAVES	% ROOT
FIELD	13.8	11.1	18.8	56.2
TUBE	36.5	8.5	26.0	28.9
GLASSHOUSE	33.0	11.1	23.6	32.3
SIGNIFICANCE	***	NS	***	***
LSD (P0.05)	4.9	3.4	2.7	4.7
NATURAL DAYLENGTH	25.9	10.4	23.0	40.6
24HOUR LIGHT	29.6	10.1	22.7	37.7
SIGNIFICANCE	NS	NS	NS	NS
LSD (P0.05)	4.1	2.7	2.2	3.9
-GIBBERELLIC ACID	23.2	12.4	24.3	40.0
+GIBBERELLIC ACID	32.2	8.1	21.4	38.4
SIGNIFICANCE	***	**	*	NS
LSD (P0.05)	4.1	2.7	2.2	3.9
COEFFICIENT OF VARIATION (%)	28.1	51.4	18.2	19.0

The mean distribution of dry matter was determined for seedlings at the start of the experiment: stem and branches 19.8 ± 6.1%; leaves 35.8 ± 8.0% and roots 44.4 ± 12.1%. The changes in distribution due to field, tube and glasshouse environments are shown in fig. 3B.38,

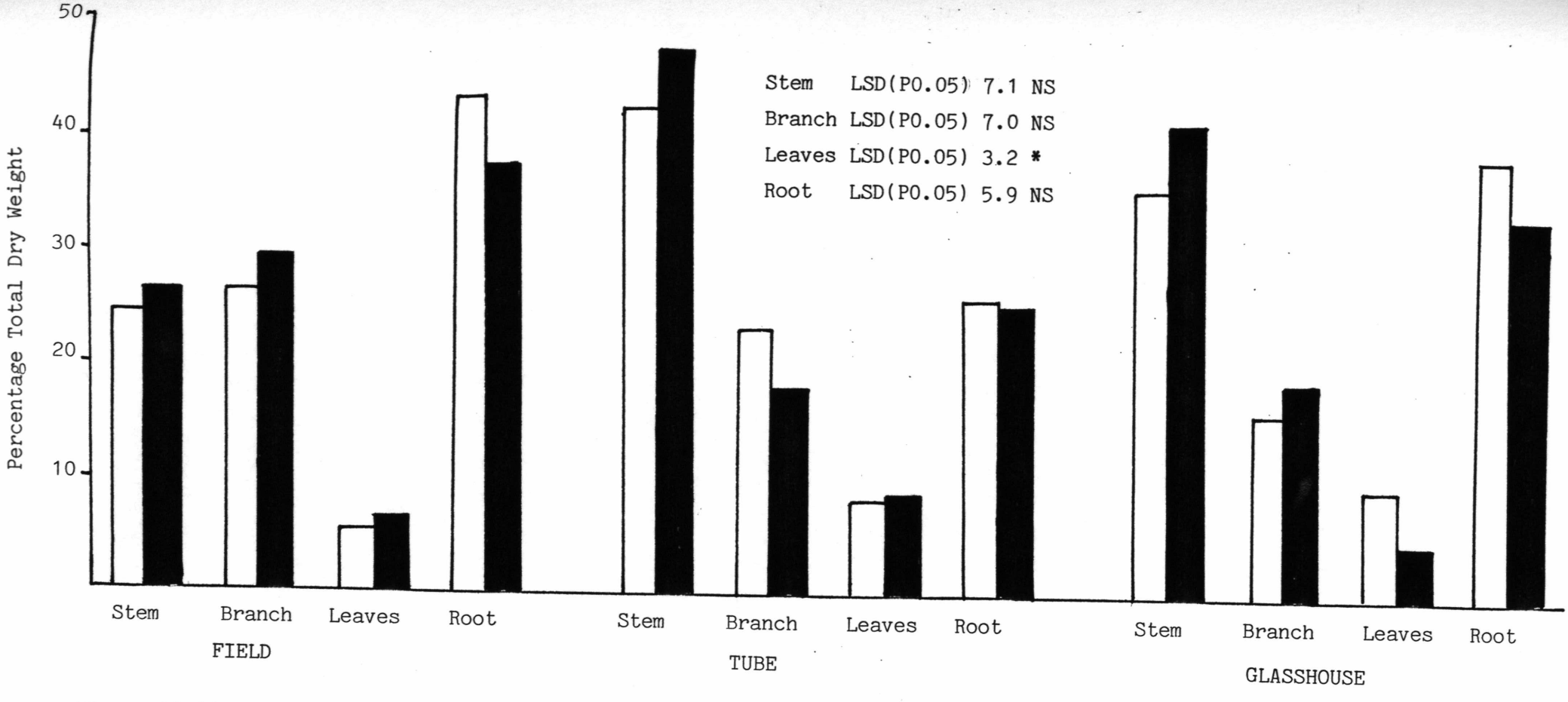


Figure 3B.36 Effect of FTG-environment, natural daylength and 24hour light (shaded columns) on the distribution of dry matter after two growing seasons (October 1984).

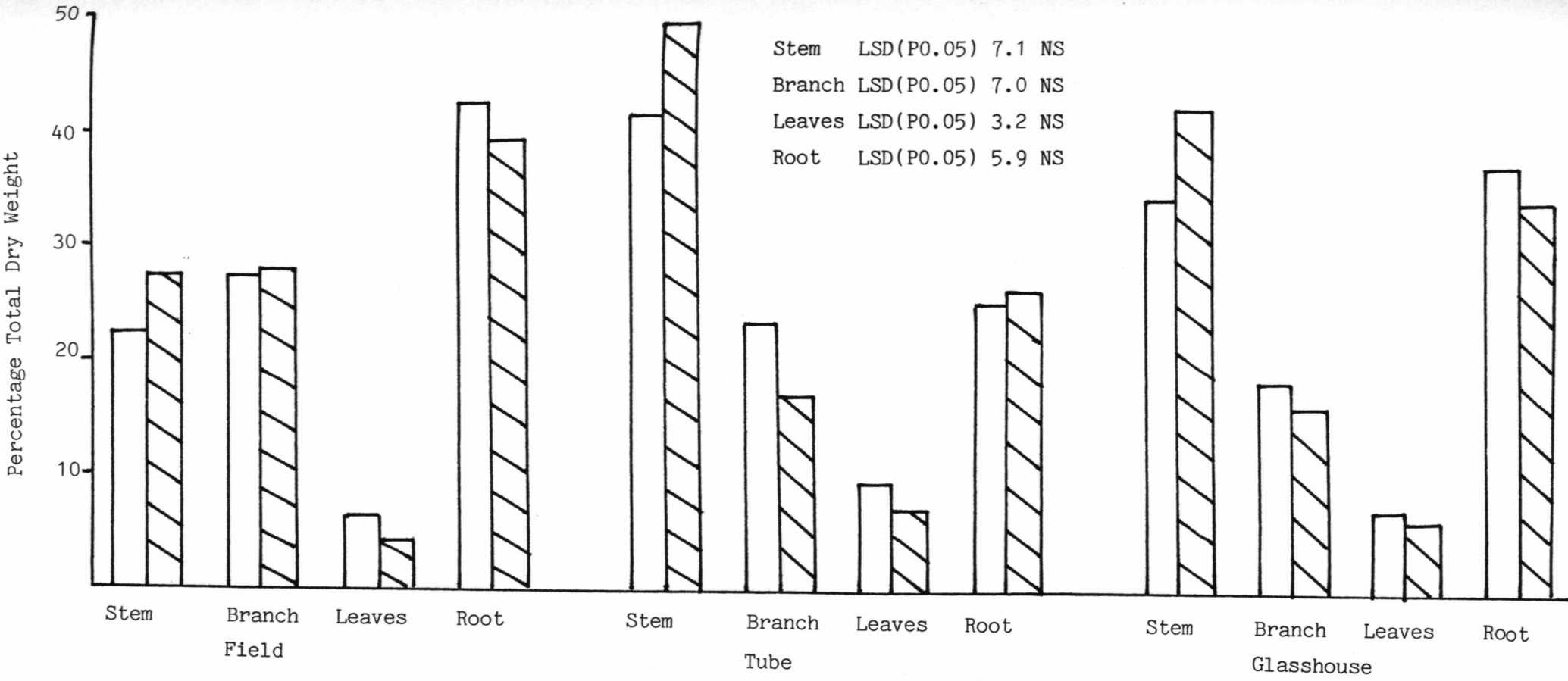


Figure 3B.37 The effect of FTG-environment and gibberellic acid (shaded columns) on the mean distribution of dry matter after two growing seasons, October 1984.

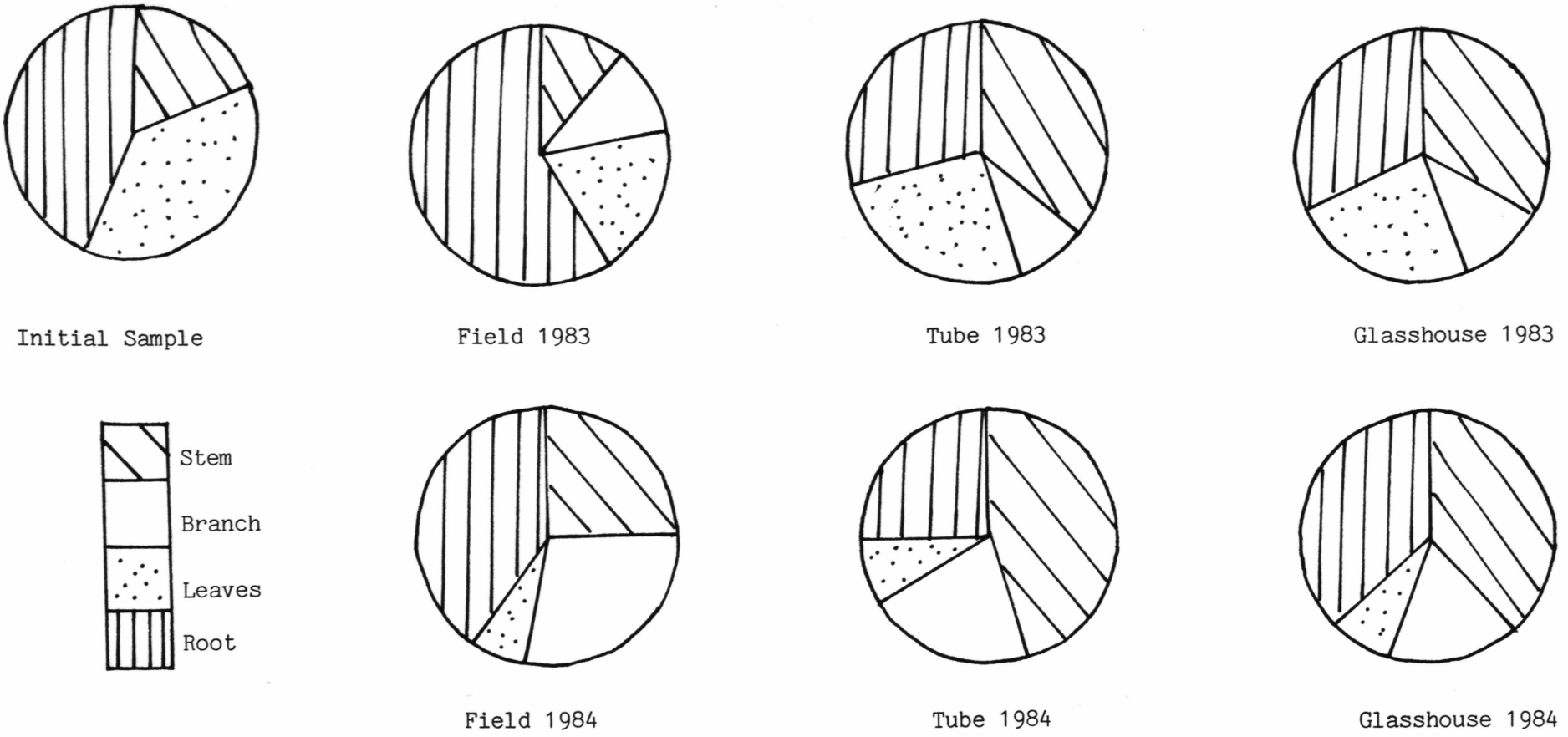


Figure 3B.38 The effect of FTG-environment on the distribution of dry matter after one (October 1983) and two (October 1984) growing seasons.

which gives the percentages of stem, branches, leaves and roots as a proportion of a circle i.e. 360°.

Table 3B.29

The effect of main factors, FTG-environment, light and hormone on the distribution of dry matter (% total dry weight) after two growing seasons, October 1984.

	% STEM	% BRANCH	% LEAVES	% ROOT
FIELD	25.3	28.0	5.9	40.8
TUBE	45.3	20.6	8.5	25.6
GLASSHOUSE	38.3	17.5	7.4	35.9
SIGNIFICANCE	***	***	NS	***
LSD (P0.05)	5.1	4.9	2.3	4.2
NATURAL DAYLENGTH	34.2	21.8	7.8	36.2
24HOUR LIGHT	38.5	22.2	6.7	32.0
SIGNIFICANCE	*	NS	NS	*
LSD (P0.05)	4.1	4.0	1.8	3.4
-GIBBERELLIC ACID	32.9	23.2	8.2	35.0
+GIBBERELLIC ACID	39.8	20.8	6.3	33.2
SIGNIFICANCE	**	NS	*	NS
LSD (P0.05)	4.1	4.0	1.8	3.4
COEFFICIENT OF VARIATION (%)	21.8	35.1	48.9	19.1

3B.19 Stem : Root Ratio

Stem:root ratio reflects the assimilate (dry matter) distribution during development, and is clearly important for growth assessment and the establishment of young trees. At the end of the first year the stem:root ratio was measured by destructive sampling. It was significantly increased in both the tube and the glasshouse environments (table 3B.30). By the end of the second year the proportion of stem dry matter in the glasshouse trees had risen but the stem:root ratio of tube trees alone was significantly greater than that of either field or glasshouse grown trees. There was no significant effect of light treatments, however gibberellic acid application had increased the

stem:root ratio of tube and glasshouse trees significantly at the end of the first growing season (fig. 3B.39).

Table 3B.30

The effect of main factors, FTG-environment, light and hormone on the mean stem:root ratio in October 1983 and 1984.

	1983	1984
FIELD	0.47	1.37
TUBE	1.59	2.75
GLASSHOUSE	1.54	1.77
SIGNIFICANCE	***	***
LSD (P0.05)	0.33	0.52
NATURAL DAYLENGTH	1.09	1.79
24HOUR LIGHT	1.32	2.14
SIGNIFICANCE	NS	NS
LSD (P0.05)	0.27	0.42
-GIBBERELLIC ACID	1.04	1.86
+GIBBERELLIC ACID	1.36	2.06
SIGNIFICANCE	*	NS
LSD (P0.05)	0.27	0.42
COEFFICIENT OF VARIATION (%)	43.1	41.1

In October 1983 the stem:root ratio for field grown trees ranged from 0.40-0.57. In contrast to this the mean stem:root ratio of GA_3-treated trees under continuous illumination in tube and glasshouse reached 1.97 and 1.93 respectively, a highly significant shift towards aerial shoot production. The initial stem:root ratio in May 1983 (n=10) was 0.50 ± 0.23 and therefore little changed by treatments in the field during the first growing season, but it was increased in the tube and glasshouse environments. For field trees the final stem:root ratio, 1984, ranged from 1.05-1.61, for glasshouse trees from 1.08-2.10 and for tube trees from 2.45-3.08, the latter, particularly high ratio being the mean for gibberellic acid treated tube trees under 24hour light.

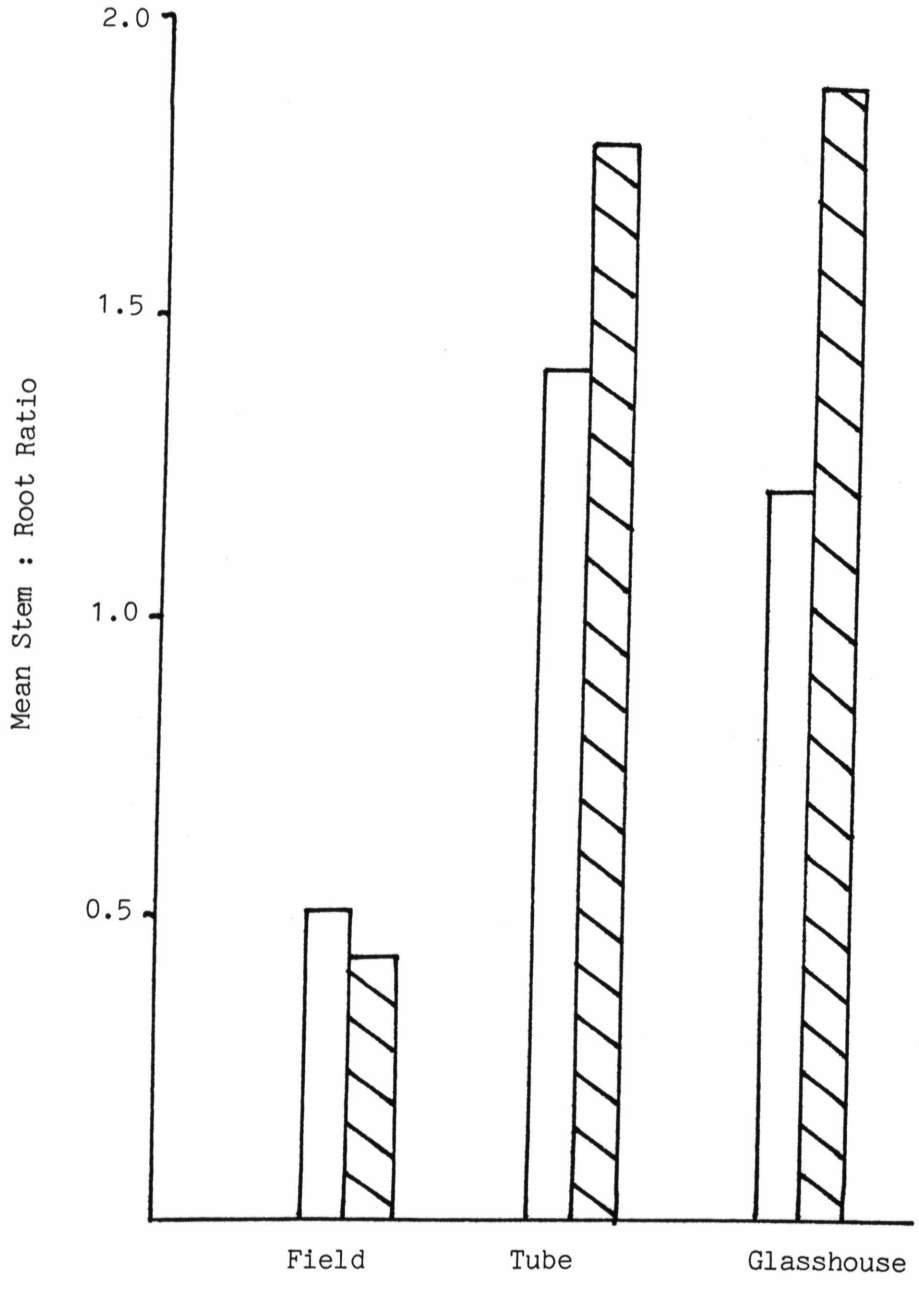


Figure 3B.39 The effect of gibberellic acid (shaded columns) on the mean stem:root ratio in the field, tube and glasshouse after one growing season, October 1983, LSD(P0.05) 0.47.

3B.20 Summary

Height growth of oak seedlings was increased in both tube and glasshouse environments, and in the absence of additional treatments growth was similar in these two environments. The increased height growth may be attributed in part to an increase in the number of growth flushes and in the length of stem produced per flush. There was also an increase in the number of nodes and mean internode length (seen only in the first growing season)

The tube environment increased the total number of branches per tree but field trees had the greastest number of branches per 10cm stem length. The degree of branching was reduced in the glasshouse but mean branch length was increased. Once the trees had emerged from the top of the tube they tended to branch thus forming a crown.

The stems of tube and glasshouse trees showed less taper than those of field trees, the stem diameter of tube trees was also decreased compared with field and glasshouse trees. However total stem volume was increased in the tube and glasshouse chiefly reflecting the increase in height growth. Transverse sections of stem indicated that the number and size of vessels was affected by the environment in which the trees were grown.

Total leaf area per tree was increased in the tube and glasshouse environments. This was not due to an increase in the total number of leaves but to an increase in the size of individual leaves. The largest leaves occurred on glasshouse trees. Specific leaf area was not affected by environment in the first year but increased in the glasshouse in the second growing season. In the second year field trees had twice the number of leaves than either tube or glasshouse trees.

Differences in leaf size and shape under different treatments were quantified using regression equations relating leaf length to leaf area. Field trees had a higher number of stomata/mm^2 of leaf area (abaxial surface), there was however no difference in stomatal index (no: stomata/no:stomata+no:epidermal cells x 100) between environments. Differences were recorded in the size of guard cells, those of field trees were wider than those in the tube and glasshouse environments, which were similar in width. Length of guard cells was similar in tube and field but reduced in glasshouse trees.

The tube environment did not affect dry matter production however there was an increase in the stem:root ratio reflecting an increase in the proportion of dry matter as stem and a decrease in the proportion of root. An increase in stem:root ratio was also seen in the glasshouse

trees, but this was accompanied by an increase in total dry weight. The stem:root ratio for glasshouse trees was similar at the end of both growing seasons, suggesting no restriction of root growth, whereas the ratio for tube trees was further increased at the end of the second year.

Gibberellic acid application increased height growth in the tube and glasshouse environments. 24hour light also increased height and diameter growth of trees in the glasshouse.Under continuous illumination glasshouse trees maintained growth through the winter months. A combination of 24hour light and gibberellic acid did not signficantly increase growth compared with GA_3 application alone i.e. the effects were not additive.

24hour light increased the number of growth flushes made by trees in the glasshouse, in contrast gibberellic acid decreased the number of flushes but increased the length of stem per flush. Gibberellic acid treatment also increased mean internode length and the total number of nodes, primarily in the glasshouse.

There were different effects of 24hour light and gibberellic acid on leaf area; the total number of leaves and total leaf area per tree were decreased by GA_3 treatment, also the mean leaf area per leaf was decreased by 24hour light, but in this case the total number of leaves was increased. Gibberellic acid increased the stomatal index of field trees with no significant effect on tube or glasshouse trees. The effects of gibberellic acid and 24hour light on the size of guard cells varied according to environment. There was no significant effect on length in the field but a decrease in width with both GA_3 and 24hour light. Length and width were increased with GA_3 and 24hour light in the glasshouse and with GA_3 in the tube, 24hour light decreased the length of guard cells in the tube envrionment.

Dry matter production was increased by 24hour light but only in the glasshouse environment. Both treatments increased the proportion of dry matter as stem with varying effects on the proportion of dry matter in the form of branches, leaves and roots. Gibberellic acid had no significant effect on the proportion of root but increased the stem: root ratio in both tube and glasshouse environments. There was no significant effect of 24hour light on stem:root ratio.

RESULTS II

PART A - EXPERIMENT II

The Effect of Tube Environment and Application of Gibberellic Acid on the Growth of Oak and Beech Seedlings in the Field.

This experiment compared the effect of the tube environment and application of gibberellic acid on the growth of two tree species, oak and beech. It also enabled comparison between the effects of tube and hormone treatments on the initial growth of oak seedlings established in the field in successive years, by comparing with the effects of these treatments on growth during the first year of the previous experiment.

4A.1 Design of Experiment

The effect of tube and gibberellic acid on the growth of oak and beech seedlings was studied in two 2 x 2 factorial, randomised block experiments in the field over the period May-October 1984. Each of the treatments was replicated 5 times. For each of the two species (oak and beech) the two treatment factors were: (a) no tube ; tube (b) -gibberellic acid ; +gibberellic acid.

The blocks, each consisting of 1 replicate of each treatment planted in two rows of 4 plants at approximately 0.75m spacing, were at right angles to the hedge at the end of the plot. Random numbers were used to allocate the trees to the different treatment/blocks after numbering the seedlings of each species in order of increasing height. Details of the seedlings used and the tube and hormone treatments are given in materials and methods.

For the purpose of statistical analysis of the experiment separate analyses of variance were carried out for the two species, oak and beech. This ensured that inherent differences between the two species did not obscure possible effects of the treatments, however comparison between the two species was possible because they were grown under similar conditions and were both included in a single randomised block design.

4A.2 Height Growth - Oak

For the height growth of oak seedlings neither main factor, tube or hormone, nor their interaction showed any significant differences throughout the year (table 4A.1). Height growth was very poor with the tallest tree only reaching 560mm. GA_3-treated trees in tubes showed some increase in height after two months, otherwise there was little growth of trees under other treatments until later in the season, when tube trees showed some increase over field trees.

4A.3 Height Growth - Beech

The tube environment had a significant effect on height growth of beech seedlings from August (table 4A.2). The interaction between tube and gibberellic acid treatment was significant from the middle of August. Figure 4A.1 gives a Richards' diagram for this interaction for 8 occasions in 1984. The tube environment alone gave the greatest height growth. GA_3-treated trees in the field and tube were similar in height at the end of the experiment both being taller than control trees.

4A.4 Branching - Oak

The average values for branch numbers and their lengths are given in table 4A.3 for both oak and beech. The final number of primary branches and the number of branches per 10cm stem length in oak were greater in the field than in tube trees; also there was a decreased amount of branching in GA_3-treated trees. The mean length of branches was similar in field and tube trees, but it was also decreased by hormone treatment. All but two of the oak seedlings used had no branches at the start of the experiment.

4A.5 Branching - Beech

Unlike the oak, for beech the total number of primary branches and the number per 10cm stem were increased by the tube environment. The two main factors had no significant effect on mean length of branches; however the interaction between the two factors was significant ($P<0.05$). A combination of both treatments gave no further increase in length of branches compared with the main effects of tube and hormone treatments alone i.e. the effects were not additive. For the beech seedlings the initial mean number of branches was 3.8 ± 2.0, number per 10cm stem 1.3 ± 0.6 and the mean length of branches 54.9 ± 22.4mm, with no significant differences between treatments.

Date	Control	+ GA_3	+ Tube	+ GA_3 + Tube	Sig.	LSD(P0.05)	CV
3.5.84	268	259	246	256	NS	31.8	9.0
31.5.84	271	264	253	261	NS	32.0	8.9
15.6.84	271	264	253	269	NS	31.0	8.6
27.6.84	273	266	253	301	NS	51.3	13.7
16.7.84	274	273	255	306	NS	54.5	14.3
1.8.84	276	273	261	308	NS	54.3	14.1
14.8.84	278	275	284	308	NS	63.0	16.0
5.9.84	284	292	309	309	NS	61.7	15.0
21.9.84	284	298	334	310	NS	87.2	20.6
8.10.84	298	298	335	310	NS	100.0	23.6

Table 4A.1 The effect of tube environment and gibberellic acid on mean height (mm) of oak grown in 1984.

	3.5.84	31.5.84	15.6.84	27.6.84	16.7.84	1.8.84	14.8.84	5.9.84	21.9.84	8.10.84
- Tube	268	291	305	324	334	335	340	354	356	360
+ Tube	274	327	370	394	430	454	480	511	528	534
Significance	NS	NS	NS	NS	NS	*	**	**	**	**
LSD(P0.05)	50.3	60.8	76.2	85.2	99.6	93.2	83.2	90.6	96.9	97.2
- GA_3	266	289	308	332	367	393	423	456	468	473
+ GA_3	276	329	366	386	397	396	398	409	415	421
Significance	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
LSD(P0.05)	50.3	60.8	76.2	85.2	99.6	93.2	83.2	90.6	96.9	97.2
Coefficient of variation (%)	19.0	20.2	23.2	24.4	26.8	24.2	20.8	21.5	22.5	22.3

Table 4A.2 The effect of the main factors, tube and hormone, on the mean height (mm) of beech seedlings, 1984.

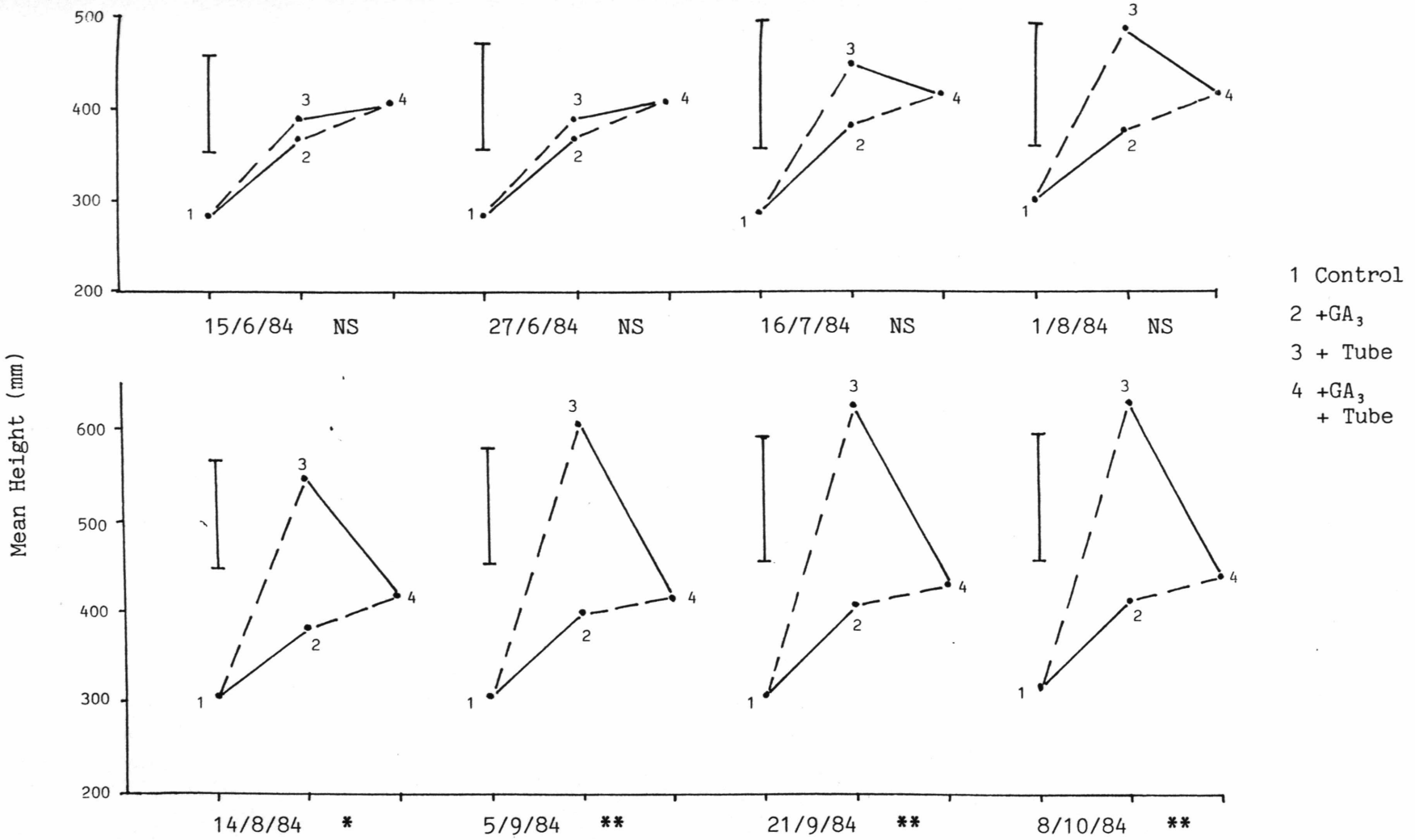


Figure 4A.1 Effect of the interaction between tube and gibberellic acid treatment on mean height (mm) of beech (1984).

	OAK			BEECH		
	Number Primary Branches	Number Branches per 10cm Stem	Mean Length (mm) of Branches	Number Primary Branches	Number Branches per 10cm Stem	Mean Length (mm) of Branches
- Tube	6.4	2.0	60.1	6.6	1.8	67.1
+ Tube	2.9	0.5	60.8	13.5	2.6	77.2
Significance	*	***	NS	***	**	**
LSD(P0.05)	2.8	0.8	38.9	3.2	0.5	14.8
- GA_3	7.0	1.9	92.8	10.2	2.1	68.6
+ GA_3	2.3	0.6	28.1	9.9	2.3	75.6
Significance	**	***	**	NS	NS	NS
LSD(P0.05)	2.8	0.8	38.9	3.2	0.5	14.8
Coefficient of variation (%)	62.2	68.3	66.1	33.2	23.3	21.0

Table 4A.3 The effect of main factors, tube and hormone, on the mean number and length of branches of oak and beech seedlings in 1984.

4A.6 Stem Diameter - Oak

Neither of the main factors, tube and hormone, had a significant effect on the mean diameter at the base or at 5cm in oak seedlings yet, there were significant interactions between the two factors (table 4A.4). Base diameter was decreased compared with the untreated controls by both tube and GA_3 treatments but the effect was not additive. The diameter at 5cm was also decreased by tube and hormone treatments alone, however there was no decrease when tube and hormone treatments were combined.

Table 4A.4

Interaction between tube and hormone, the effect on mean stem diameter (mm) of oak seedlings 1984.

	INITIAL BASE DIAMETER	FINAL BASE DIAMETER	INITIAL DIAMATER AT 5CM	FINAL DIAMETER AT 5CM
NO TUBE $-GA_3$	6.0	13.4	3.8	6.4
NO TUBE $+GA_3$	6.2	10.4	4.0	4.8
+ TUBE $-GA_3$	5.4	10.2	3.6	5.0
+ TUBE $+GA_3$	5.8	10.8	3.4	6.6
SIGNIFICANCE	NS	*	NS	**
LSD (P0.05)	0.9	2.3	0.6	1.6
COEFFICIENT OF VARIATION (%)	11.0	14.8	12.3	20.3

4A.7 Stem Diameter - Beech

The tube environment had a significant effect on the base diameter of beech seedlings (table 4A.5), with mean increases of 2.2mm and 1.8mm occurring in the presence and absence of gibberellic acid respectively. The diameter at 5cm was not significantly affected by either tube or hormone treatments.

Table 4A.5

The effect of the main factors, tube and hormone, on the mean stem diameter (mm) of beech seedlings 1984.

	INITIAL BASE DIAMETER	FINAL BASE DIAMETER	INITIAL DIAMETER AT 5CM	FINAL DIAMETER AT 5CM
NO TUBE	3.9	8.5	2.9	6.9
+ TUBE	4.0	10.5	3.0	7.8
SIGNIFICANCE	NS	**	NS	NS
LSD (P0.05)	0.4	1.3	0.5	1.1
-GIBBERELLIC ACID	4.0	9.9	3.0	7.5
+GIBBERELLIC ACID	3.9	9.1	2.9	7.2
SIGNIFICANCE	NS	NS	NS	NS
LSD (P0.05)	0.4	1.3	0.5	1.1
COEFFICIENT OF VARIATION (%)	10.6	14.3	18.6	15.4

4A.8 Leaf Area - Oak

The final mean number of leaves and the total leaf area per plant of oak seedlings were significantly decreased by gibberellic acid (table 4A.6). The mean number of leaves was also substantially reduced by the tube treatment. Neither mean leaf area per leaf nor mean leaf weight were significantly affected by the tube or GA_3 treatments. However the specific leaf area was significantly reduced by GA_3 treatment. This effect, on specific leaf area only, occurred with a combination of tube and hormone treatments (fig. 4A.2).

4A.9 Leaf Area - Beech

The final number of leaves and mean total leaf area of beech seedlings were increased by tube treatment and decreased by GA_3 application (table 4A.7). As with oak the mean leaf area per leaf and leaf weight per leaf were not significantly affected by tube or hormone treatments, however specific leaf area was increased by both treatments. The interactions between tube and GA_3 were not significant.

	Initial Number of Leaves	Final Number of Leaves	Final Total Leaf Area (cm^2)	Final Mean Leaf Area per Leaf (cm^2)	Final Mean Leaf Area per Leaf (cm^2)	Specific Leaf Area (cm^2/g)
- Tube	15.5	70.1	648	9.9	0.072	136.4
+ Tube	14.1	40.5	461	12.8	0.092	141.4
Significance	NS	*	NS	NS	NS	NS
LSD(P0.05)	2.4	23.4	220.3	3.2	0.024	12.8
- GA_3	15.7	80.8	815	10.8	0.075	145.5
+ GA_3	13.9	29.8	294	11.8	0.090	132.3
Significance	NS	***	***	NS	NS	*
LSD(P0.05)	2.4	23.4	220.3	3.2	0.024	12.8
Coefficient of variation (%)	16.9	43.5	40.8	29.0	29.7	9.5

Table 4A.6 The effect of main factors, tube and hormone, on the mean number, area and weight of leaves of oak, 1984.

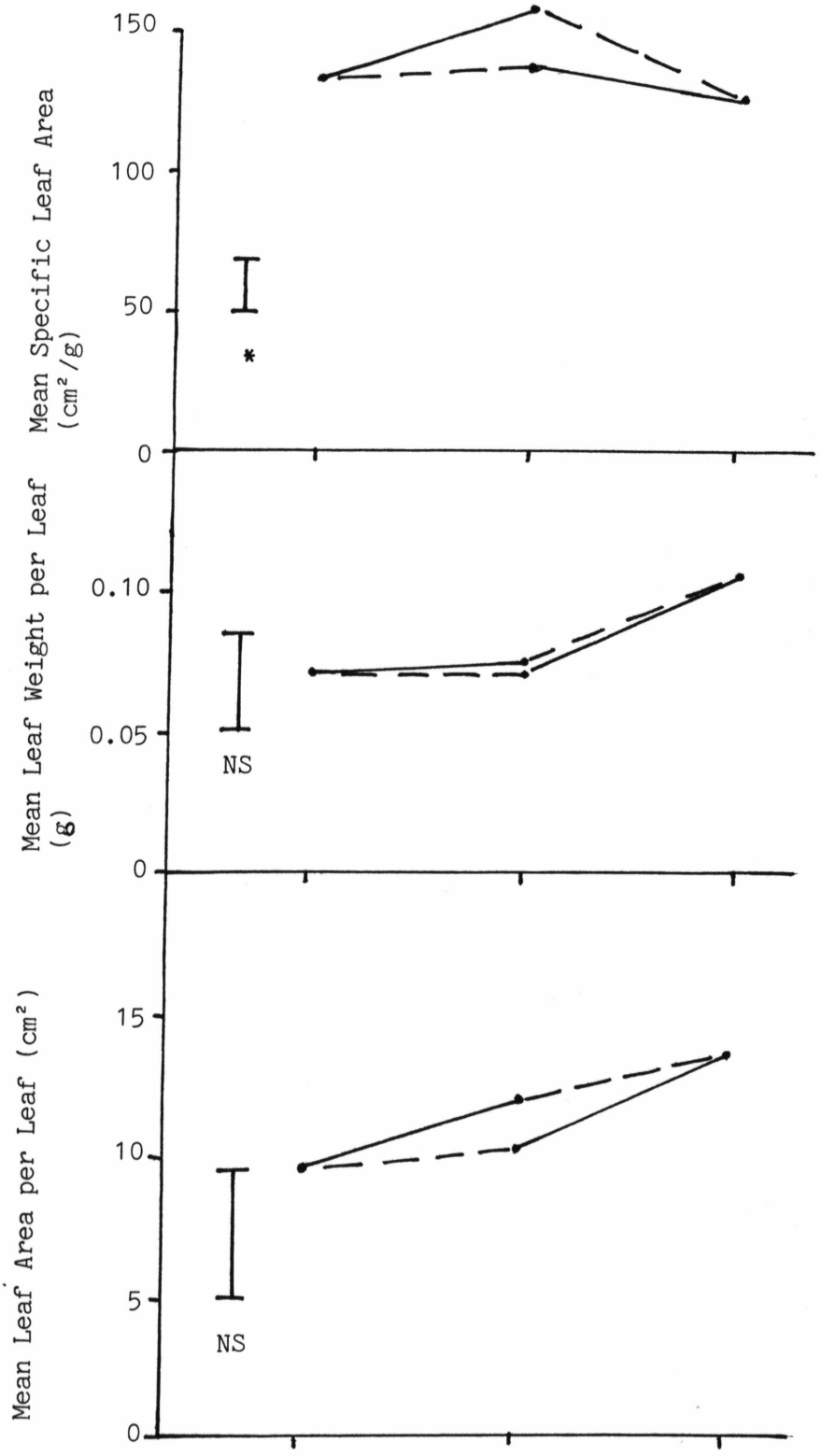


Figure 4A.2 The effect of tube environment and gibberellic acid treatment on mean specific leaf area (cm^2/g leaf dry wt), mean leaf area (cm^2) and mean leaf dry weight (g) of oak, 1984.

——— $-GA_3$ — — — $+GA_3$

	Initial Number of Leaves	Final Number of Leaves	Final Total Leaf Area (cm^2)	Final Mean Leaf Area per Leaf (cm^2)	Final Mean Leaf Weight (g)	Specific Leaf Area (cm^2/g)
- Tube	18.7	34.5	178	6.0	0.046	136.1
+ Tube	18.0	108.4	562	5.7	0.036	158.1
Significance	NS	***	***	NS	NS	*
LSD(P0.05)	6.9	37.1	192.6	3.1	0.024	19.3
- GA_3	16.1	92.1	531	5.5	0.042	131.2
+ GA_3	20.6	50.8	208	6.1	0.040	163.0
Significance	NS	*	**	NS	NS	**
LSD(P0.05)	6.9	37.1	192.6	3.1	0.024	19.3
Coefficient of variation (%)	38.5	53.3	53.4	54.9	60.5	13.5

Table 4A.7 The effect of main factors, tube and hormone on the mean number, area and weight of leaves of beech, 1984.

4A.10 Total Dry Weight - Oak and Beech

Total dry weight was significantly increased by the tube envrionment in beech, whereas GA_3 treatment decreased total dry weight of both oak and beech (table 4A.8). However for oak there was a significant interaction between tube and GA_3 treatments, the total dry weight of oak being decreased by tube and hormone treatments alone, but no further decrease occurred with a combination of both treatments (fig. 4A.3).

Table 4A.8

The effect of main factors, tube and hormone,on the mean total dry weight (g) of oak and beech,1984.

	OAK	BEECH
INITIAL WEIGHT (n=20)	6.0 ± 2.4	1.6 ± 0.6
NO TUBE	19.5	10.3
+ TUBE	16.7	17.1
SIGNIFICANCE	NS	*
LSD (P0.05)	4.3	5.3
-GIBBERELLIC ACID	21.0	17.3
+GIBBERELLIC ACID	15.3	10.1
SIGNIFICANCE	*	**
LSD (P0.05)	4.3	5.3
COEFFICIENT OF VARIATION (%)	24.2	37.5

4A.11 Distribution of Dry Matter - Oak

For oak the tube environment had no significant effect on the distribution of dry matter within the plant, however GA_3 treatment significantly increased the proportion of stem and roots and decreased that of branches and leaves (fig. 4A.4). Although not significantly different the proportion of stem was greater, and the percentage of branches and leaves decreased with a combination of tube and hormone treatments as compared with GA_3 treatment alone. The distribution of dry matter of oak had altered from that of the initial

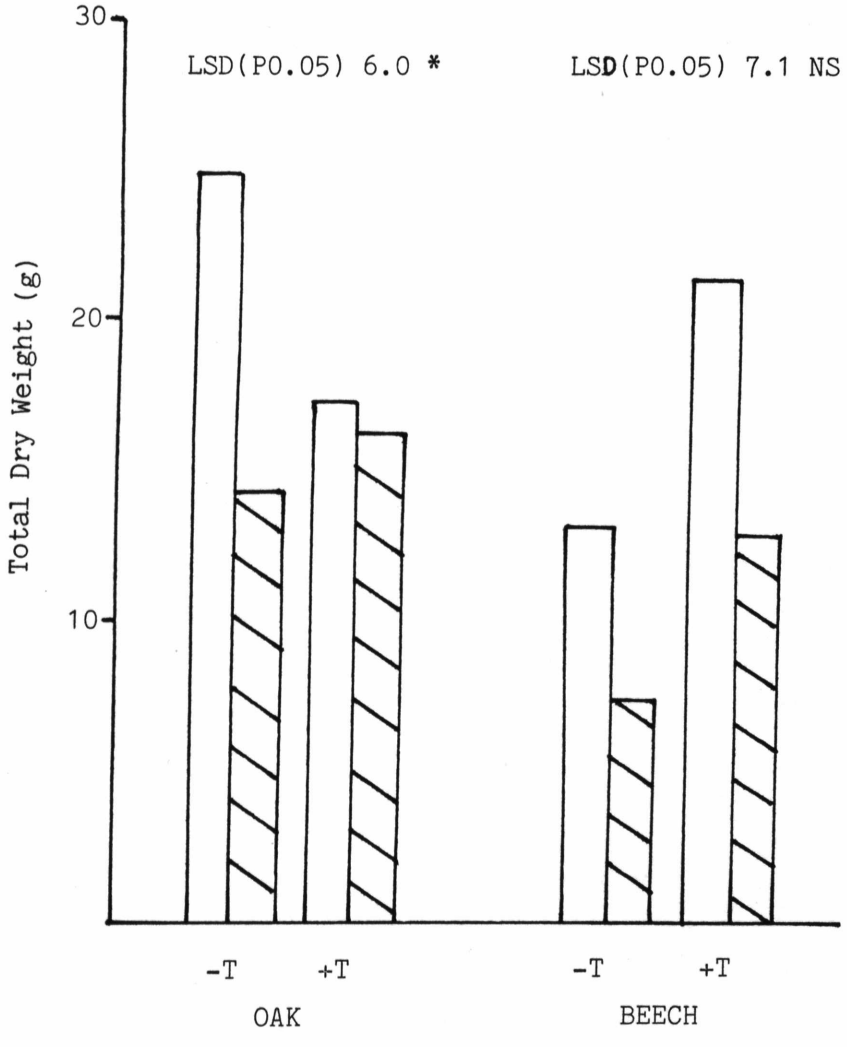


Figure 4A.3 The effect of tube (T) and gibberellic acid (shaded columns) on the mean total dry weight (g) of oak and beech seedlings 1984.

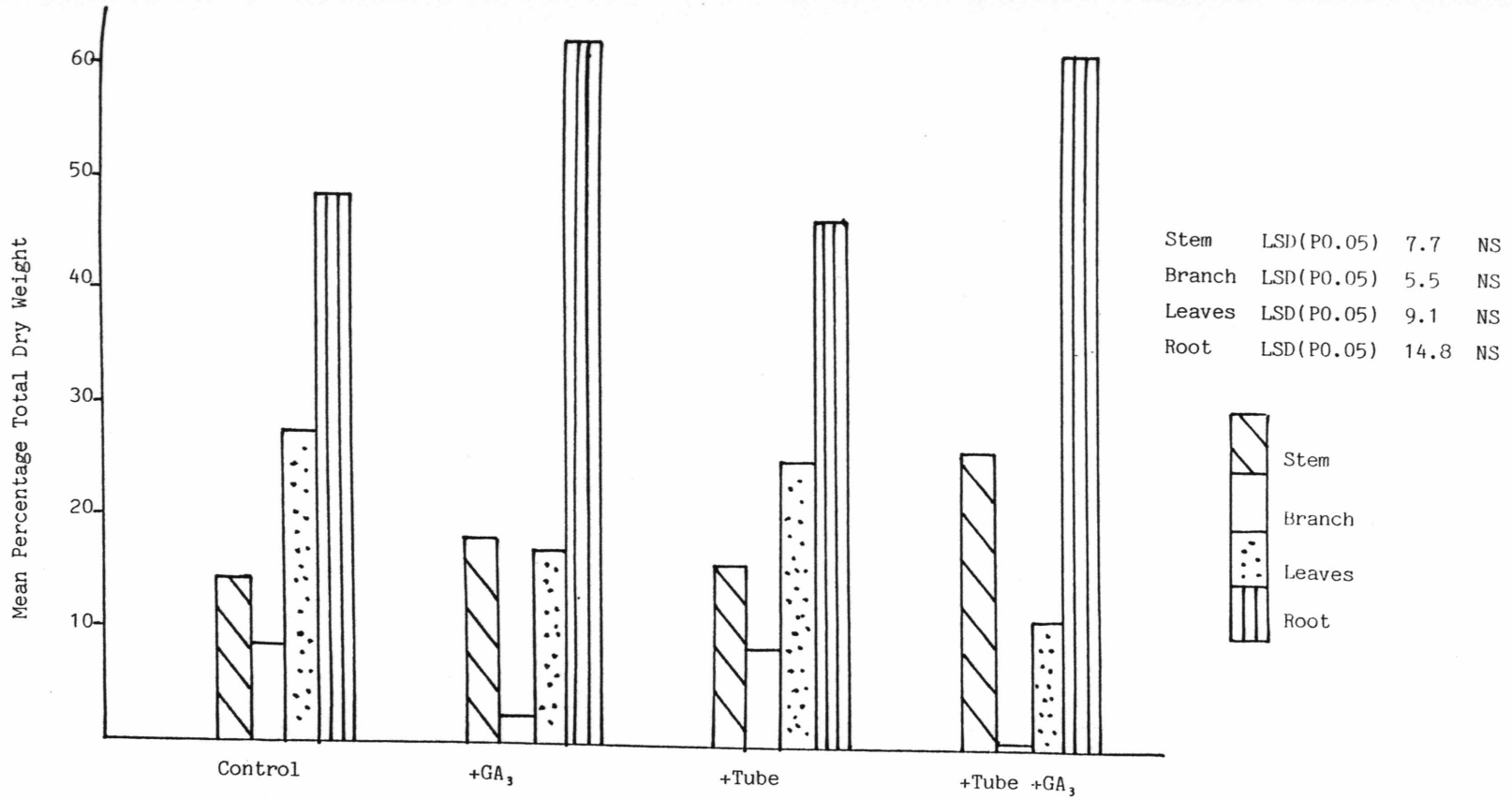


Figure 4A.4 Distribution of dry matter between stem, branch, leaves and root of oak as affected by tube and GA_3 treatments.

sample (n=20) in which stem + branches was 22.6 ± 5.2%, leaves 46.1 ± 12.6% and root 31.4 ± 8.9% of the total dry weight.

4A.12 Distribution of Dry Matter - Beech

For beech the tube environment had a significant effect on the proportion of leaves only, GA_3 significantly increased the proportion of stem and branches and decreased that of leaves and root (table 4A.9). The percentage of root with a combination of tube and GA_3 was similar to that produced by the GA_3 treatment alone (fig. 4A.5). The initial distribution of dry matter in the beech seedlings (n=20) was stem + branches 28.6 ± 5.8%, leaves 19.8 ± 8.2% and roots 51.7 ± 9.3%.

Table 4A.9

The effect of the main factors, tube and hormone, on the distribution of dry matter, expressed as percentage of total dry weight, of beech, October 1984.

	% STEM	% BRANCH	% LEAVES	% ROOT
NO TUBE	42.3	11.2	11.8	34.8
+ TUBE	39.2	11.3	20.3	29.2
SIGNIFICANCE	NS	NS	***	NS
LSD (P0.05)	4.4	5.5	4.3	6.3
-GIBBERELLIC ACID	32.4	8.3	21.2	38.1
+GIBBERELLIC ACID	49.0	14.2	10.9	25.9
SIGNIFICANCE	***	*	***	**
LSD (P0.05)	4.4	5.5	4.3	6.3
COEFFICIENT OF VARIATION (%)	11.1	50.6	27.3	20.1

4A.13 Stem : Root Ratio - Oak and Beech

Tube environment had no significant effect on stem:root ratio of oak or beech, however GA_3 significantly increased the stem:root ratio in beech (table 4A.10). There was no significant interaction between tube and hormone for either oak or beech. The initial mean stem:root ratio for oak (n=20) was 0.76 ± 0.23 and beech (n=20) 0.58 ± 0.18, over the experimental period it was decreased by all treatments in oak and increased in beech.

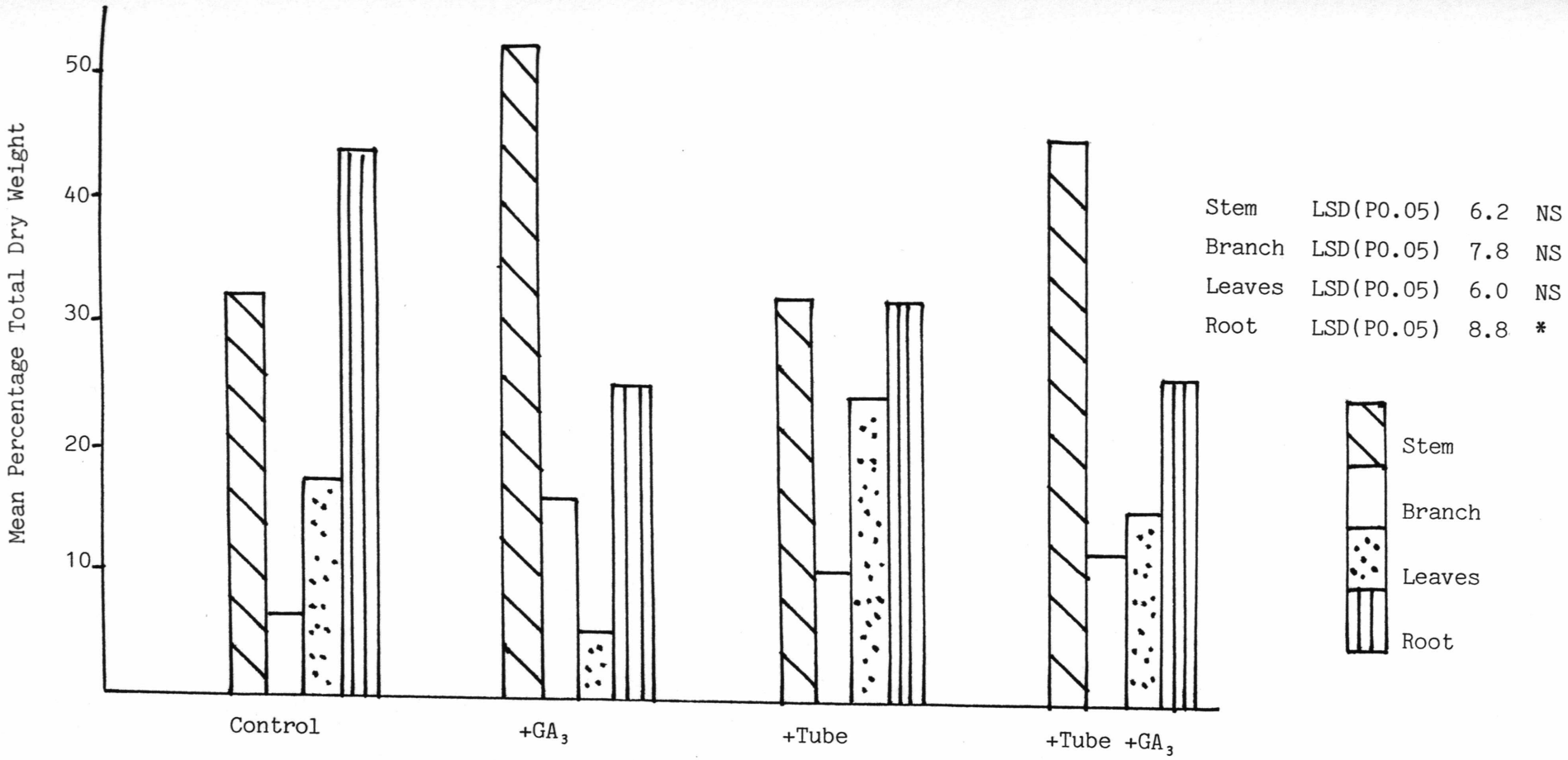


Figure 4A.5 The distribution of dry matter between stem, branch, leaves and root of beech as affected by tube environment and GA_3 treatments.

Table 4A.10

The effect of the main factors, tube and hormone,on the mean stem:root ratio of oak and beech, 1984.

	OAK	BEECH
NO TUBE	0.43	1.86
+ TUBE	0.55	1.86
SIGNIFICANCE	NS	NS
LSD (P0.05)	0.22	0.66
-GIBBERELLIC ACID	0.57	1.14
+GIBBERELLIC ACID	0.41	2.58
SIGNIFICANCE	NS	***
LSD (P0.05)	0.22	0.66
COEFFICIENT OF VARIATION (%)	44.9	36.1

4A.14 Summary

Height growth of oak seedlings was poor in 1984 in comparison with the growth achieved in the first experiment of 1983, there were no significant effects of tube environment or gibberellic acid. Although height growth was not significantly affected there was a decrease in the number and length of branches and stem diameter with the tube and hormone treatments. Combined with these changes the total number of leaves and total leaf area of oak were decreased with gibberellic acid treatment, and the number of leaves also decreased in the tube.

The tube environment had no significant effect on the total dry weight, distribution of dry matter or stem:root ratio of oak. Dry matter production was however decreased by gibberellic acid application, the proportion of dry matter as stem and roots were increased, with no effect on stem:root ratio, but the proportion of branches and leaves decreased.

The growth of beech was increased by both the tube environment and gibberellic acid application. Gibberellic acid had a similar effect on growth in both field and tube environments, in contrast to the results obtained for oak in the previous experiment. The number and length of branches were increased by tube and hormone treatments, but stem

diameter was increased only in the tube. Also increased by the tube environment were the number of leaves and total leaf area, with no significant effect on individual leaf size.

Unlike oak the total dry weight of beech was increased in the tube environment and in particular the proportion of dry matter as leaves was increased. Gibberellic acid also decreased total dry weight of beech. However the stem:root ratio was significantly increased reflecting an increase in the proportion of dry matter as stem and branches and a decrease in that as roots.

PART B - EXPERIMENT III

The Effect of Light Duration and Gibberellic Acid, Combined Factorially, on Two Year Old Oak and Beech Trees in the Glasshouse.

The comparison between oak (Q.petraea) and beech was continued in two 2 x 2 factorial experiments, June-October 1984, to study the effects of light duration and hormone (GA_3) on the growth of 2 year old trees in the glasshouse.

4B.1 Materials and Methods

There were four treatments with 5 replicates of each treatment for each of the two species. The two treatment factors were:
Light: natural daylength; 24hour light
Hormone: -gibberellic acid; +gibberellic acid
The natural daylength and 24hour light treatments were separated and given in different areas of the same glasshouse, the trees being arranged at random on the benches. The trees were assigned to treatments using random numbers after ordering the trees in approximately descending order of size (height). As in the previous experiment separate analyses were carried out for the two species. Details of the trees used and the 24hour light and gibberellic acid treatments are given in material and methods.

4B.2 Height Growth - Oak

In table 4B.1 the effects of the main factors light and gibberellic acid on the mean cumulative increase in height of oak trees are presented. The interaction between light and gibberellic acid never reached significance throughout the experiment. 24hour light had no significant effect but gibberellic acid increased height growth in the first part of the experimental period.

4B.3 Height Growth - Beech

Both hormone and light had a significant effect on the height growth of 2year old beech in the glasshouse (table 4B.2). Gibberellic acid increased height growth and unlike oak this effect was maintained until the end of the experimental period. 24hour light only became significant in September. The interaction between light and gibberellic acid was not significant throughout the experimental period.

	Natural Daylength	24 Hour Light	Sig.	$LSD_{(P0.05)}$	- GA_3	+ GA_3	Sig.	$LSD_{(P0.05)}$
15.6.84	4.5	11.5	NS	8.5	7.5	8.5	NS	8.5
27.6.84	143	190	NS	106	62	271	***	106
16.7.84	246	216	NS	203	83	380	**	203
27.7.84	298	266	NS	233	141	423	*	233
14.8.84	320	308	NS	234	197	431	*	234
5.9.84	336	432	NS	201	346	422	NS	201
21.9.84	378	509	NS	195	435	452	NS	195
6.11.84	400	586	NS	243	490	497	NS	243

Table 4B.1 The effect of main factors, light and gibberellic acid application on mean cumulative height increase (mm) of 2 year old oak in the glasshouse.

	Natural Daylength	24 Hour Light	Sig.	$LSD_{(P0.05)}$	- GA_3	+ GA_3	Sig.	$LSD_{(P0.05)}$
15.6.84	18.5	9.0	NS	23.2	16.0	11.5	NS	23.2
27.6.84	47.0	60.5	NS	39.9	37.0	70.5	NS	39.9
16.7.84	147	137	NS	49.0	77	207	***	49.0
27.7.84	161	162	NS	57.1	91	232	***	57.1
14.8.84	175	239	NS	107	139	275	*	107
5.9.84	108	276	NS	124	163	293	*	124
21.9.84	186	316	*	118	188	315	*	118
6.11.84	186	316	*	118	188	315	*	118

Table 4B.2 The effect of main factors, light and gibberellic acid application on mean cumulative increase in height (mm) of 2 year old beech in the glasshouse.

	OAK			BEECH		
	Number Primary Branches	Number Secondary Branches	Mean Length Primary Branches (mm)	Number Primary Branches	Number Secondary Branches	Mean Length Primary Branches (mm)
Natural Daylength	19.0	13.6	139.0	22.1	42.1	154.0
24 Hour Light	21.6	15.2	168.0	24.2	58.1	200.1
Significance	NS	NS	NS	NS	*	*
LSD(P0.05)	4.5	3.8	60.5	3.3	15.5	35.5
- GA_3	21.1	14.5	140.0	22.3	37.8	164.8
+ GA_3	19.6	14.4	167.0	24.0	62.4	189.2
Significance	NS	NS	NS	NS	**	NS
LSD(P0.05)	4.6	3.8	58.5	3.5	15.5	35.1
Covariate	**	***	NS	***	*	NS
Coefficient of variation (%)	23.2	27.1	39.0	14.3	32.3	20.5

Table 4B.3 The effect of light and gibberellic acid on the mean number and length of branches, adjusted for covariate, of 2 year old oak and beech (n=10) in the glasshouse.

4B.4 Branching - Oak and Beech

Due to differences between trees at the beginning of the experiment it was decided to use the initial measures of number of primary and secondary branches and mean length of primary branches as covariates in the analyses of variance. Light and GA_3 had no significant effect on the mean number and length of branches of the 2year old oak. However the number of secondary branches of beech was increased by 24hour light and gibberellic acid and the mean length of primary branches was increased by 24hour light (table 4B.3). There was no significant effect on the number of primary branches in beech.

4B.5 Stem Diameter - Oak and Beech

The increase in diameter at the base of the stem and at a height of 5cm was not significantly affected by either 24hour light or gibberellic acid in both species (table 4B.4)

Table 4B.4

The effect of main factors, light and gibberellic acid application on mean increase in stem diameter (mm) of 2year old oak and beech in the glasshouse.

	OAK		BEECH	
	BASE DIAMETER	DIAMETER AT 5CM	BASE DIAMETER	DIAMETER AT 5CM
NATURAL DAYLENGTH	4.2	3.6	3.6	2.8
24HOUR LIGHT	4.5	3.2	3.8	2.9
SIGNIFICANCE	NS	NS	NS	NS
LSD (P0.05)	2.5	1.6	1.3	1.4
-GIBBERELLIC AICD	4.8	3.9	3.5	2.6
+GIBBERELLIC ACID	3.9	2.9	3.9	3.1
SIGNIFICANCE	NS	NS	NS	NS
LSD (P0.05)	2.5	1.6	1.3	1.4

4B.6 Leaf Area - Oak

There were no significant differences in the final number of surviving leaves of oak however the total leaf area and mean leaf area per leaf were decreased by GA_3 application (table 4B.5). Mean leaf weight per leaf was also decreased by hormone treatment however this

	Initial Number Leaves	Final Number Leaves	Final Total Leaf Area (cm^2)	Final Mean Leaf Area per Leaf (cm^2)	Final Mean Leaf Weight (g)	Specific Leaf Area (cm^2/g)
Natural Daylength	180	367	3413	9.5	0.056	171.3
24 Hour Light	177	460	4324	9.9	0.062	160.1
Significance	NS	NS	NS	NS	NS	NS
LSD(P0.05)	57.4	131.5	1580	3.3	0.019	37.9
-Gibberellic acid	176	431	4876	11.8	0.071	170.8
+Gibberellic acid	180	396	2861	7.7	0.047	160.7
Significance	NS	NS	*	*	*	NS
LSD(P0.05)	57.4	131.5	1580	3.3	0.019	37.9
Coefficient of variation (%)	33.9	33.4	42.9	36.2	33.8	24.0

Table 4B.5 The effect of the main factors, light and hormone, on the mean number, area (cm^2) and weight (g) of leaves of 2 year old oak in the glasshouse.

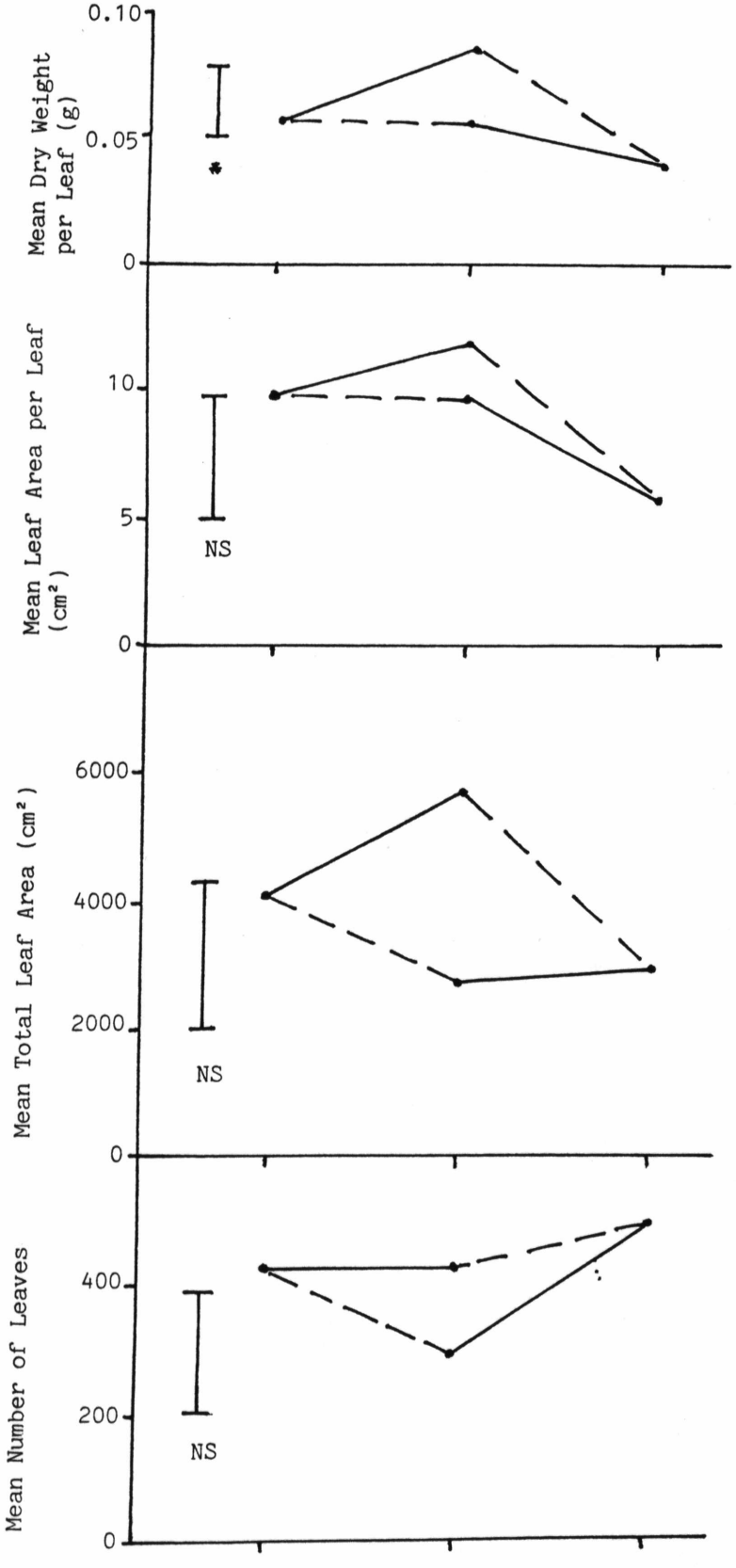


Figure 4B.1 The effect of daylength and gibberellic acid on the mean number, area and weight of leaves of 2 year old oak in the glasshouse. - - - - - GA_3 ~~ + GA_3. ——— Natural daylength ~~ 24hour light.

	Initial Number Leaves	Final Number Leaves	Final Total Leaf Area (cm^2)	Final Mean Leaf Area per Leaf (cm^2)	Final Mean Leaf Weight (g)	Specific Leaf Area (cm^2/g)
Natural Daylength	298	322	1916	5.8	0.030	193.0
24 Hour Light	240	640	3678	5.6	0.030	187.6
Significance	NS	NS	NS	NS	NS	NS
LSD(P0.05)	92.6	301.7	1675	1.7	0.009	27.8
-Gibberellic acid	251	470	3373	6.8	0.036	190.8
+Gibberellic acid	291	474	2220	4.6	0.024	189.8
Significance	NS	NS	NS	*	*	NS
LSD(P0.05)	92.6	301.7	1675	1.7	0.009	27.8
Coefficient of variation (%)	36.0	67.0	62.9	30.5	30.8	15.3

Table 4B.6 The effect of main factors, light and hormone, on the mean number, area (cm^2) and weight (g) of leaves of 2 year old beech in the glasshouse.

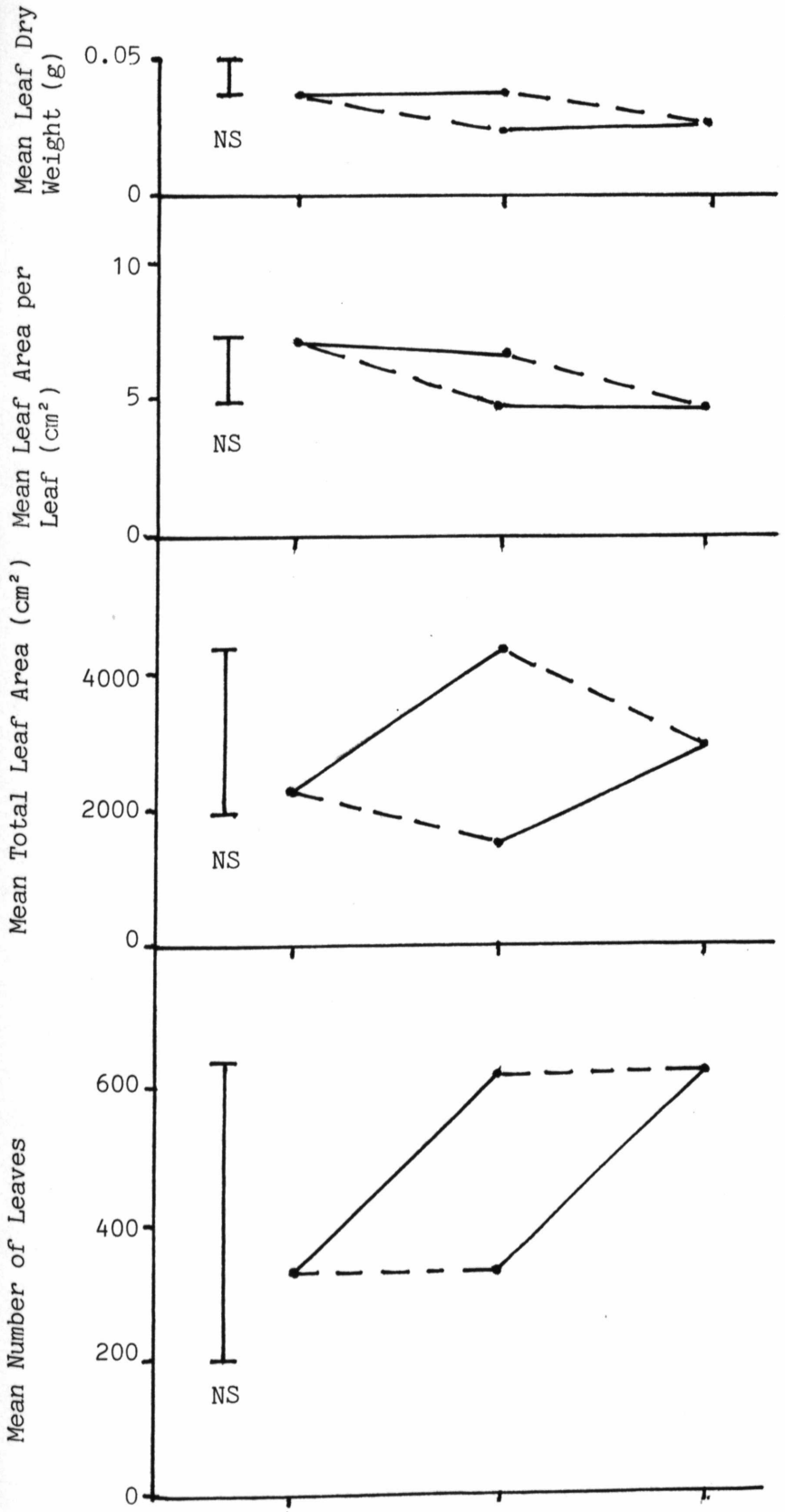


Figure 4B.2 The effect of daylength and gibberellic acid on the mean number, area and weight of leaves of 2 year old beech in the glasshouse.

- - - - $-GA_3$ ~ $+GA_3$ ——— Natural Daylength ~ 24 Hour Light

effect only occurred under 24hour light, 24hour light alone led to an increase in leaf dry weight (fig. 4B.1). Specific leaf area was not significantly affected by treatments.

4B.7 Leaf Area - Beech

For beech there were no significant differences in final number of surviving leaves or total leaf area(table 4B.6). Mean leaf area and mean leaf dry weight per leaf were significantly decreased by GA_3 treatment under both light regimes (fig. 4B.2), though specific leaf area was not significantly affected.

4B.8 Total Dry Weight - Oak and Beech

Daylength had no significant effect on the total dry weight of either oak or beech, gibberellic acid treatment however significantly decreased the total dry weight of oak (table 4B.7). The interaction between daylength and GA_3 was not significant. The decrease in dry weight of oak with gibberellic acid occurred under both daylength treatments.

Table 4B.7

The effect of the main factors, light and hormone, on the mean total dry weight (g) of 2year old oak and beech in the glasshouse.

	OAK	BEECH
NATURAL DAYLENGTH	88.9	75.1
24HOUR LIGHT	105.9	101.8
SIGNIFICANCE	NS	NS
LSD (P0.05)	33.9	34.2
-GIBBERELLIC ACID	114.8	88.0
+GIBBERELLIC ACID	80.0	88.9
SIGNIFICANCE	*	NS
LSD (P0.05)	33.9	34.2
COEFFICIENT OF VARIATION (%)	36.5	40.6

4B.9 Distribution of Dry Matter - Oak

For oak daylength and GA_3 treatments had no significant effect on the distribution of dry matter within the plant (table 4B.8). The interaction between daylength and hormone was also not significant. However the distribution of dry matter had altered from that prior to treatment when the proportion of stem + branches was 33.9 ± 6.1%, leaves 14.1 ± 2.7% and root 52.0 ± 4.8% of the total dry weight.

Table 4B.8

The effect of main factors, daylength and hormone, on the distribution of dry matter, expressed as percentage of total dry weight, of 2year old oak in the glasshouse.

	% STEM	% BRANCH	% LEAVES	% ROOT
NATURAL DAYLENGTH	29.5	12.5	23.3	34.7
24HOUR LIGHT	29.9	13.9	25.6	30.6
SIGNIFICANCE	NS	NS	NS	NS
LSD (P0.05)	4.6	5.3	5.3	5.8
-GIBBERELLIC AICD	29.5	11.4	25.5	33.6
+GIBBERELLIC ACID	29.8	15.1	23.4	31.7
SIGNIFICANCE	NS	NS	NS	NS
LSD (P0.05)	4.6	5.3	5.3	5.8
COEFFICIENT OF VARIATION (%)	16.3	41.9	22.9	18.8

4B.10 Distribution of Dry Matter - Beech

For beech there was a significant decrease in percentage root under 24hour light, with no significant effect on percentage stem, branches and leaves (table 4B.9). Gibberellic acid increased the percentage stem and decreased percentage leaves with no significant effect on the proportion of branches and roots. The interaction between light and hormone was not significant. The dry weight of beech proir to treatment was distributed as follows: stem + branches 47.3 ±2.5%, leaves 15.7 ± 2.4 and roots 37.0 ± 2.4% of the total dry weight.

Table 4B.9

The effect of main factors, light and hormone, on the distribution of dry matter, expressed as percentage total dry weight, of 2year old beech in the glasshouse.

	% STEM	% BRANCH	% LEAVES	% ROOT
NATURAL DAYLENGTH	34.4	19.4	13.3	32.8
24HOUR LIGHT	38.0	20.2	16.6	25.2
SIGNIFICANCE	NS	NS	NS	**
LSD (P0.05)	8.2	3.3	7.3	4.6
-GIBBERELLIC ACID	31.9	18.6	18.5	31.0
+GIBBERELLIC ACID	40.5	21.0	11.4	27.0
SIGNIFICANCE	*	NS	*	NS
LSD (P0.05)	8.2	3.3	7.3	4.6
COEFFICIENT OF VARIATION (%)	23.7	17.8	51.0	16.6

4B.11 Stem : Root Ratio - Oak and Beech

For both oak and beech there was a significant increase in stem: root ratio with 24hour light, and for beech a significant increase with gibberellic aicd (table 4B.10). For oak there was some increase with gibberellic acid under 24hour light, though this was not significant (fig.4B.3).

The initial mean stem:root ratio for beech (n=20) was 1.29 ± 0.13 and oak (n=20) 0.47 ± 0.17. At the end of the experiment non-GA_3 treated beech trees under natural daylength had a similar stem:root ratio to the initial sample, for the other treatments this ratio had approximately doubled. For oak there was an increase in stem:root ratio for all treatments indicating greater stem compared with root growth.

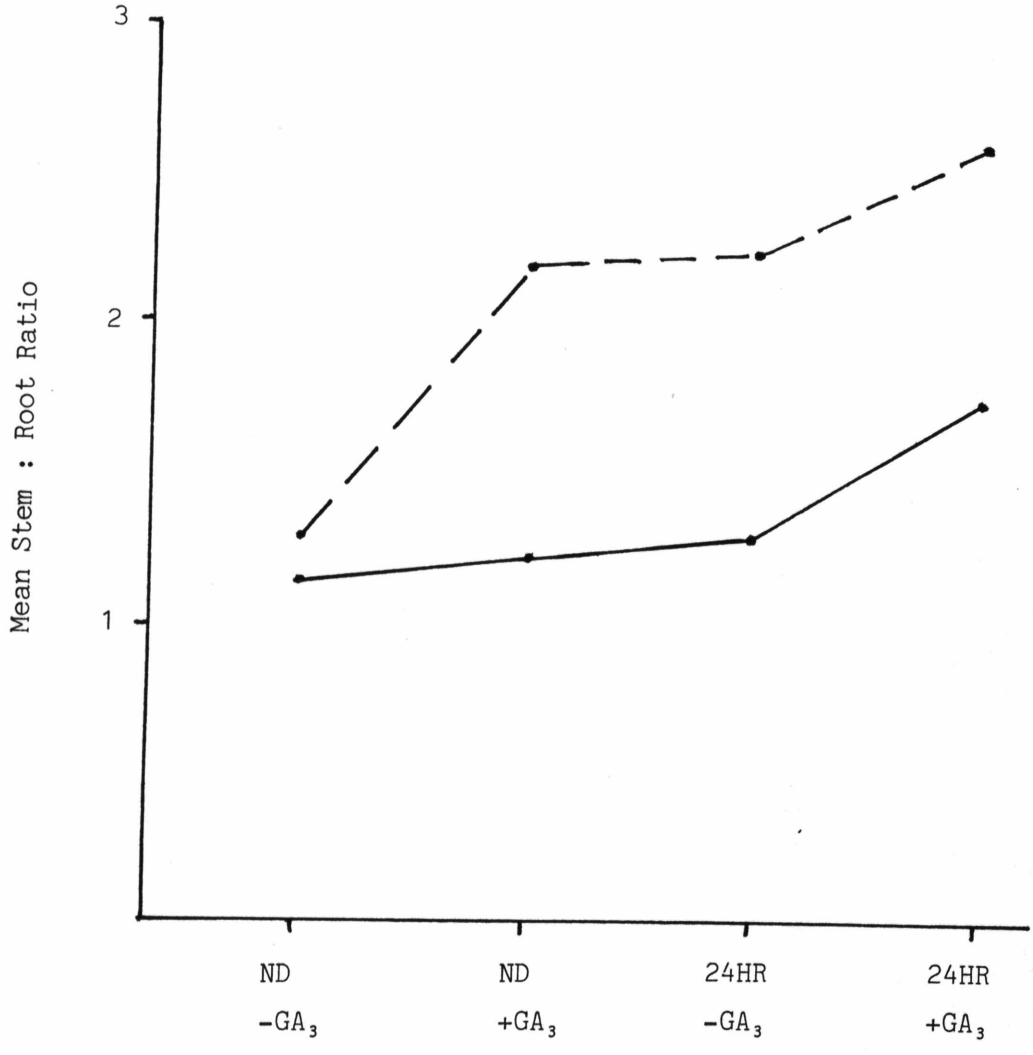


Figure 4B.3 The effect of light duration (ND = natural daylength, 24HR = 24hour light) and gibberellic acid (GA_3) on the mean stem:root ratio of oak (——) LSD(P0.05) 0.38 and beech (- - -) LSD(P0.05) 0.76 in the glasshouse.

Table 4B.10

The effect of main factors, daylength and hormone, on the mean stem:root ratio of 2year old oak and beech in the glasshouse.

	OAK	BEECH
NATURAL DAYLENGTH	1.18	1.74
24HOUR LIGHT	1.51	2.39
SIGNIFICANCE	*	*
LSD (P0.05)	0.27	0.54
-GIBBERELLIC ACID	1.21	1.75
+GIBBERELLIC ACID	1.48	2.38
SIGNIFICANCE	NS	*
LSD (P0.05)	0.27	0.54
COEFFICIENT OF VARIATION (%)	21.0	27.4

4B.12 Summary

Height growth of 2 year old oak, grown in the glasshouse, can also be stimulated by gibberellic acid, though 24hour light had no significant effect. There was no significant effect on stem diameter, or degree of branching. The distribution of dry matter of oak was not affected by 24hour light or gibberellic acid, though total dry weight was decreased by gibberellic acid.

Height growth of 2 year old beech was increased by both GA_3 application and 24hour light, the effect of extending the photoperiod only becoming apparent as the natural daylength shortened. The number of primary branches was not significantly affected but the mean length of branches was increased by 24hour light. The number of secondary branches was increased by both 24hour light and gibberellic acid. Total dry weight of beech was not affected by treatments but the proportion of dry matter as root was decreased by 24hour light and that as stem increased, while that as leaves was decreased by GA_3.

RESULTS III

PART A - EXPERIMENT IV

A Controlled Environment Study to Examine the Effect of Temperature and Gibberellic Acid on the Growth of Oak

5A.1 Materials and Methods

Measurements of temperature in the field and tube taken in the summer of 1983 showed that the tube temperature could exceed 30°C and was often about 10°C higher than ambient. The temperatures used in this experiment were based on meteorological data for June, July and August 1983 when the overall mean minimum and maximum temperatures were 12.9± 2.8°C and 21.8±3.6°C respectively, a mean range of 9°C.

In a 2 x 2 factorial experiment seedling oak were subjected to two day/night temperature regimes: 20°C/12°C and 30°C/12°C, with a 12hour photoperiod (8hours natural daylight plus 4hours tungsten lighting). The effect of gibberellic acid treatment was combined with the temperature treatment i.e. half of the trees in each temperature regime being treated with 50ppm GA_3, as described in materials and methods, the others serving as controls.

There were 5 replicates for each treatment. The experiment ran from June-September 1984 and was carried out in two adjacent controlled environment cabinets. Temperature and light regimes were controlled, but no attempt was made to control relative humidity within the cabinets. Seedlings were raised in the glasshouse but not given a period of "hardening-off". The plants, in 15cm pots, were arranged at random within the cabinets and moved periodically to different positions to minimise any edge effects.

5A.2 Environment

The maximum and minimum temperatures within the cabinets used for this study were monitored throughout the experimental period (n=92days). For the 20°C/12°C day/night temperature regime the mean maximum temperature was 23.7±2.1°C and mean minimum temperature 11.1±1.6°C. For the higher day/night temperature regime, 30°C/12°C, the mean maximum and minimum temperatures were 31.0±0.9°C and 10.6±0.4°C respectively.

The temperature and humidity within the cabinets were also measured on 3days at hourly intervals from 1000-1600hr (n=21). The mean temperatures for this series of measurements were 19.0±2.0°C and 31.4±1.3°C

for the 20°C/12°C and 30°C/12°C treatments respectively, and the mean relative humidities 61.5 ±17.5% and 85.9±5.2% respectively. On sunny days light cloth shades were pulled down in front of the cabinets to prevent overheating, this however also reduced light levels.

The soil temperature was measured using mercury-in-glass thermometers pushed into individual pots. Measurements, taken on 6days, were made at hourly intervals through the day from 1000-1600hr, a different pot being used on each occasion. Mean results (table 5A.1) show that the soil temperature increased gradually to that of the air during the day. Although not followed, the soil must have cooled again - probably at similar rates - during the low temperature nights.

Table 5A.1

Mean hourly readings recording changes in soil temperature (°C) (n=6) in the two day/night temperature regimes.

TIME (hours)	20°C/12°C	30°C/12°C
1000	14.3 ± 1.1	18.8 ± 1.5
1100	17.0 ± 0.9	25.3 ± 1.2
1200	18.0 ± 0.6	27.7 ± 0.6
1300	18.6 ± 0.4	29.3 ± 0.9
1400	19.2 ± 0.2	30.4 ± 0.8
1500	19.8 ± 0.5	30.8 ± 0.7
1600	19.9 ± 0.2	31.5 ± 1.0

5A.3 Height Growth

There were significant differences between both temperature and gibberellic acid treatments (fig. 5A.1), with gibberellic acid leading to almost a doubling of height growth under both temperature regimes. However the interaction between temperature and gibberellic acid was not significant. Height growth of seedlings not treated with gibberellic acid was restricted to the first three weeks of the experimental period with no further increase in height occurring after completion of this initial growth flush. However with gibberellic acid treatment seedlings maintained growth over a longer period of time. Several GA_3-treated seedlings in the higher day/night temperature regime suffered damage to the leading shoot, visible as a blackening of the shoot tip, possibly due to desiccation. This may partly explain the lack of

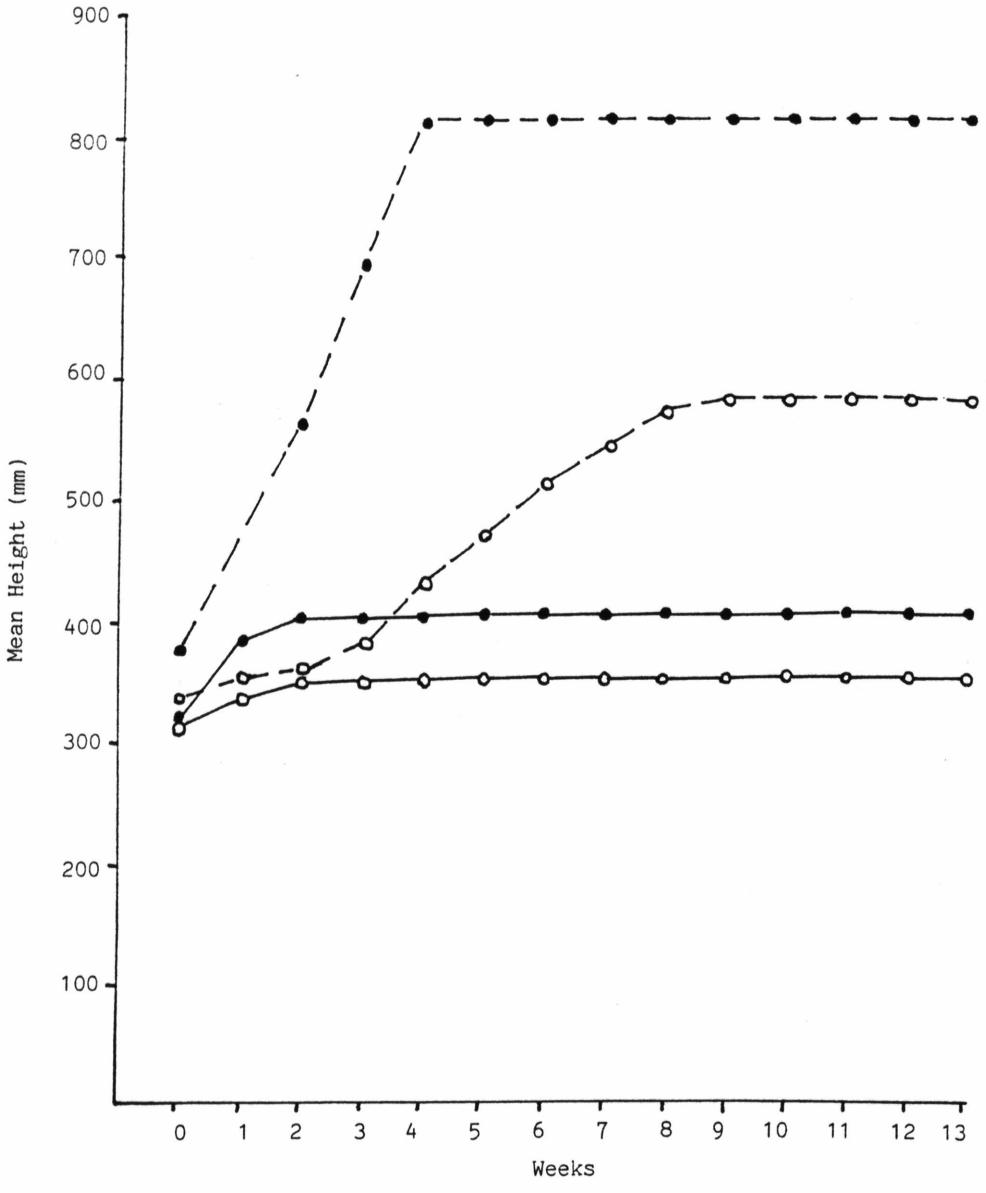


Figure 5A.1 Mean height (mm) of oak seedlings under two day/night temperature regimes: 20°C/12°C (O); 30°c/12°C (●) with (---) and without (——) gibberellic acid application.

further height growth with this treatment after the 5th week of the experiment.

During the experimental period only one flush of new growth or none at all was made regardless of treatment. The number of seedlings flushing in each treatment during the experimental period is shown in table 5A.2 together with the mean length of shoot produced during this 3rd flush. All seedlings had completed two growth flushes prior to treatment.

Table 5A.2

The effect of two day/night temperature regimes and gibberellic acid application on the mean number of growth flushes and the length of new shoot produced during 13 weeks of growth.

	Initial number flushes	Final number flushes	Number of seedlings undergoing 1 flush	Mean length (mm) of 3rd flush
20°C/12°C $-GA_3$	2	2.2	1	205
20°C/12°C $+GA_3$	2	2.6	3	395
30°C/12°C $-GA_3$	2	2.6	3	153
30°C/12°C $+GA_3$	2	2.8	4	545

The final total number of nodes and mean internode lengths for the whole seedling are given in table 5A.3, the means have been adjusted to take into account the number of nodes present and the mean internode lengths prior to treatment, which are also tabulated. Temperature and GA_3 treatment had no significant effect on the total number of nodes made, though there was some increase with gibberellic acid. Gibberellic acid however significantly increased the mean internode length particularly in the higher day/night temperature regime.

Table 5A.3

The effect of the main factors: day/night temperature and hormone on the mean total number of nodes and mean internode length. Final means adjusted taking the initial values as covariate.

	Initial number nodes	Final number nodes	Initial mean internode length (mm)	Final mean internode length (mm)
20°C/12°C	24.4	33.1	13.0	14.3
30°C/12°C	25.4	36.3	13.5	15.3
Significance	NS	NS	NS	NS
LSD (P0.05)	3.5	7.4	1.8	2.1
-Gibberellic acid	24.4	31.2	12.5	13.1
+Gibberellic acid	25.4	38.2	14.0	16.6
Significance	NS	NS	NS	**
LSD (P0.05)	3.5	7.4	1.8	2.2
Covariate		**		*
Coefficient of variation (%)	14.7	22.3	14.4	14.4

5A.4 Branching

The number of branches and their mean lengths were very variable and not significantly affected by treatments. The number of branches increased by 1-2 branches on five seedlings, on the remaining seedlings the number of branches remained the same but their mean length increased. Mean increase in branch length was 8.8±3.4mm.

5A.5 Stem Diameter

Stem diameter at the base and at 5cm were significantly increased by the 30°C/12°C day/night temperature regime, the diameter at 5cm was also increased by GA_3 treatment (table 5A.4). The interaction between temperature and hormone was not significant.

Table 5A.4

The effect of two day/night temperature regimes and gibberellic acid on the stem diameter (mm) in a controlled environment study.

	Initial base diameter	Final base diameter	Initial diameter at 5cm	Final diameter at 5cm
20°C/12°C	5.2	8.0	3.3	5.1
30°C/12°C	5.4	9.5	3.6	6.4
Significance	NS	*	NS	*
LSD (P0.05)	1.2	1.3	0.8	1.1
-Gibberellic acid	5.2	8.5	3.5	5.0
+Gibberellic acid	5.4	9.0	3.4	6.6
Significance	NS	NS	NS	**
LSD (P0.05)	1.2	1.3	0.8	1.1
Coefficient of variation (%)	24.1	16.0	25.5	20.4

5A.6 Leaf Area

There were no significant differences in number of leaves, total leaf area, mean leaf area per leaf or mean leaf dry weight per leaf between temperature and hormone treatments. The interaction between temperature and hormone was also not significant. There was a mean increase in number of leaves per seedling of 8.55 ± 2.6. The mean final total leaf area was $510.0 \pm 48.6 cm^2$, mean leaf area per leaf $17.4 \pm 1.7 cm^2$ and mean leaf dry weight per leaf $0.096 \pm 0.008 g$.

5A.7 Total Dry Weight

Mean total dry weight of seedlings under the two day/night temperature regimes, 20°C/12°C and 30°C/12°C, were $11.9 \pm 1.4 g$ and $13.8 \pm 1.4 g$ respectively. Gibberellic acid also had no significant effect, without GA_3 treatment the mean total dry weight was $12.5 \pm 1.4 g$, with GA_3 treatment $13.2 \pm 1.5 g$.

5A.8 Distribution of Dry Matter

Higher temperature and gibberellic acid significantly increased the proportion of dry matter as stem and decreased that of root, with no significant effect on the proportion of leaf material (table 5A.5). The distribution of dry matter as three fractions stem (S), leaf (L) and root (R) are shown in figure 5A.2 for the initial sample and for the four treatments after 13 weeks growth. The percentage of leaf matter decreased generally and the percentage of roots increased except in GA_3-treated trees under 30°C/12°C temperature regime. The percentage stem was also increased but not in GA_3-treated trees at 20°C/12°C.

Table 5A.5

The effect of main factors, day/night temperature and hormone on the distribution of dry matter, expressed as percentage total dry weight.

	% Stem	% Leaves	% Root
20°C/12°C	31.2	22.6	46.2
30°C/12°C	43.6	22.8	33.6
Significance	**	NS	*
LSD (P0.05)	8.8	5.0	10.9
-Gibberellic acid	24.9	24.5	50.7
+Gibberellic acid	49.9	21.0	29.1
Significance	***	NS	***
LSD (P0.05)	8.8	5.0	10.9
Coefficient of variation (%)	25.0	23.0	28.9

5A.9 Stem : Root Ratio

Stem:root ratio was significantly affected by the treatments imposed, with gibberellic acid increasing the ratio under both temperature regimes (table 5A.6). For temperature treatments without GA_3 the stem:root ratio had decreased compared with the initial mean stem:root ratio of 1.23 ± 0.57. The largest increase occurred in GA_3-treated trees in the 30°C/12°C day/night temperature regime.

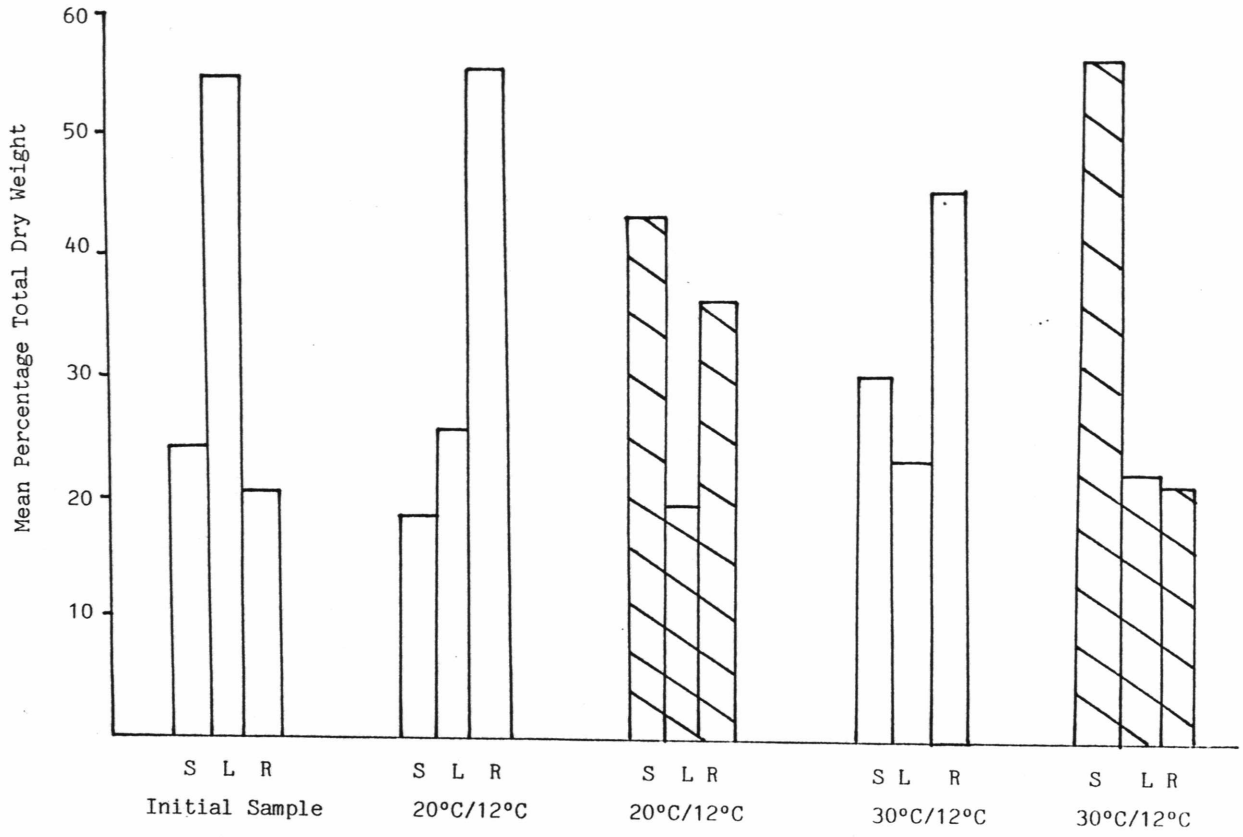


Figure 5A.2 The effect of two day/night temperature regimes and gibberellic acid (shaded columns) on the distribution of dry matter between stem (S), leaves (L) and roots (R).

Table 5A.6

The effect of two day/night temperature regimes and gibberellic acid, LSD (P0.05) 0.70, on mean stem:root ratio of dry weights. Interaction not significant.

	20°C/12°C	30°C/12°C	Mean	
- GA_3	0.39	0.79	0.59	***
+ GA_3	1.42	2.59	2.01	
Mean	0.91	1.69		
	*			

PART B - EXPERIMENT V

The Effect of Shading and Gibberellic Acid on the Growth of Oak Seedlings in the Glasshouse.

5B.1 Materials and Methods

The effect of different ranges of light intensity and gibberellic acid application (as described in materials and methods) on the growth of oak was studied in the glasshouse in a factorial experiment, May-August 1985. The three light regimes used were: a control treatment with no shading (1) and two degrees of shading achieved using $1m^3$ metal frames covered on all sides with one or two layers of a muslin-like cloth, treatments (2) and (3) respectively. The frames were placed on the glasshouse bench over the seedlings. One half of these had been treated with gibberellic acid. Five replicates of each of the $+GA_3$ and $-GA_3$ treatments were placed at random in the different light conditions, also during the experiment their positions were changed at intervals to minimise possible edge effects. Temperature, humidity and light levels were measured for each shade treatment on a number of days at approximately 2 hourly intervals between 0900-1900hrs.

5B.2 Environment

Table 5B.1 shows the mean light levels (PAR), temperature and relative humidity in the three light treatments. Mean light intensity was reduced by 58.9% by one layer of cloth compared with no shade and further reduced by 50.3% between the lighter and heavier shade treatments. Temperature was not significantly different however there was an increase in humidity in the heaviest shade treatment.

Table 5B.1

Mean (n=50) light (PAR 400-700nm), temperature and relative humidity in the three shade treatments.

	No Shade (1)	Shade (2)	Shade (3)		LSD(P0.05)
Light ($\mu molm^{-2}s^{-1}$)	353	145	72	***	91.5
Temperature (°C)	25.9	26.3	25.6	NS	1.7
Humidity (%RH)	53.1	54.7	63.6	***	5.5

5B.3 Height Growth

The effect of shade on height growth was not significant until the final measurement in August (table 5B.2), however gibberellic acid gave a significant increase more than doubling the height in all three treatments. Although the interaction between shade and hormone was not statistically significant the greatest increase in height was produced with gibberellic acid in the heaviest shade treatment (i.e. 185.5% over the unshaded controls) (fig. 5B.1).

Table 5B.2

The effect of shading treatments and gibberellic acid application on mean height (mm) of oak seedlings in the glasshouse.

Date	14.5.85	13.6.85	11.7.85	8.8.85
No Shade (1)	160.0	351.0	407.0	437.0
Shade (2)	147.0	372.0	434.0	454.0
Shade (3)	155.5	440.0	548.0	616.0
Significance	NS	NS	NS	*
LSD (P0.05)	34.9	99.9	154.4	148.4
-Gibberellic acid	147.3	242.0	309.0	323.0
+Gibberellic acid	161.0	533.0	616.0	683.0
Significance	NS	***	***	***
LSD (P0.05)	28.5	81.5	126.1	121.1
Coefficient of variation (%)	24.5	27.9	36.2	32.0

The final number of growth flushes made by the seedlings was not significantly affected by the shade and hormone treatments (LSD (P0.05) 1.0). The length of shoot produced by each flush was recorded and the mean value, together with the number of seedlings involved are tabulated in table 5B.3. If flushes are separated into pre- and post-treatment after the second flush GA_3 appears to increase the length of shoot produced during the 3rd flush in each level of shade. Fewer seedlings had 4th and 5th flushes but again there appeared to be an increase with GA_3 and with shading when compared with the control treatment.

The effect of shade and GA_3 on the total number of nodes present and the mean internode length at the end of the experimental period

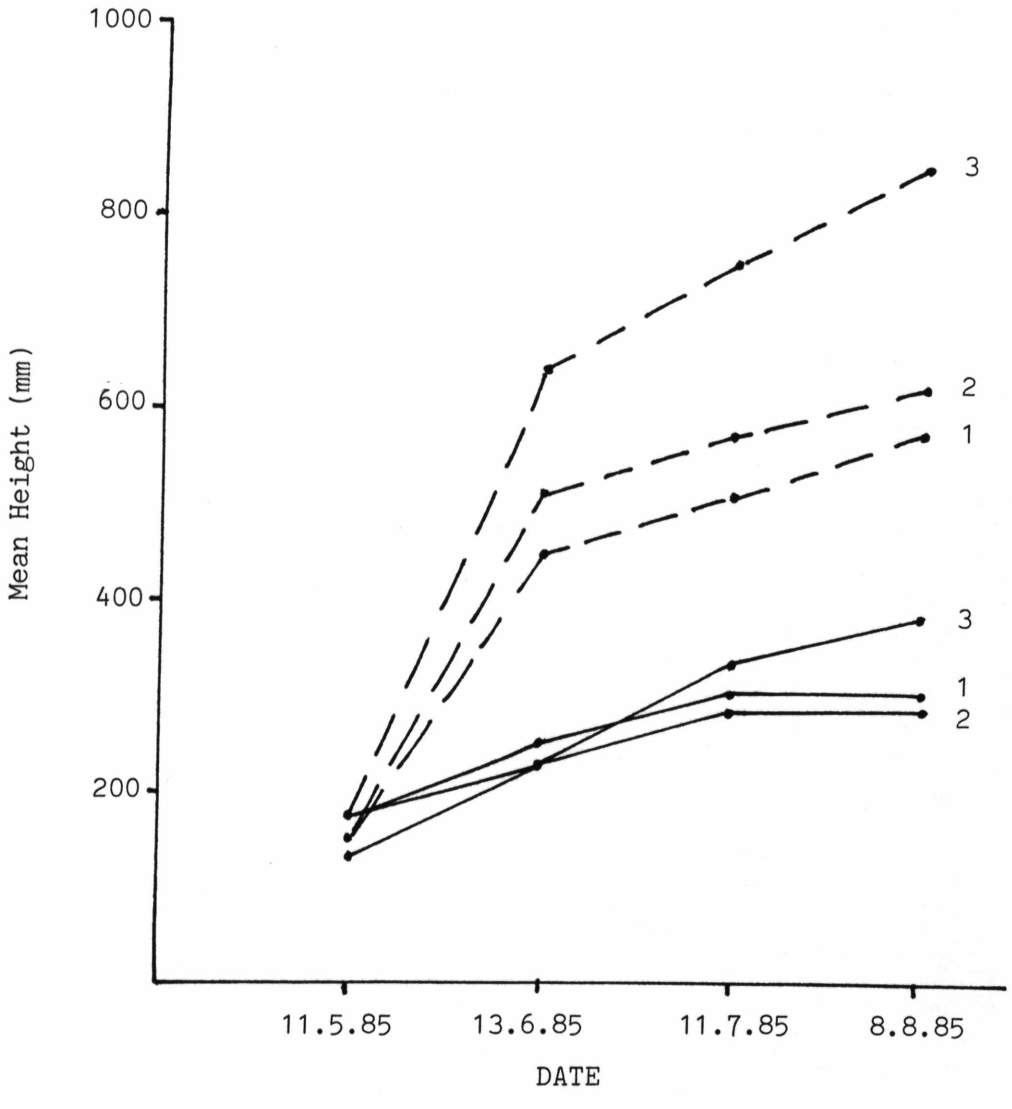


Figure 5B.1 The effect of three degrees of shading (1 no shade (100%), 2 one layer of cloth (41.1%), 3 two layers of cloth (20.4%)) and gibberellic acid (– – –) on the mean height (mm) of oak.

		Initial Number Flushes	Final Number Flushes	Mean Length (mm) 1st Flush	Mean length (mm) 2nd Flush	Mean Length (mm) 3rd Flush	Mean Length (mm) 4th Flush	Mean Length (mm) 5th Flush
No Shade (1)	$-GA_3$	2.2	3.6	105 (5)	44 (5)	91 (5)	57 (2)	175 (1)
No Shade (1)	$+GA_3$	2.0	3.8	88 (5)	55 (5)	304 (5)	162 (4)	
Shade (2)	$-GA_3$	1.8	3.4	103 (5)	52 (5)	79 (4)	118 (3)	
Shade (2)	$+GA_3$	2.2	3.5	101 (4)	47 (4)	397 (4)	145 (1)	150 (1)
Shade (3)	$-GA_3$	1.8	3.4	102 (5)	54 (5)	133 (5)	215 (1)	245 (1)
Shade (3)	$+GA_3$	2.2	4.0	118 (5)	44 (5)	306 (5)	383 (5)	

Table 5B.3 The effect of shade and gibberellic acid on the mean number of growth flushes of oak and the mean shoot length (mm) of each flush, number of seedlings given in brackets.
(Shade (2) - 1 layer of cloth, Shade (3) - 2 layers of cloth)

are given in table 5B.4. The results have been adjusted taking the initial measurements as covariate as it was thought that the number of nodes present and mean internode length prior to treatment may influence further node production. However covariate was only significant in considering the final mean length of all internodes. There was no significant interaction between shade and GA_3 treatments but the total number of nodes and mean internode length were increased by the heaviest shade treatment and by gibberellic acid (fig. 5B.2).

Table 5B.4

The effect of main factors, shade and hormone on the mean total number of nodes and mean internode length (covariate initial node number / length).

	Final Total Number Nodes	Mean Internode Length (mm)
No shade (1)	20.5	10.6
Shade (2)	22.8	12.3
Shade (3)	31.0	14.3
Significance	*	**
LSD (P0.05)	8.0	2.2
-Gibberellic acid	16.6	10.5
+Gibberellic acid	33.0	14.2
Significance	***	***
LSD (P0.05)	6.8	1.8
Covariate	NS	*
Coefficient of variation (%)	34.7	19.2

5B.4 Branching

There were no significant differences in number and length of branches. The largest number of branches were produced by trees in the "no shade" treatment without GA_3 (fig. 5B.3). For the other treatments a maximum of 2 out of the 5 replicates produced branches. The mean length was greatest in GA_3 treated trees in one of the shade treatments, however this was due to a single long branch (probably aberrant) in one of the seedlings.

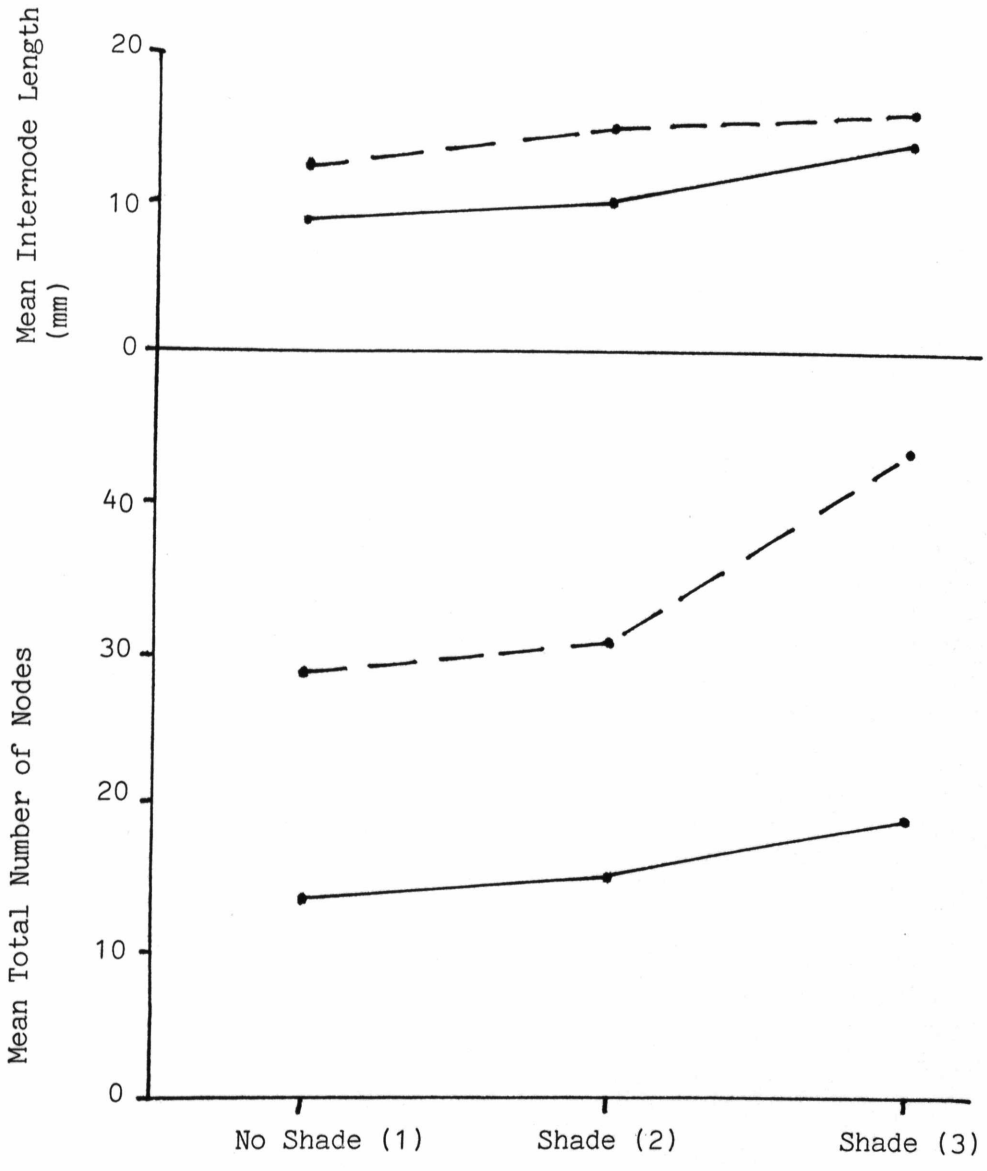


Figure 5B.2 The effect of shade and hormone (+GA_3 - - -) on the mean number of nodes, LSD(P0.05) 11.9, and mean internode length (mm), LSD(P0.05) 3.4, of oak in the glasshouse.

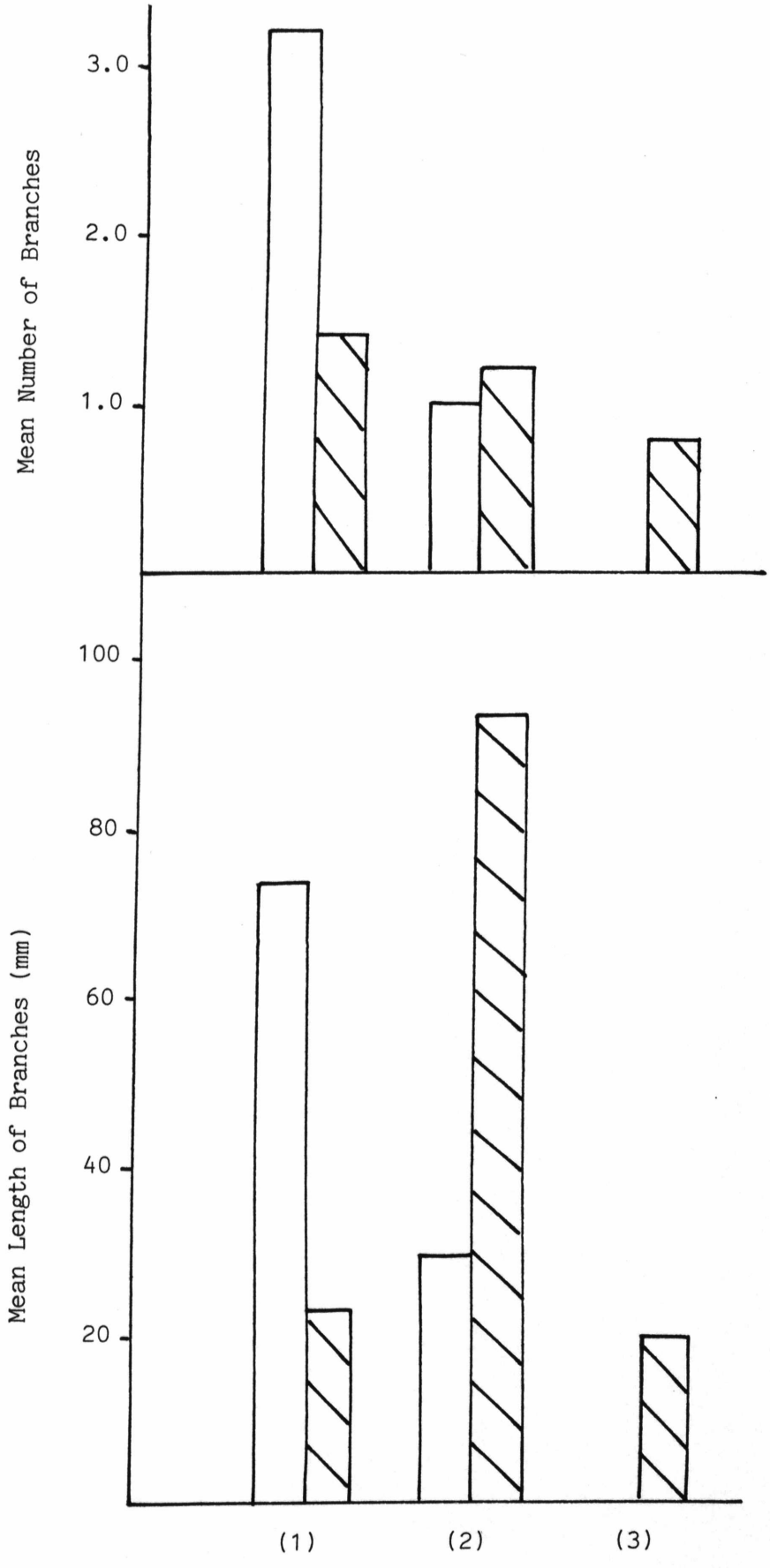


Figure 5B.3 The effect of shade, (1) no shade, (2) 1 layer of cloth, (3) 2 layers of cloth, and gibberellic acid (shaded columns) on the mean number of branches, LSD(P0.05) 2.8, and mean length (mm) of branches, LSD(P0.05) 92.3, of oak in the glasshouse.

5B.5 Stem Diameter

Shade and hormone treatments had no significant effect on stem diameter at the base (table 5B.5). However the diameter at 5cm was significantly increased by gibberellic acid in the three light treatmeants. The interaction between shade and hormone was not statistically significant, however there was some increase in base diameter with GA_3 under one layer of cloth.

Table 5B.5

The effect of shade and hormone on the mean stem diameter (mm) of oak seedlings in the glasshouse.

	Initial Base Diameter	Final Base Diameter	Initial Diameter at 5cm	Final Diameter at 5cm
No Shade (1)	4.3	7.2	2.9	5.2
Shade (2)	4.3	7.4	2.8	5.1
Shade (3)	4.5	7.2	2.9	4.9
Significance	NS	NS	NS	NS
LSD (P0.05)	0.5	1.3	0.4	0.8
-Gibberellic acid	4.3	6.8	2.9	4.4
+Gibberellic acid	4.3	7.8	2.8	5.7
Significance	NS	NS	NS	***
LSD (P0.05)	0.4	1.1	0.3	0.6
Coefficient of variation (%)	13.8	19.5	16.6	17.1

5B.6 Leaf Area

The effect of shade and gibberellic acid application on the mean leaf number, leaf area and weight are given in table 5B.6. Initial leaf area was determined using the exponential relationship between leaf length (mm) and leaf area (mm^2): Area = 0.3848 Length $^{1.9750}$ (r=0.963). This relationship was derived using an initial sample of 15 seedlings (178 leaves) taken from seedlings raised in the glasshouse for 1985 experiments. Final area measurements were made using the automatic area measurement system.

The final total number of leaves and the increase in leaf number

	No Shade	Shade (2)	Shade (3)	Sig.	$LSD_{(P0.05)}$	- GA_3	+ GA_3	Sig.	$LSD_{(P0.05)}$	Coeff. of Var.
Initial number of leaves	13.1	11.2	9.8	NS	3.5	11.0	11.7	NS	2.8	33.8
Final number of leaves	52.0	41.0	40.8	NS	22.1	33.7	55.5	*	18.0	53.6
Increase in leaf number	38.9	29.4	31.0	NS	20.2	22.7	43.5	*	16.5	65.8
Initial total leaf area (cm^2)	203	141	163	NS	53.7	162	175	NS	43.9	34.5
Final total leaf area (cm^2)	541	470	602	NS	226	435	640	NS	185	45.5
Increase in total leaf area (cm^2)	339	322	439	NS	199	273	460	*	163	58.9
Initial mean leaf area (cm^2)	16.0	12.3	16.8	*	3.8	14.7	15.4	NS	3.1	27.5
Final mean leaf area (cm^2)	10.9	11.6	15.8	NS	4.4	13.3	12.3	NS	3.6	37.3
Mean leaf weight (g)	0.077	0.067	0.076	NS	0.021	0.079	0.068	NS	0.017	31.0
Specific leaf area (cm^2/g lf dry wt)	138.3	172.8	213.1	***	32.2	161.7	187.8	NS	26.3	19.9

Table 5B.6 The effect of shade and GA_3 on the mean leaf number, area (cm^2) and leaf weight (g) of oak seedlings in the glasshouse.

over the 3month experimental period were significantly greater in GA_3 treated trees in all treatments. The interaction was not significant, but for non-GA_3 treated trees the increase in number of leaves was greatest in the no-shade treatment and least in the heaviest shade treatment, but this pattern was altered in GA_3-treated trees (fig.5B.4).

The final total leaf area was also analysed taking the initial leaf area as covariate. Due to a significant interaction (P0.05) between treatments at the start of the experiment. This analysis showed a significant increase in total leaf area with gibberellic acid (fig. 5B.5).

There was no significant effect of shade and GA_3 treatments on mean leaf area per leaf or mean leaf weight per leaf. Analysis of final mean leaf area taking initial mean leaf area as covariate also showed no significant differences between treatments. Specific leaf area showed a significant increase from no shade to the heaviest shade treatment. The interaction between shade and GA_3 was not significant, the increase in specific leaf area with increasing shade occurred both in non-GA_3 and GA_3 treated trees.

5B.7 Total Dry Weight

Total dry weight was not significantly affected by the shade treatments however there was an increase in dry weight with gibberellic acid (table 5B.7). The interaction between shade and GA_3 was not significant (LSD (P0.05) 6.87). There was a decrease in dry weight in the shaded treatments compared with the no-shade treatment, gibberellic acid increased the total dry weight of seedlings under these shade treatments so their dry weight was similar to the no-shade trees (fig. 5B.6).

Table 5B.7

The effect of shade, LSD (P0.05) 4.86, and gibberellic acid LSD (P0.05) 3.97, on the mean total dry weight (g) of oak seedlings in the glasshouse.

	No Shade (1)	Shade (2)	Shade (3)	Mean	
- GA_3	11.19	5.59	6.38	7.72	
+ GA_3	11.61	12.67	11.61	11.96	*
Mean	11.40	9.13	8.99		
		NS			

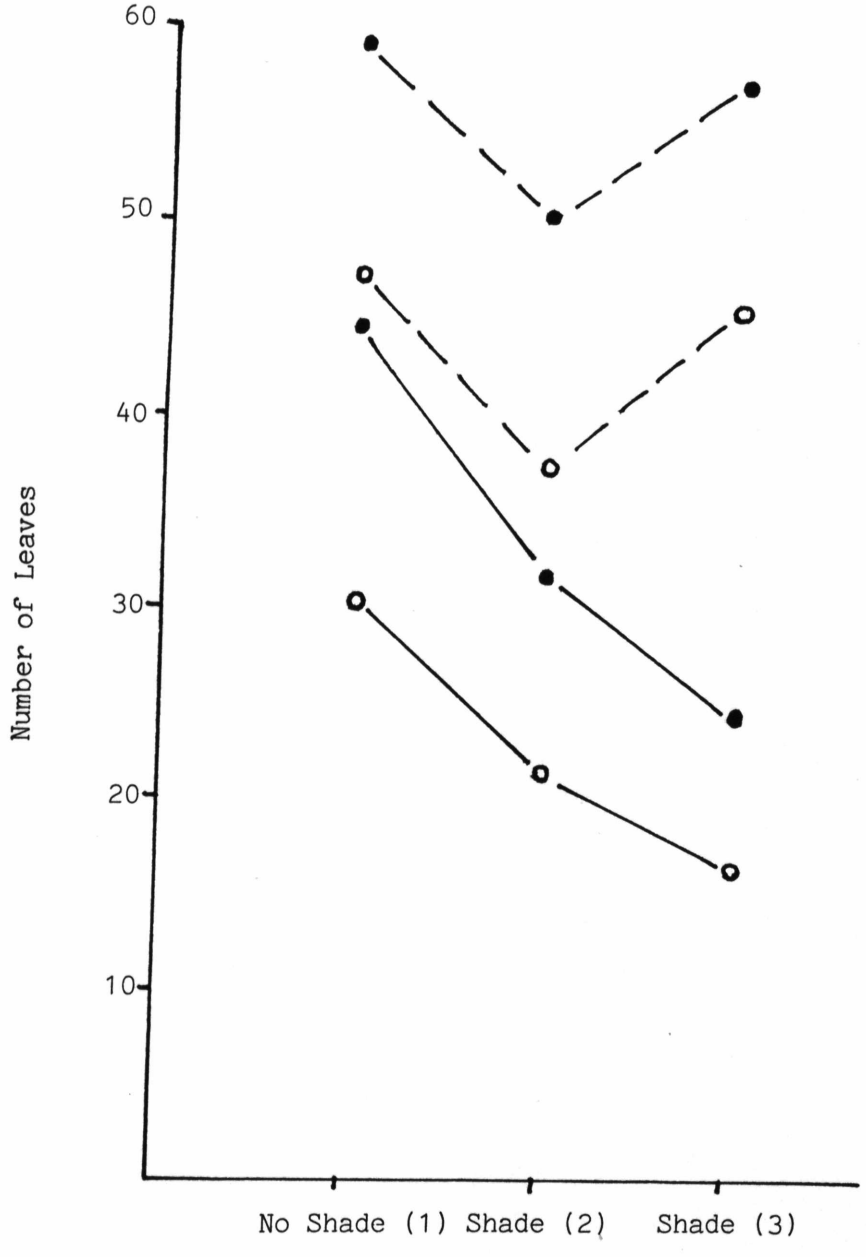


Figure 5B.4 The effect of shade and GA_3 (– – –) on the mean number (●) LSD(P0.05) 31.3 and mean increase in leaf number (o) LSD(P0.05) 28.5 of oak in the glasshouse.

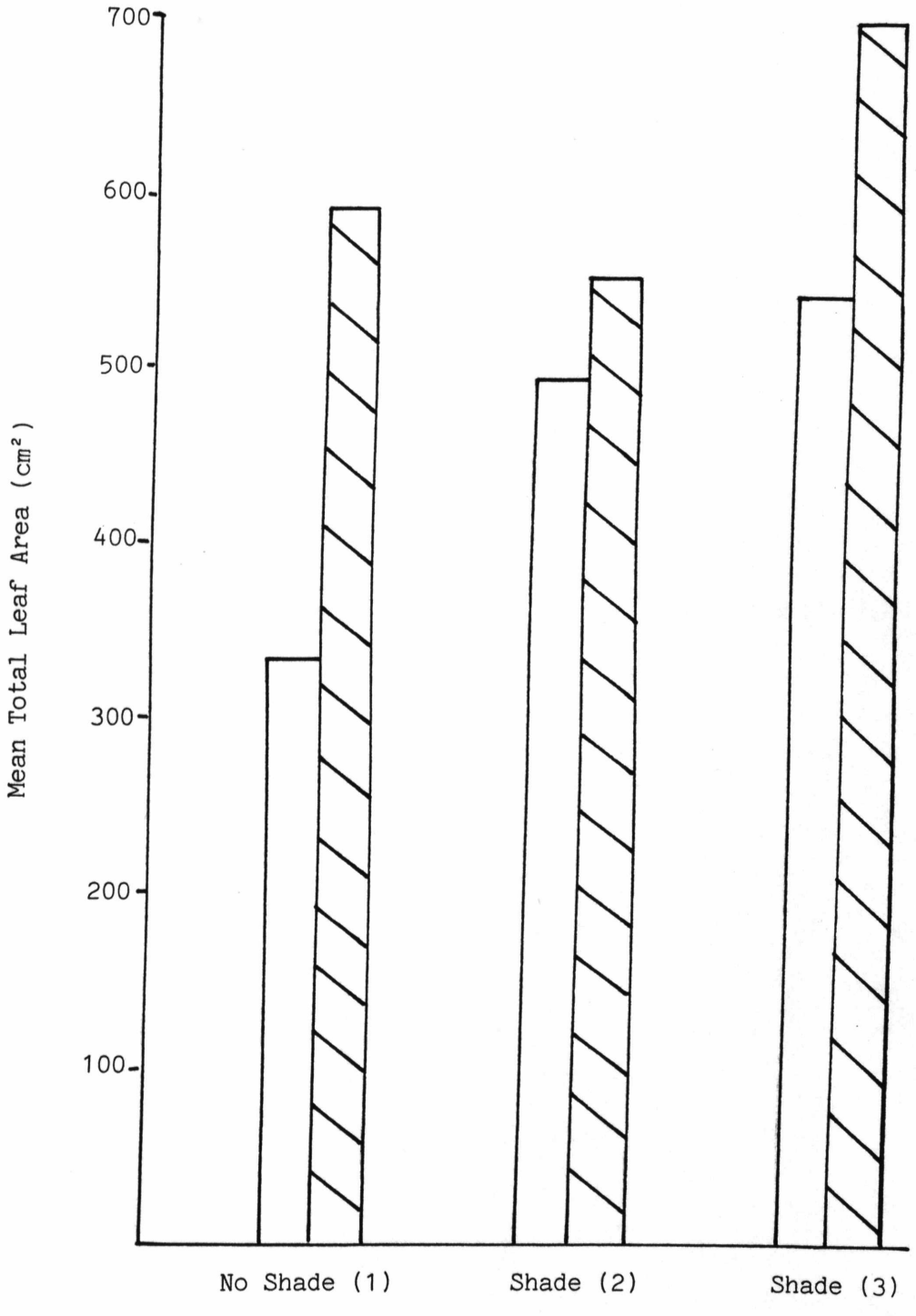


Figure 5B.5 The effect of shade and gibberellic acid (shaded columns) on the mean total leaf area (cm²), LSD(P0.05) 283.9, of oak in the glasshouse. Means adjusted taking initial total leaf area as covariate.

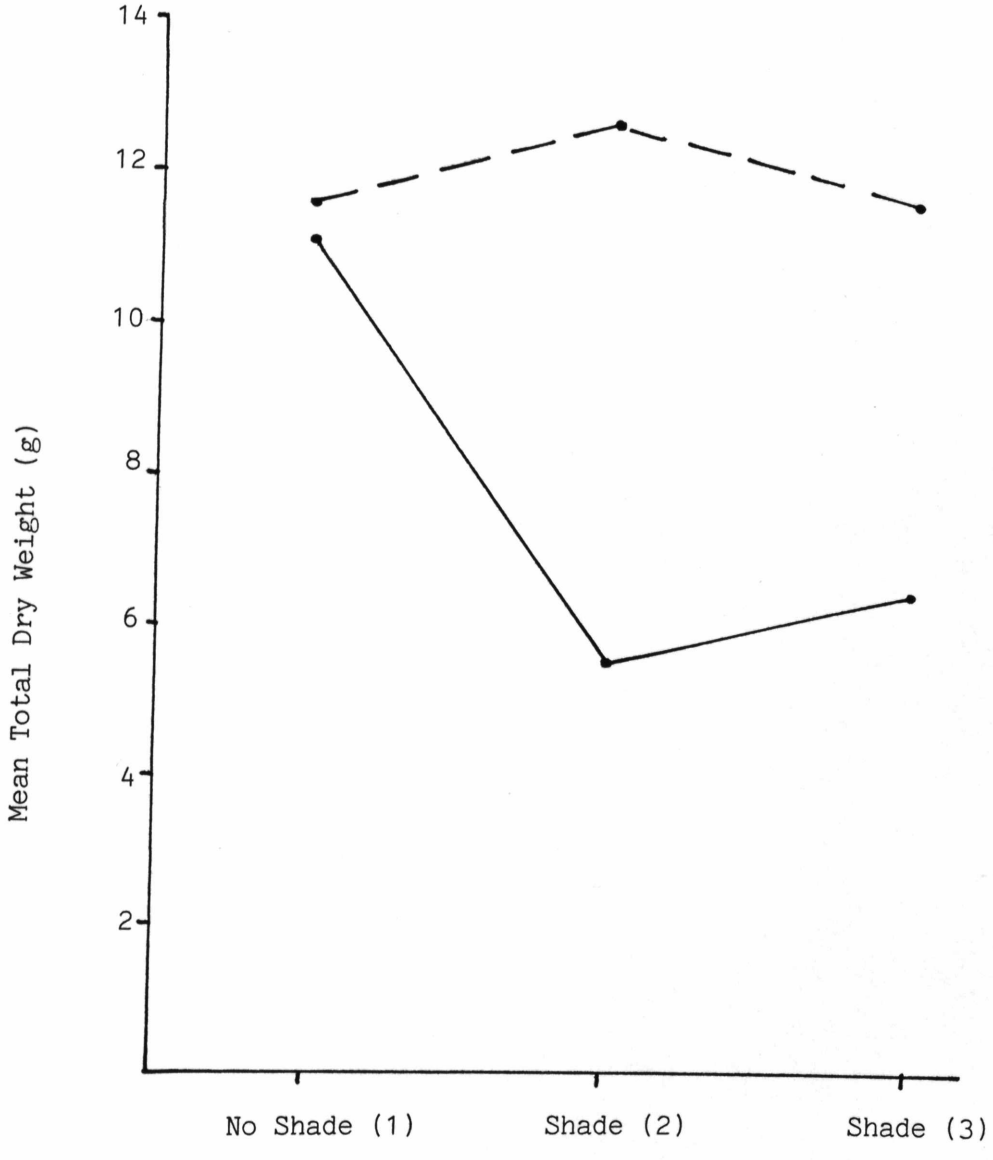


Figure 5B.6 The effect of shade and gibberellic acid application ($+GA_3$ – – –) on the mean total dry weight (g) of oak in the glasshouse.

5B.8 Distribution of Dry Matter

Shade had no significant effect on the distribution of dry matter however gibberellic acid significantly increased percentage stem and decrease percentage leaves with no effect on percentage roots (table 5B.8). The interaction between shade and GA_3 was not significant, the increase in percentage stem and leaves with gibberellic acid occurred in each of the three light treatments. The proportion of roots decreased in no-shade and heaviest shade treatment but not in the middle level of shade, though these differences were not significant (fig. 5B.7).

Table 5B.8

The effect of shade and GA_3 on the distribution of dry matter, expressed as percentage total dry weight, of oak in the glasshouse.

	% Stem	% Leaves	% Root
No Shade (1)	30.6	37.0	32.4
Shade (2)	29.6	32.7	37.8
Shade (3)	33.9	32.5	33.5
Significance	NS	NS	NS
LSD (P0.05)	5.0	8.7	11.2
-Gibberellic Acid	26.5	38.2	35.3
+Gibberellic Acid	36.2	30.0	33.9
Significance	***	*	NS
LSD (P0.05)	4.1	7.1	9.1
Coefficient of Variation (%)	17.2	27.7	34.9

5B.9 Stem : Root Ratio

Stem:root ratio was not significantly affected by shade or GA_3 treatments (table 5B.9). The interaction was also not significnat (LSD (P0.05) 0.74), though there was some increase in stem:root ratio with gibberellic acid in no-shade and the heaviest shade treatments with no effect in the middle level of shade (fig. 5B.8). All treatments showed an increase in stem:root ratio compared with the initial mean stem:root ratio prior to treatment (0.57 ± 0.15).

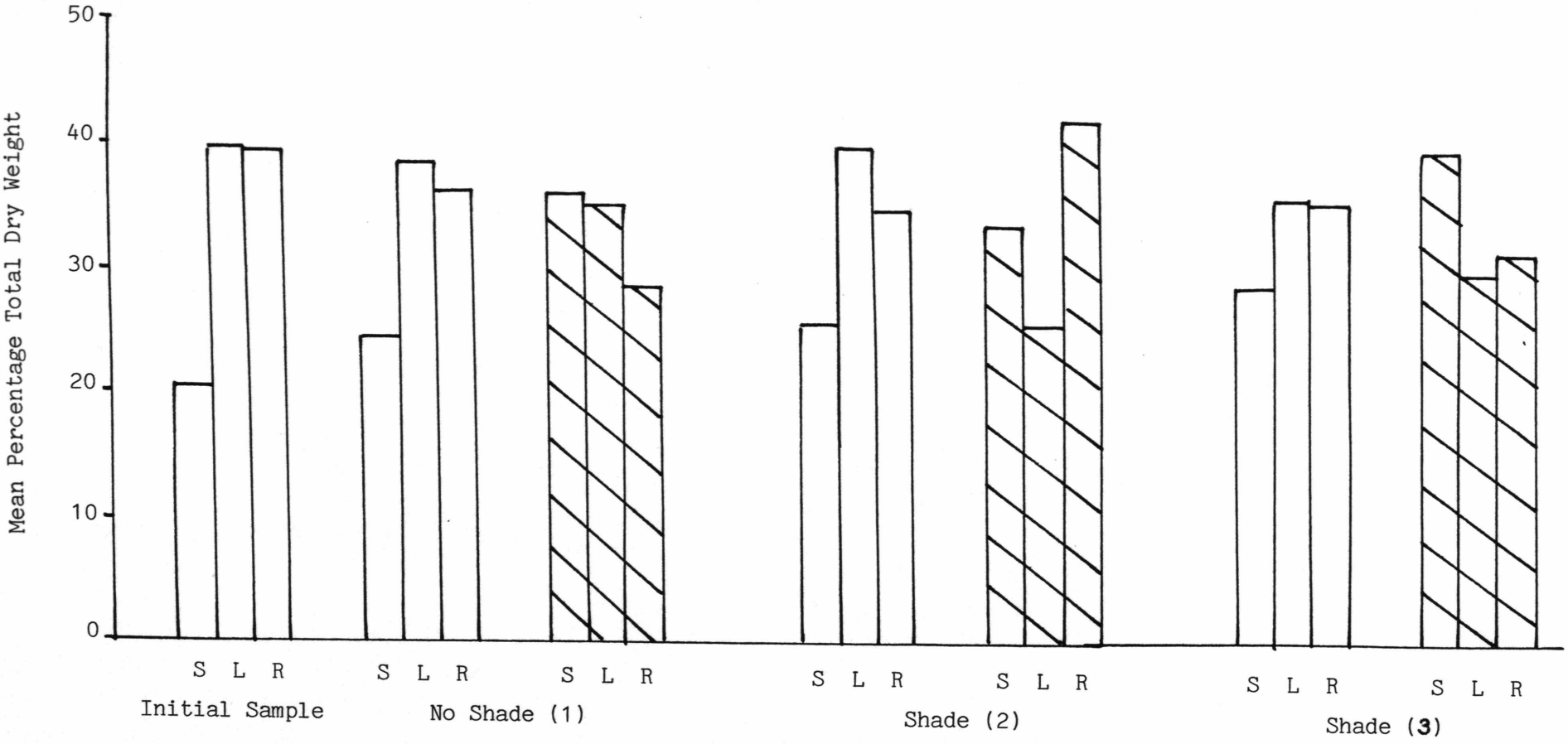


Figure 5B.7 The effect of shade and gibberellic acid (shaded columns) on the distribution of dry matter between stem (S), LSD(P0.05) 7.0, leaves (L), LSD(P0.05) 12.3 and root (R), LSD(P0.05) 15.8, of oak in the glasshouse. (Shade (2) = 1 layer of cloth, Shade (3) = 2 layers of cloth).

Table 5B.9

The effect of shade, LSD (P0.05) 0.52, and gibberellic acid, LSD (P0.05) 0.43, on the mean stem:root ratio of oak in the glasshouse.

	No Shade (1)	Shade (2)	Shade (3)	Mean	
- GA_3	0.81	0.87	0.92	0.87	NS
+ GA_3	1.55	0.83	1.38	1.25	
Mean	1.18	0.85	1.15		
		NS			

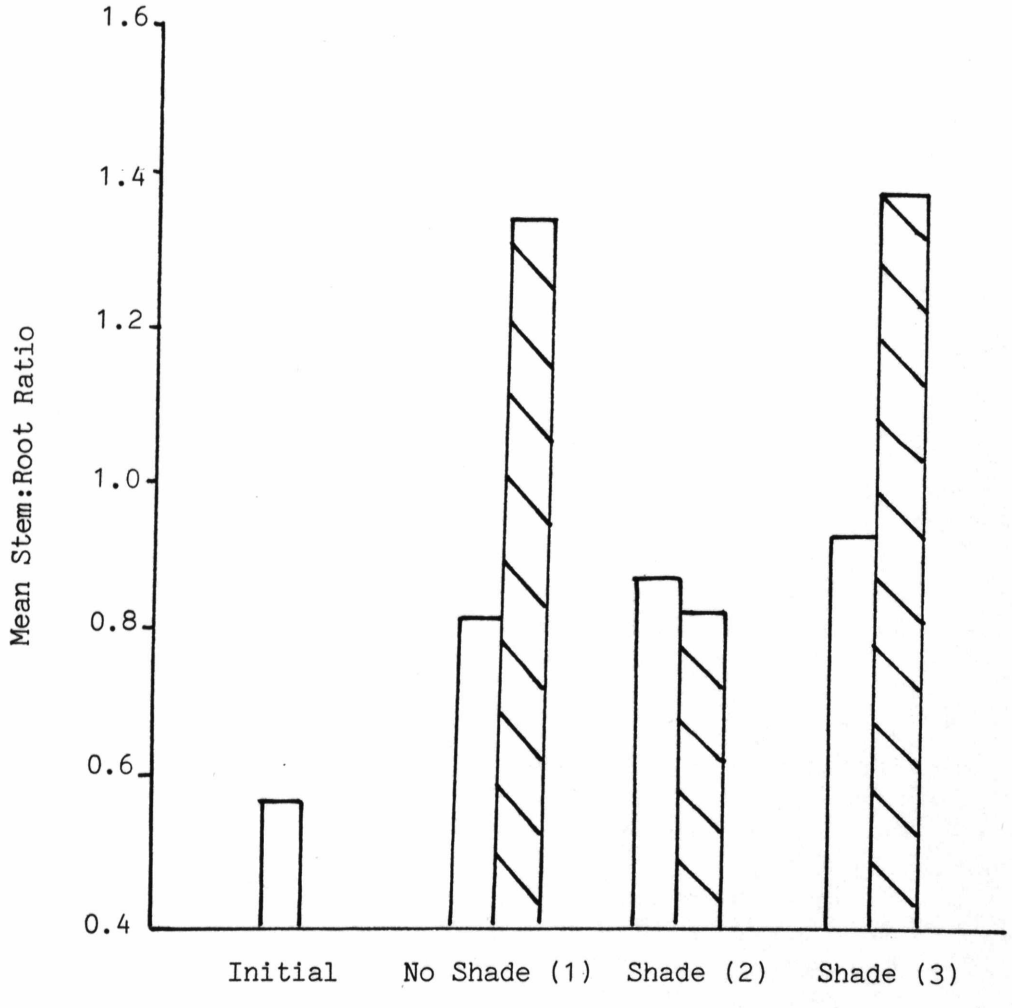


Figure 5B.8 The effect of shade and gibberellic acid (shaded columns) on the mean stem:root ratio of oak in the glasshouse.

PART C - EXPERIMENT VI

The Effect of Different Concentrations and Repeated Applications to Oak Seedlings of Gibberellic Acid in the Field.

5C.1 Materials and Methods

Two experiments were carried out to examine the effects of different concentrations of gibberellic acid on the growth of young oak. The concentrations of GA_3 used increased in steps by a factor of 3 (50ppm, 150ppm, 450ppm and 1350ppm) applied once as a foliar spray to run-off at the beginning of each experiment. Control trees were sprayed with a solution containing 10% ethanol and 0.05% Tween 20 only but no hormone. The first experiment was carried out from May-November 1984, the second from May-August 1985.

A second experiment, to examine the effects of repeated applications of GA_3, was also carried out between May-August 1985. For this experiment trees were either sprayed to run-off once, twice or three times with a solution containing 50ppm GA_3, control trees were given no hormone treatment. Each consecutive spraying was carried out at approximately monthly intervals when height measurements were also taken.

Five replicates of each treatment were used in all experiments, trees being assigned to the treatments using random numbers after ordering the trees according to initial height. This allowed a randomised block design to be used for these experiments; the blocks, each containing 1 replicate of each treatment, were planted at right angles to a coniferous hedge at the end of the plot.

5C.2 Height Growth - Experiments with Single Application

Height growth during the first of the experiments to examine the effect of different concentrations of gibberellic acid was relatively poor compared with earlier experiments (table 5C.1). A significant increase in height was caused by the highest concentration of GA_3 by June, other treatments i.e. 150ppm and 450ppm, also gave a slight, though statistically non-significant, increase in growth early in the growing season. Control trees however did not increase in height until later in the year (fig. 5C.1).

Better overall growth was obtained during the second, though shorter experiment, but again the results did not reach significance (table 5C.2). There was an immediate effect on height growth of

Date of Measurement	Control	50ppm	150ppm	450ppm	1350ppm	Sig.	LSD(P0.05)	Coefficient of variation (%)
3.5.84	292	350	335	364	345	NS	52.9	11.7
30.5.84	294	352	335	364	351	NS	51.8	11.4
15.6.84	294	352	335	364	405	*	67.2	14.4
27.6.84	294	355	354	378	429	*	82.3	17.0
16.7.84	298	357	355	378	429	NS	85.2	17.5
30.7.84	305	357	357	378	429	NS	84.4	17.3
14.8.84	317	359	357	378	429	NS	85.6	17.4
5.9.84	317	359	357	379	429	NS	87.1	17.7
6.11.84	322	362	357	379	434	NS	82.5	16.6

Table 5C.1 The effect of different concentrations of gibberellic acid on mean height (mm) of oak, 1984.

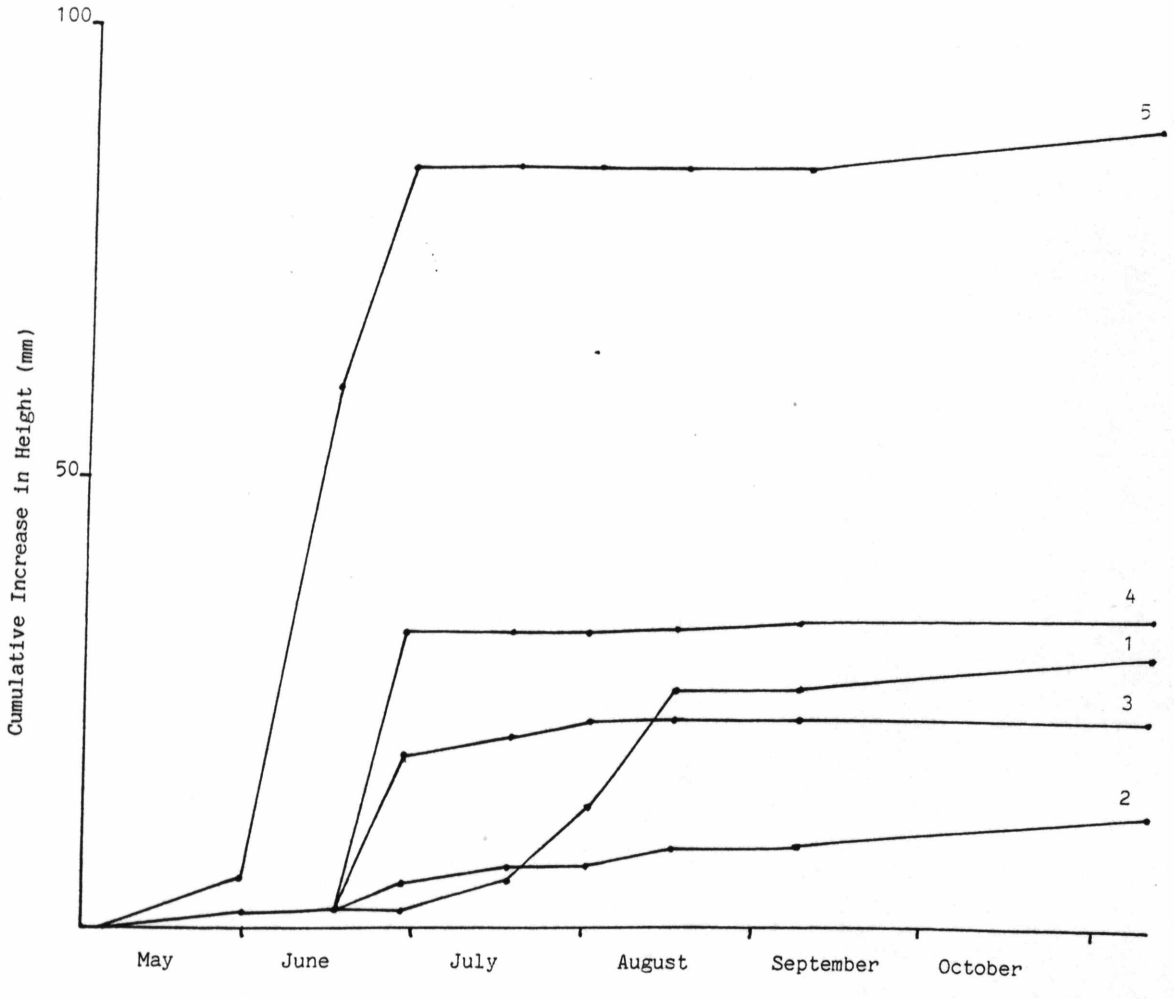


Figure 5C.1 1984 experiment, cumulative increase in mean height of young oak trees treated with different concentrations of gibberellic acid.

(1) No GA_3 (2) 50ppm (3) 150ppm (4) 450ppm (5) 1350ppm

1350ppm GA_3 and some increase with 150ppm and 450ppm GA_3. The final heights show an increase with increasing concentration of gibberellic acid (fig. 5C.2). Block effects were not significant in either of the experiments.

Table 5C.2

Mean height (mm) of oak treated with different concentrations of the hormone, gibberellic acid, 1985.

Date	Control	50ppm	150ppm	450ppm	1350ppm		LSD(P0.05)
13/5/85	166	202	153	162	169	NS	62
13/6/85	175	215	167	177	212	NS	70
11/7/85	175	221	208	197	244	NS	90
8/8/85	177	227	213	256	307	NS	113

The poor growth achieved by seedlings in the first of the experiments examining the effect of different concentrations of gibberellic acid was reflected in the number of seedlings which had produced at least one growth flush during the experimental period (table 5C.3). When considering the growth of branches as well as flushes of the main stem more seedlings were involved. There appeared to be an incease in length of shoot made during the flush and mean internode length with increasing gibberellic acid concentration, though, in view of the lack of statistical confirmation, any inferences drawn from such data must be treated with caution.

Results for the second experiment, in 1985, showed the number of seedlings making at least one growth flush during the experimental period to increase with increasing concentration of hormone (table 5C.4). There also appeared to be some increase in the length of the shoot produced during the flush with the higher concentrations of gibberellic acid, though again the results must be treated with caution.

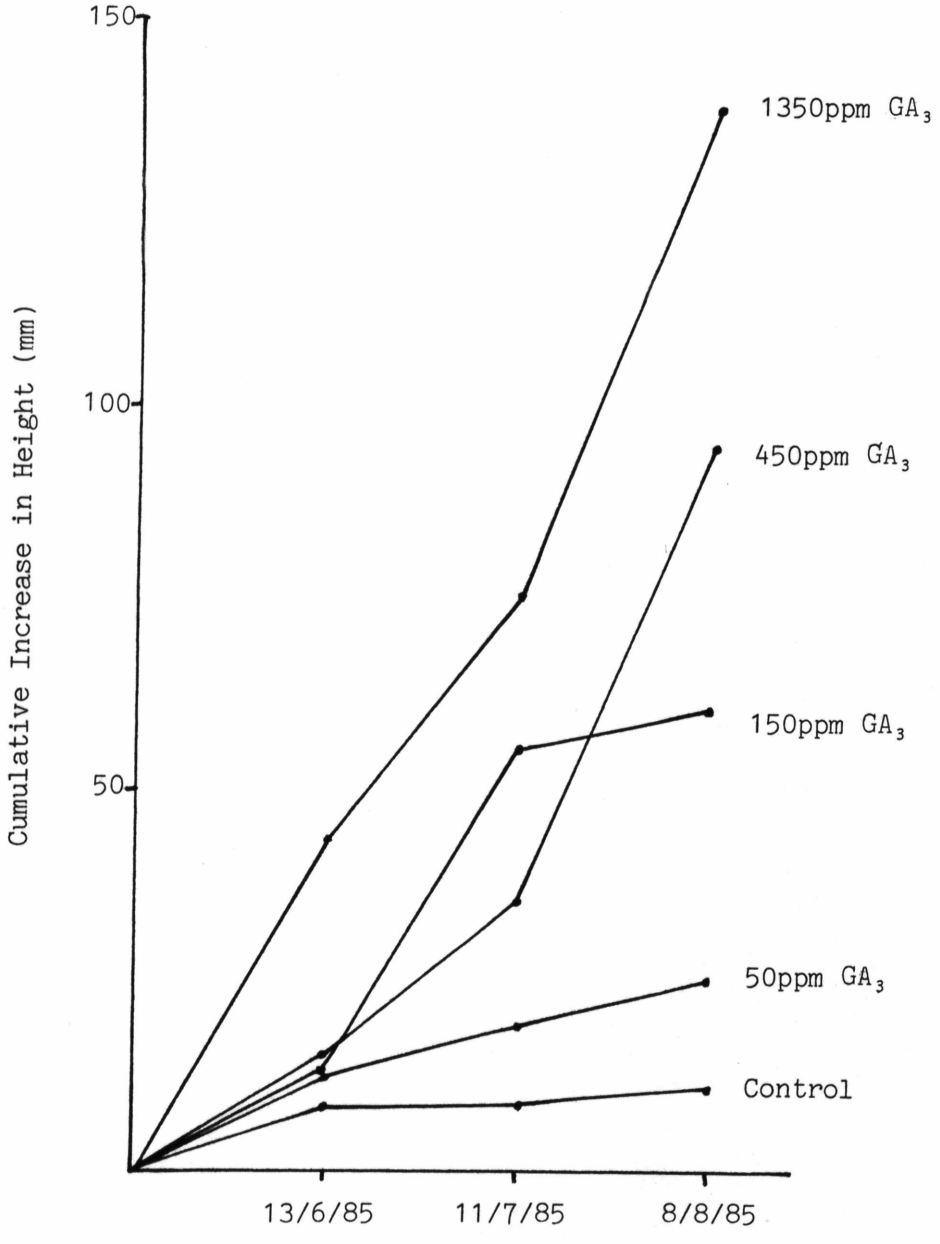


Figure 5C.2 1985 experiment, cumulative increase in mean height of young oak trees treated with different concentrations of gibberellic acid.

ppm GA_3	Initial Mean Number Flushes	Final Mean Number Flushes	Number Seedlings Gaining 1 Flush	Mean Number Flushes Stem + Branches	Number Seedlings Flushing Stem + Branches	Mean Length (mm) Shoot Produced 3rd Flush	Mean Number of Nodes Produced in 3rd Flush	Mean Internode Length (mm)
0	2.0	2.4	2	2.6	3	60.0	8.5	7.2
50	2.0	2.2	1	3.0	5	20.0	5.0	4.0
150	2.0	2.4	2	3.0	5	40.0	9.0	4.4
450	2.0	2.2	1	2.6	3	50.0	9.0	5.5
1350	2.0	2.8	4	2.8	4	107.5	10.7	7.3

Table 5C.3 The effect of different concentrations of gibberellic acid on the number of flushes, number of seedlings making an additional growth flush during the experimental period, 1984, and shoot growth details.

Table 5C.4

The effect of different concentrations of gibberellic acid on the mean number of flushes, number of seedlings producing an additional growth flush during the experimental period, 1985, and the mean length of the growth flush.

ppm GA_3	Initial mean number flushes	Final mean number flushes	Number of seedlings gaining 1 flush	Mean length (mm) shoot produced during additional flush
0	1.8	1.8	0	
50	2.4	2.8	2	37.5
150	2.0	2.4	2	130.0
450	2.0	2.8	4	180.7
1350	1.6	2.6	5	129.0

5C.3 Height Growth - Experiment on Repeated GA_3 Application

The effect of repeated applications of gibberellic acid on height growth is given in table 5C.5. Only one group of trees showed an increase in height after each had been given one application of gibberellic acid, though the actual difference in height was not significant. At the end of the second month trees which had had only one application of GA_3 showed no further increase in growth, whereas those given a second application had increased in height, though again this was not statistically significant (fig. 5C.3). After another month there was a significant increase in height growth of trees which had been given a third application of gibberellin. Block effects were not significant.

Table 5C.5

The effect of repeated applications of gibberellic acid (50ppm) on cumulative increase in mean height (mm) of oak seedlings in the field. (x1 = one application, x2 = two applications, x3 = three applications).

Date	Control	x 1	x 2	x 3		LSD(P0.05)	CV
13/5/85	168	142	166	153	NS	76	35
13/6/85	175	200	172	160	NS	79	33
11/7/85	175	203	201	200	NS	80	30
8/8/85	184	205	231	401	*	130	37

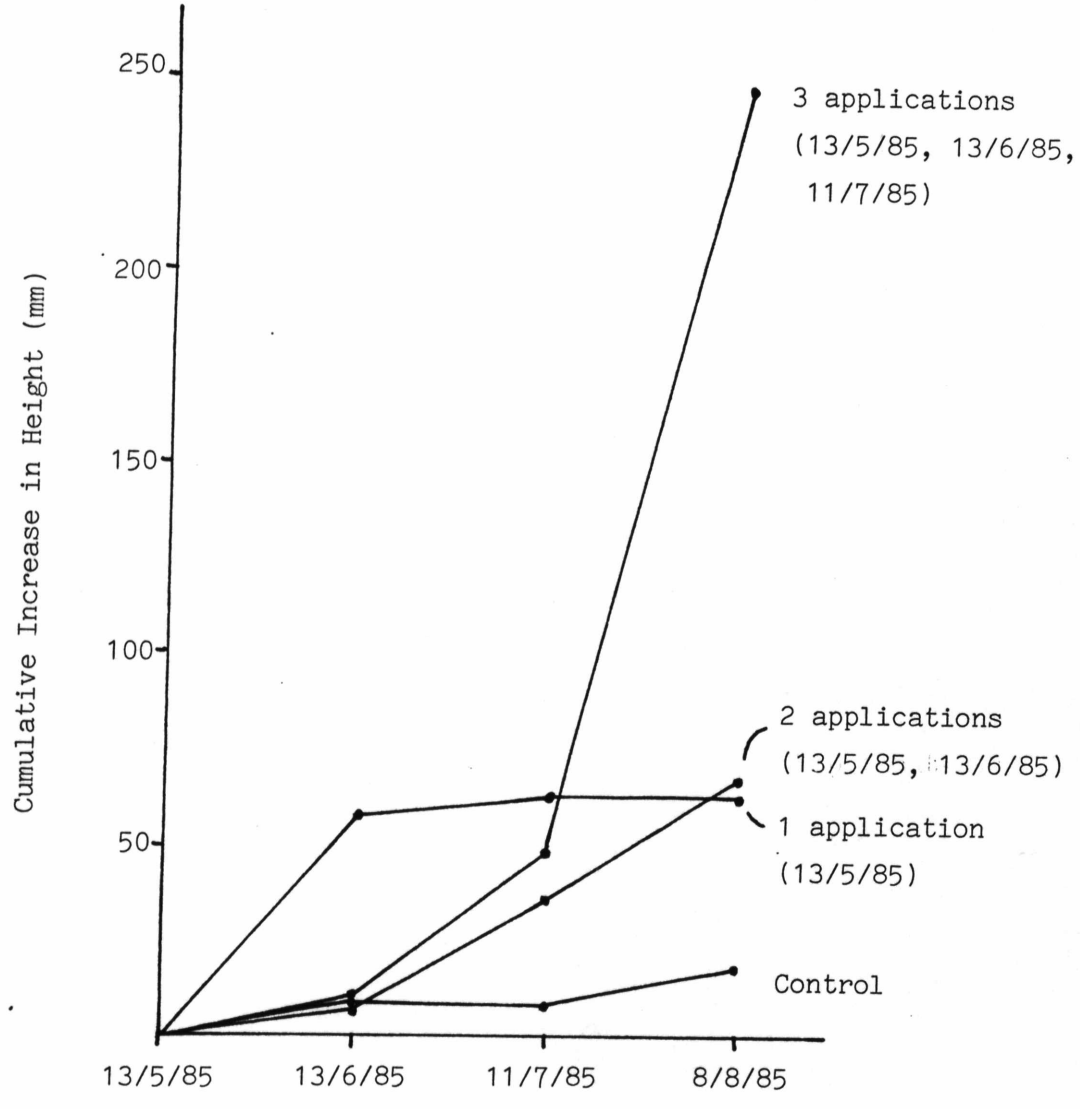


Figure 5C.3 The effect of repeated applications of gibberellic acid (50ppm GA_3) on cumulative increase in mean height (mm) of oak seedlings in the field.

The number of seedlings making one growth flush during the experimental period and the mean length of the shoot produced by the flush appeared to increase with the number of applications of gibberellic acid (table 5C.6), though again the results must be treated with caution.

Table 5C.6

The effect of repeated applications of gibberellic acid on the mean number of flushes, number of seedlings producing an additional growth flush and the mean length of the flush.

Number of applications of GA_3	Initial mean number flushes	Final mean number flushes	Number seedlings gaining 1 flush	Mean length (mm) of shoot for the flush
0	2.0	2.2	1	20.0
x 1	2.0	2.6	3	78.3
x 2	2.0	2.8	4	76.2
x 3	2.0	2.8	4	278.7

5C.4 Branching

The effect of different concentrations of gibberellic acid on the number of branches formed was masked by the high coefficient of variation, however there was a significant decrease in total number of branches and the number per 10cm stem between the control and hormone treated trees in the second experiment (table 5C.7). The general trend was for branching to decrease with increasing concentration of gibberellic acid.

There were no significant differences in branching between treatments involving different numbers of applications of gibberellic acid. Mean length was greatest in those trees which had been given three applications of gibberellic acid, the total number and number of branches per 10cm stem was greater in the control trees (fig. 5C.4).

5C.5 Stem Diameter

Basal diameter was not significantly affected by different concentrations of gibberellic acid (table 5C.8), however in the 1985 experiment all GA_3 treatments showed an increase in base diameter compared with the control trees. The diameter at 5cm did show a significant increase with gibberellic acid in 1984, though there was no

	Control	50ppm	150ppm	450ppm	1350ppm	Sig.	LSD(P0.05)	CV
1984 Experiment								
Number of Primary Branches	3.6	3.4	2.8	1.2	2.2	NS	3.1	88.8
Number Branches per 10cm Stem Length	1.1	0.9	0.8	0.3	0.5	NS	0.9	87.5
Mean Length Branches (mm)	94.0	73.0	42.0	59.0	11.0	NS	84.2	112.5
1985 Experiment								
Number of Primary Branches	6.6	1.4	0.8	0.8	1.0	***	2.5	88.1
Number Branches per 10cm Stem Length	3.8	0.7	0.5	0.3	0.3	***	1.2	78.3
Mean Length Branches (mm)	46.8	17.8	11.7	29.3	30.5	NS	41.6	114.1

Table 5C.7 The effect of different concentrations of gibberellic acid on the mean number and length (mm) of branches of young oak trees grown in the field, results from two experiments 1984 and 1985.

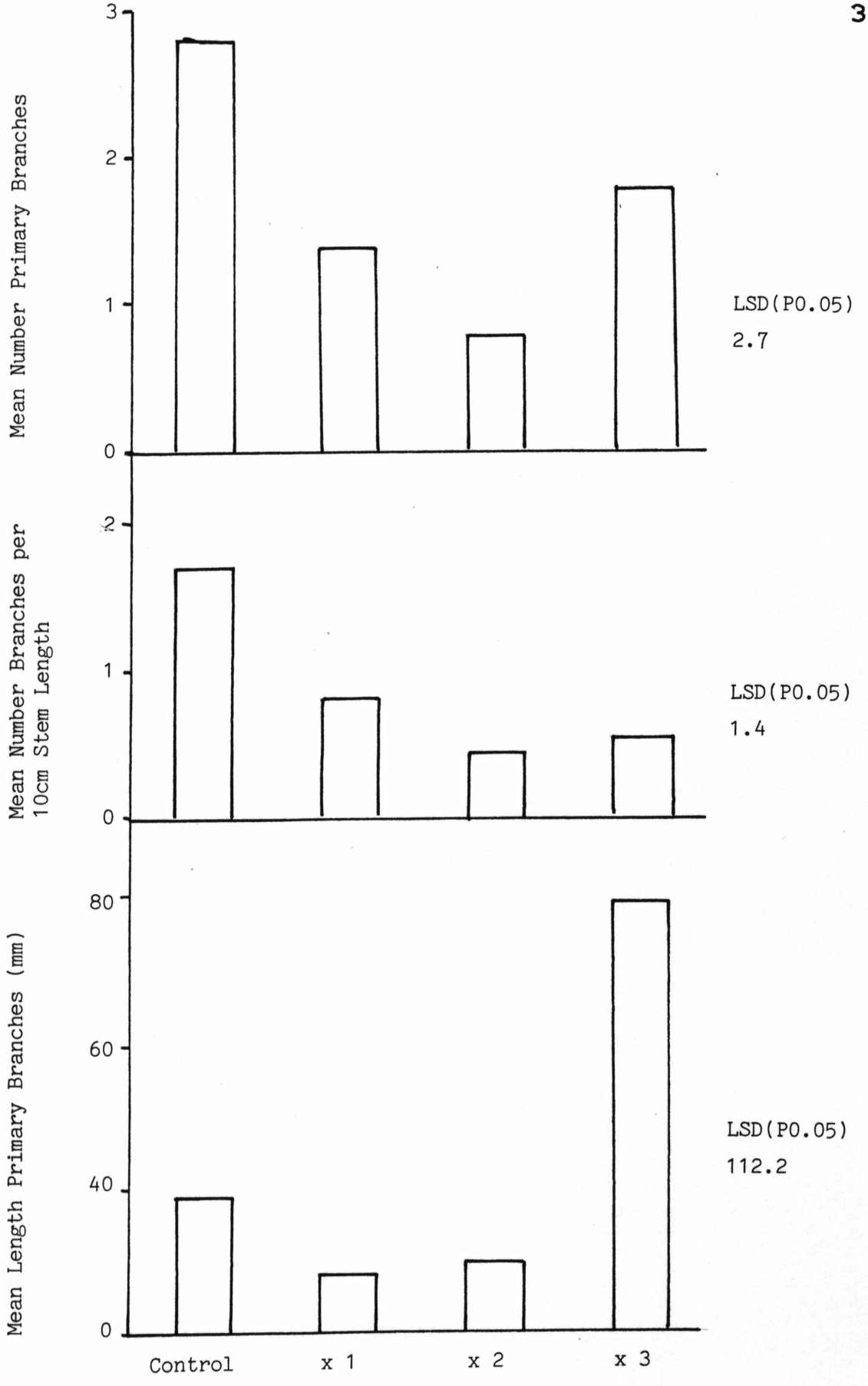


Figure 5C.4 Effect of repeated applications of 50ppm gibberellic acid on the mean number and length of branches of oak. Control = No GA_3, x 1 = one application, x 2 = two applications, x 3 = three applications.

	Control	50ppm	150ppm	450ppm	1350ppm	Sig.	LSD(P0.05)	CV
1984 Experiment								
Initial Base Diameter	6.4	6.2	6.6	7.0	6.8	NS	1.3	14.8
Final Base Diameter	13.0	12.6	11.4	12.2	12.0	NS	2.0	12.5
Initial Diameter at 5cm	4.2	4.2	4.2	4.2	4.4	NS	0.8	14.2
Final Diameter at 5cm	5.6	7.4	6.6	7.8	7.6	*	1.3	13.4
1985 Experiment								
Initial Base Diameter	4.8	4.6	4.4	4.6	4.4	NS	1.1	18.2
Final Base Diameter	6.8	8.2	7.4	9.0	8.4	NS	2.1	19.9
Initial Diameter at 5cm	2.6	3.0	2.8	3.0	2.8	NS	0.7	19.0
Final Diameter at 5cm	4.0	5.2	5.2	6.4	5.2	NS	2.1	30.6

Table 5C.8 The effect of different concentrations of gibberellic acid on mean stem diameter (mm) of oak seedlings in two separate experiments.

clear trend relative to concentration of hormone. There were no significant differences in diameter at 5cm in the second experiment, nor were there any significant block effects in either experiment.

Repeated applications of 50ppm gibberellic acid had no significant effect on base diameter, although there was some increase with three applications of hormone (table 5C.9). The diameter at 5cm was significantly increased by three applications of hormone, with the diameter at this height showing an increase with each application of hormone applied.

Table 5C.9

The effect of repeated applications of gibberellic acid (50ppm) on the mean stem diameter (mm) of oak seedlings in the field (x1 = one application, x2 = two applications, x3 = three applications).

	Control	x 1	x 2	x 3		LSD(P0.05)	CV
Initial base diameter	5.0	5.0	4.8	4.6	NS	1.2	18.1
Final base diameter	6.8	6.8	6.8	8.6	NS	1.8	17.9
Initial diam. at 5cm	3.0	3.0	3.2	3.0	NS	0.3	7.3
Final diam. at 5cm	4.4	4.8	5.4	6.8	*	1.5	20.3

5C.6 Leaf Area - Experiments With Single Application

Results for leaf number, leaf area and weight for the first of the two experiments examining the effect of different concentrations of gibberellic acid on oak are given in table 5C.10. The seedlings were planted out at the beginning of May 1984, during a period of cold weather with strong north-easterly winds there was some leaf damage to the seedlings, in some cases resulting in loss of leaves, hence the reduction in mean leaf number by the end of May. There were no significant differences in final number of leaves though hormone treated trees tended to have fewer leaves. The total leaf area was significatly reduced by GA_3 treatment, though there was no clear relation between total area and concentration of GA_3; nor were there any significant differences in mean leaf area per leaf, mean leaf weight per leaf or specific leaf area.

	Control	50ppm	150ppm	450ppm	1350ppm	sig.	LSD(P0.05)	CV
Initial Number Leaves	19.8	15.8	15.6	15.6	15.6	NS	4.7	21.1
Number Leaves 30.5.84	19.4	13.0	10.6	13.0	11.4	NS	6.4	35.6
Final Number Leaves	51.4	37.6	34.0	23.0	21.0	NS	26.3	58.7
Total Leaf Area (cm^2)	745	435	290	389	251	*	307	54.4
Mean Leaf Area per Leaf (cm^2)	17.2	11.6	9.6	16.0	13.3	NS	7.1	39.3
Mean Dry Wt per Leaf (g)	0.135	0.081	0.075	0.134	0.103	NS	0.058	40.7
Specific Leaf Area (cm^2/g)	127.8	145.5	123.3	122.5	131.5	NS	21.9	12.5

Table 5C.10 The effect of different concentrations of gibberellic acid on mean leaf number, area and weight for oak in the field, 1984.

Results for the second, 1985, experiment are given in table 5C.11. Initial leaf area was determined using the exponential relationship between leaf length and leaf area: Area = 0.3848 Length $^{1.975}$ as derived in the previous experiment (V). The final number of leaves was significantly reduced by hormone treatment, but there were no significant differences in total leaf area or mean leaf area per leaf. The total leaf area was however greater in control trees and there was a decrease in mean area per leaf in all treatments compared with the initial measurements.Mean dry weight per leaf and specific leaf area were not significantly different.

5C.7 Leaf Area - Experiment on Repeated GA_3 Application

The effect of repeated applications of 50ppm gibberellic acid on leaf number, area and weight of oak seedlings are given in table 5C.12. The initial leaf area was again estimated using the relationship between leaf length and area: Area = 0.3848 Length $^{1.9750}$. There were no significant differences in number of leaves, total leaf area or mean leaf area per leaf, however there was a general reduction in mean area per leaf with all treatments compared with the initial measurements. Mean weight per leaf was not significantly affected, though there was a decrease with increasing number of applications of gibberellic acid. There was no significant effect on specific leaf area.

5C.8 Total Dry Weight

The use of different concentrations of gibberellic acid had no significant effect on the total dry weight of oak in either of the experiments (table 5C.13). However in the 1984 experiment control trees had a greater dry weight than those treated with 1350ppm GA_3, trees given 50ppm, 150ppm and 450ppm GA_3 had intermediate dry weights. No such trend was visible in the second experiment. The initial mean total dry weight was greater for the 1984 experiment, 6.0 ± 2.4g (n=20) than in 1985, 2.5 ± 0.5g (n=5). The use of repeated application of 50ppm GA_3 had no significant effect on the total dry weight, the mean dry weight for all treatments lay between 9.0 - 10.0g (LSD(P0.05) 4.4).

	Control	50ppm	150ppm	450ppm	1350ppm	Sig.	LSD(P0.05)	CV
Initial Number Leaves	10.2	14.0	10.4	11.4	10.4	NS	4.8	31.7
Final Number Leaves	48.8	20.6	17.4	24.6	28.4	*	20.6	54.9
Initial Total Area (cm^2)	194	236	148	203	141	NS	114	46.3
Final Total Area (cm^2)	351	241	189	216	166	NS	184	59.0
Initial Area per Leaf (cm^2)	18.7	17.3	14.3	17.2	14.8	NS	6.8	30.8
Final Area per Leaf (cm^2)	6.8	12.6	11.1	9.7	6.1	NS	5.3	42.9
Mean Dry Wt per Leaf (g)	0.041	0.089	0.074	0.065	0.041	NS	0.039	46.6
Specific Leaf Area (cm^2/g)	165.7	141.6	154.5	150.8	152.2	NS	22.7	11.1

Table 5C.11 The effect of different concentrations of gibberellic acid on mean leaf number, area and weight of oak in the field, 1985.

	Control	x 1	x 2	x 3	Sig.	LSD(P0.05)	CV
Initial Number Leaves	11.0	10.6	10.8	10.6	NS	3.9	26.7
Final Number Leaves	25.6	27.4	22.4	27.2	NS	14.4	40.9
Initial Total Leaf Area (cm^2)	168	176	156	159	NS	69.7	30.7
Final Total Leaf Area (cm^2)	257	259	222	249	NS	98.5	29.0
Initial Area per Leaf (cm^2)	15.6	16.9	14.0	15.9	NS	4.2	19.7
Final Area per Leaf (cm^2)	11.6	12.4	10.2	9.7	NS	6.3	41.6
Mean Dry Wt per Leaf (g)	0.082	0.073	0.066	0.059	NS	0.045	46.6
Specific Leaf Area (cm^2/g)	150.0	185.7	155.9	166.4	NS	55.1	24.3

Table 5C.12 The effect of repeated applications of 50ppm GA_3 on mean leaf number, area and weight of oak seedlings in the field. (x 1 = one application, x 2 = two applications, x 3 = three applications).

Table 5C.13

The effect of different concentrations of gibberellic acid on the mean total dry weight (g) of oak in two separate experiments.

	Control	50ppm	150ppm	450ppm	1350ppm		LSD(P0.05)	CV
1984	30.6	24.1	21.8	24.2	18.7	NS	8.3	26.1
1985	8.4	10.8	7.7	10.6	7.0	NS	5.3	48.9

5C.9 Distribution of Dry Matter - Experiments With Single Application

The percentage distribution of dry matter within the plants given different concentrations of gibberellic acid is shown in table 5C.14. For the 1984 experiment there were no significant differences, although percentage stem increased with increasing GA_3 and percentgae leaves decreased with all concentrations of GA_3. Significant differences were observed at the end of the second experiment, the increase in percentage stem with increasing GA_3 and decrease in percentage leaves compared with the control trees was confirmed. The percentage of dry matter in the form of roots appeared little affected by treatment with different concentrations of gibberellic acid. Compared with the distribution of dry matter prior to treatment there was an increase in percentage stem and percentage root and a decrease in percentage leaves.

5C.10 Distribution of Dry Matter - Experiment on Repeated GA_3 Application

Increasing the number of applications of GA_3 had a significant effect on increasing percentage stem (table 5C.15). There were no significant differences in percentage leaves and percentage roots, however the proportion of roots does show a decrease with increasing number of applications of gibberellic acid. For all treatments the percentage leaves was decreased compared with the initial sample and percentage roots increased, percentage stem was only increased by three applications of GA_3.

	Initial	Control	50ppm	150ppm	450ppm	1350ppm	Sig.	LSD(P0.05)	CV
1984 Experiment									
Stem	22.6 ± 5.1	24.7	25.3	21.5	30.1	32.5	NS	9.3	25.8
Leaves	46.0 ± 12.6	18.9	12.8	11.0	11.3	10.2	NS	6.1	35.6
Root	31.4 ± 8.9	56.3	61.8	67.8	52.3	57.3	NS	13.9	17.5
1985 Experiment									
Stem	19.0 ± 4.3	17.7	23.0	26.6	28.9	32.2	*	8.9	26.0
Leaves	32.2 ± 5.3	23.5	15.8	15.9	14.6	15.2	*	6.2	27.3
Root	48.7 ± 8.3	58.6	61.2	57.5	56.5	52.7	NS	10.8	14.1

Table 5C.14 Distribution of dry matter of oak seedlings, expressed as percentage total dry weight, as affected by different concentrations of gibberellic acid, in two separate experiments.

Table 5C.15

Distribution of dry matter of oak seedlings, expressed as percentage total dry weight, as affected by repeated applications of GA_3 (50ppm). One application - x1, two applications - x2, three applications - x3.

	Initial	Control	x 1	x 2	x 3		LSD(P0.05)
Stem	22.8 ± 3.1	15.7	20.1	24.8	35.8	**	10.1
Leaves	38.2 ± 4.8	18.5	16.3	17.8	15.3	NS	6.9
Root	39.0 ± 3.6	65.7	63.6	57.5	48.9	NS	13.3

5C.11 Stem : Root Ratio

No significant differences were apparent between treatments with different concentrations of gibberellic acid (table 5C.16). No clear trends were visible in the first experiment, but the stem:root ratio of the trees after 3 month's growth in 1985 showed an increase with increasing concentration of gibberellic acid. The initial mean stem: root ratio in 1984 (n=20) was 0.76 ± 0.23 and in 1985 (n=5) 0.41 ± 0.17, therefore stem:root ratio was decreased by all treatments in 1984 and only increased by 1350ppm GA_3 in the 1985 experiment.

Table 5C.16

The effect of different concentrations of gibberellic acid on the mean stem:root ratio of oak in two separate experiments.

	Control	50ppm	150ppm	450ppm	1350ppm		LSD(P0.05)
1984	0.47	0.42	0.33	0.45	0.57	NS	0.21
1985	0.31	0.04	0.49	0.54	0.66	NS	0.26

Stem:root ratio of dry weight was significantly ($P<0.05$) affected by the number of applications of gibberellic acid applied to the seedlings (fig. 5C.5), with a significant increase occurring with three applications. The initial stem:root ratio for trees used in this experiment was 0.59 ± 0.10 and therefore the stem:root ratio was reduced by all treatments except three applications of GA_3.

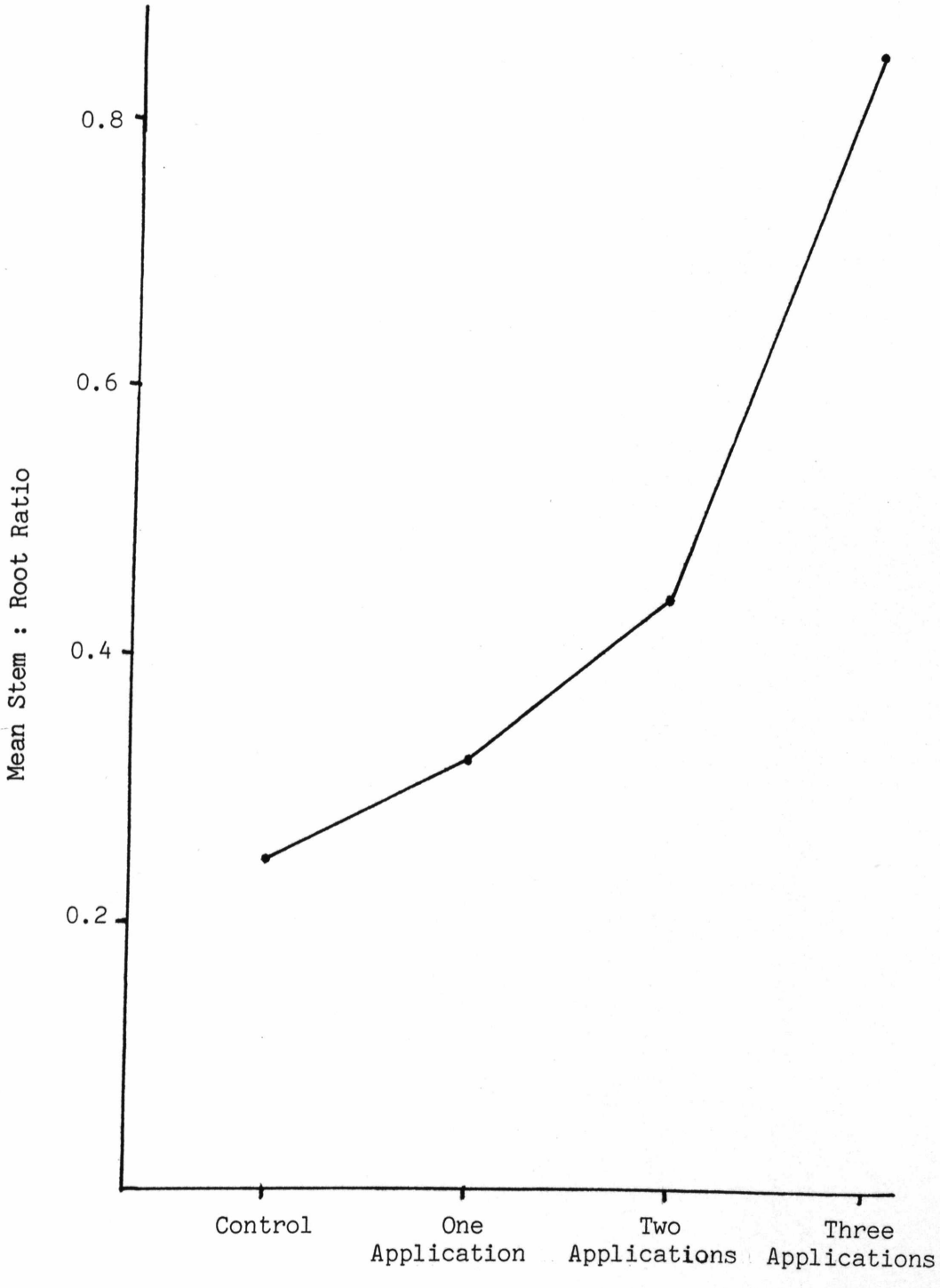


Figure 5C.5 The effect of repeated applications of 50ppm gibberellic acid on mean stem:root ratio of dry weight of oak seedlings in the field, LSD(P0.05) 0.44.

PART D - SUMMARY

Results confirmed the findings of the previous experiments that height growth of oak seedlings can be increased with the application of gibberellic acid as a foliar spray. This effect occurring under the different environmental conditions of growth cabinets, glasshouse and in the field. Greater height growth was achieved with increasing concentrations or the number of applications of gibberellic acid used. GA_3 increased height growth under two day/night temperature regimes by extending growth over a longer period of time, thus increasing the length of shoot produced in each growth flush, and also by increasing mean internode length. Higher day/night temperature (30°C/12°C) alone had no significant effect on height growth, however decreasing light intensity by shading did increase height growth.

The effect of GA_3 on stem diameter was variable but in general it appeared to increase stem diameter. Higher day/night temperature increased the base diameter but no significant differences were found between shading treatments. The number of branches produced under the different treatments was too variable to show any clear trends.

In the glasshouse experiment GA_3 increased the total number of leaves and the total leaf area, specific leaf area increased with increasing level of shade. However in the field experiments there was a decrease in the total number of leaves and total leaf area per tree with GA_3 compared with control trees.

The production of dry matter was not significantly affected by day/night temperature or shading, however the distribution of dry matter within the plant was altered. A higher day/night temperature (30°C/12°C) regime increased the proportion of stem and decreased that of root. Similarly gibberellic acid increased the proportion of dry matter as stem, the effect of GA_3 on stem:root ratio was increased at the higher day/night temperature regime. Increasing the concentration of GA_3 applied also increased the stem:root ratio.

Results from these experiments were highly variable which may have obscured possible treatment effects. The number of seedlings available for use was limilted thus restricting the number of replicates which could be used for each treatment. The duration of the experiments may also have been too short to show any real differences between treatments. Weather conditions are another factor contributing to differences in results obtained in similar experiments carried out in 1984 and 1985 growing seasons. Moreover the seedlings were unfortunately raised from different seed sources in the two years.

DISCUSSION

6.1 General and Meteorological Considerations

The work of Tuley (1982b, 1983, 1985) has focussed attention on the fact that the height growth of oak can be increased inside tube shelters. This study was designed to examine the environmental conditions in such tubes and how the growth of oak is affected by tube shelters, and how this compares with other methods which have proved successful in enhancing the growth of oak i.e. glasshouse conditions with manipulation of daylength and also the application of gibberellic acid (Nitsch 1957b, Vogt 1970, Larson and Palashev 1973, Schwabe 1976, Smith and Schwabe 1984), also by fertilisation (Foster and Farmer 1970) and CO_2 enrichment (Milhet and Costes 1984).

The ability to accelerate growth by such techniques could offer substantial advantages over present practices. In the glasshouse seedlings of plantable size could be produced in a much shorter time, they could also be produced throughout the year by using extended daylength which delays or prevents the onset of dormancy (Nitsch 1957a, Vince-Prue 1975). Tube shelters also have the advantage that they protect young trees from mammal damage and aid chemical weed control (Evans 1984a). Oak may be described as having weak 'apical control' since branch growth often equals or exceeds that of the terminal shoot (Longman and Coutts 1974), trees with 'better' form i.e. fewer branches, straighter stems would be desirable for timber production. In tube shelters or in the glasshouse, an improved growth habit may be induced.

Oak for timber was chiefly grown under the shelterwood system. Under this system there is the gradual removal of the entire stand in a series of partial cuttings which extend over a fraction of the rotation (Hawley and Smith 1954). Replacement of the stands is by natural regeneration. The initial density of planting was very high in order to encourage the development of straight, natural pruned boles. If the plants are given too much space in the early stages they grow into short, spreading trees thus reducing the value of the timber (Hawley and Smith 1954). Under conditions of low light intensity, as found in densely planted stands, the main axis elongates as much as possible to reach the light at the canopy level, while lateral branches are suppressed. Hence apical dominance is environmentally re-inforced.

While it was part of this study to make physical determinations of several environmental factors (temperature, humidity, CO_2, light

levels) which constitute the environment in the tube shelters, glasshouse and field, and modify growth, the other aspects of these studies was to identify and compare their effects on growth in the three conditions. In addition to modification of the levels of assimilate, water content, the internal factors, particularly the balance between plant growth regulators,operating must also be taken into account (Kramer and Kozlowski 1979, Bachelard 1980). The effect of one growth regulator i.e. gibberellic acid (GA_3) was studied, specifically by way of exogenous application.

Levels of environmental factors were initially sampled by spot readings, the radiation, temperature and humidity was determined simultaneously in field, tube and glasshouse environments. Replicate samples were taken each corresponding to a particular tree, so analyses of variance could be used to determine whether differences between environments were significant. Even small differences in the environment e.g. temperatures which just exceed optimum may have an effect on growth especially over longer periods of time (Steponkus 1981).

It was of course realized that spot readings record the situation only at a given time, and despite some time difference between the first and final samples taken in a series of measurements, consistent differences were recorded between environments. A series of spot readings therefore represents an average over space and time. The time factor involved in sampling is of greater importance with more rapidly changing variables such as radiation (Woodward 1985). To overcome this difficulty where a series of spot readings had to be taken over an extended period, a Latin square design was used (Cox 1958). Only one sensor was used in each environment at any one time, (due to the difficulty in setting up and controlling many sensors), sampling might thus have been improved with the use of more sensors to sample each environment over a wider area (Woodward 1985).

Of the sensors used the temperature sensors, platinum resistance thermometers and thermocouples proved relatively reliable, they were fairly easily calibrated and the calibration remained relatively stable. The humidity sensors however proved more difficult to calibrate and the calibration was less stable with time. They therefore required more frequent checking.

Supplementing the spot readings the environmental factors were also sampled and recorded using a computer-based data logging system (Persuard and Viriden 1984). This allowed the environments to be sampled more frequently, the results representing the average of

many readings, unfortunately here too only one sensor could be used in each environment. While this eliminated any systematic instrument errors, simultaneity could not be achieved.

Relationships between data-logging results for field, tube and glasshouse environments and meteorological data were derived with the object of obtaining calculated values for those days for which no primary data were available. However caution had to be exercised, such that calculations must stay within the limits of the data used to derive the original regression equation. Such relationships then represent a correlation technique which determine the degree of dependence of microclimate parameters on factors of the macroclimate (Holmes and Dingle 1965). Such expression of dependence of one variable on another does not elucidate the underlying principles, in particular caution must be exercised before cause and effect relationships between two variables may be assumed, even if statistical significance is obtained. Conversely statistically insignificant results may be rejected where a cause and effect relationship may exist but is masked by other factors (Holmes and Dingle 1965).

Byrne (1970) highlights the underlying theory and outlines some of the problems associated with the sampling and recording of data using a data-logging system. The frequency of sampling required is dependent upon the nature of the environmental variable being measured. Sampling time must be adequate to pick up small changes in the environmental parameters but not so frequent that superfluous data are accumulated (Woodward 1985). In this study several environmental parameters were recorded using a single data-logging system. The sampling time was chosen arbitrarily and this clearly represents a compromise, as each parameter may ideally require a different sampling frequency. Other errors, which must be considered include those connected with the calibration of the sensors, or the effects of temperature on calibration stability.

Infra-red gas analysis was used to measure the CO_2 concentation of air, an infra-red gas analyser (IRGA) was available and it is also a simple, relatively reliable technique. Potential sources of error e.g. vibration, temperature (Šesták, Čatský and Jarvis 1971) were recognised and these were, as far as possible, minimised. As the absorption bands of CO_2 and H_2O overlap filters were used, and ideally samples should also be dried (Parkinson 1971). The standard gas mixtures used to calibrate the IRGA were dried but samples taken in the three environments were not dried. The higher the water content of the

air, as in the tube environment, the greater the potential error. The syringe technique used for sampling was an adaptation of the inflation system as described by Šesták, Čatský and Jarvis (1971).

The field environment was considered as 'control' and the tube and glasshouse environments as modifications of the field conditions. The physical environment in the field was entirely controlled by the weather, except for photoperiod, however, the soil was well cultivated and a suitable site was chosen for the tree species to be grown, as recommended by Blatchford (1978); this also applied when trees were grown within tube shelters. The field environment is associated with the highest radiation levels, it is also more exposed to wind. It is possible, however, to modify the field environment to some extent, as in this study, by using artificially extended daylengths. It would seem that this may only be practicable on an experimental scale, but use of light-break techniques might be adapted to field use. Gibberellic acid can also be applied to trees, preferably prior to planting when trees are of small and managable size.

6.2 The Physical Environment

The environment inside the tube suffers from a decrease in radiation, the tube material will itself absorb radiation and must have a scattering effect, moreover it may also have had a small effect on the spectral composition of light entering the tube, though any such changes were not measured in this study. The tube material does contain a UV-inhibitor to help extend the life of the plastic shelter.

As suggested by Tuley (1980) the temperature within the tube was increased (Table 3A.2), it could also be higher than in the glasshouse environment (Figure 3A.8). Since the temperature effects must have been radiation dependent the tube environment was subject to rapid changes in temperature particularly on sunny mornings (Figure 3A.7), there was also a greater range in temperature than in the field (Table 3A.5). Night temperature could be lower than in the field.

Very high humidities, close to saturation were recorded in the tube during the summer months (Table 3A.8). The high humidities would tend to decrease the vapour pressure deficit between leaf and the surrounding air despite the increased temperature which would tend to increase vapour pressure deficit (Helms 1976). While leaf temperature normally tend to be lower than air temperature, due to evaporative cooling, these high humidities were reflected in smaller negative or even positive differences between leaf and air temperature within

the tube (Figure 3A.17). A decrease in vapour pressure deficit would tend to reduce transpiration and perhaps also the uptake of water and nutrients from the soil. However stomata of tube trees may be able to remain open enabling an increase in uptake of CO_2. A combination of high temperature and low CO_2, as was found in the tube, would lead to wide opening of stomata (Meidner and Mansfield 1968).

Other environmental factors of the tube environment, which were not specifically measured but may have had some effect on tree growth, included mechanical restriction, and therefore lack of stem movement and also reduced air movement and CO_2 exchange. The action of wind tends to decrease height (Rees and Dixon 1980a) and stem growth (Grace 1977). Also at high wind speeds some cuticular damage occurs to Q.robur (Dixon and Grace 1984), such damage is more likely to occur under field conditions.

Perhaps somewhat unexpectedly CO_2 levels in the lower part of the tube were actually higher than in the field, the extra CO_2 being derived partly from the soil. There was a greater vertical range in CO_2 concentration within the tube during the day, the sharp decreases occurring in the centre of the tube amongst the bulk of the leaf material. CO_2 levels were also affected by the size of the tree within the tube, radiation levels amongst the leaves of the tree were similar in tube and glasshouse at the beginning of the season but was reduced in the tube in September. Reduced CO_2 flux within the tube was also seen in accumulation of respiratory CO_2 at night.

Prevailing weather conditions exerted a major effect on the tube microclimate, as seen in the linear relationship between shortwave radiation and also mean air temperature and their corresponding meteorological data. This was not found with humidity where the tube and the tree within it must have had the predominant influence on tube humidity. Once a tree emerged from the top of the tube, as happened in one season during the first experiment in 1983, the tree is clearly subjected to two environments as highlighted by the buds within the tube opening before those on the same tree outside the shelter, also noted by Tuley (1985).

The glasshouse offers a more controllable environment, it is less dependent in terms of temperature on field conditions. Humidity tends to be similar to or lower than in the field and radiation levels are reduced (Edwards 1968). Both day and night temperature are increased in the glasshouse compared with those in the field. There is freer exchange of air than in the tube, the glasshouse is also ventilated

during the day and has a larger volume than a tube shelter. The glasshouse environment can be controlled in terms of temperature, also light quality through supplementary lighting (Cathey and Campbell 1980), and quantity including length of photoperiod. However, since most glasshouse plants are grown in containers, as were the trees in this study, there is a restriction on root volume which was not imposed in either the field or tube environment.

6.3 Effects on Tree Growth

Height growth over one growing season was increased 213.5-219.8% in the tube and glasshouse environments compared with growth in the field. Tuley (1980) recorded an increase in height growth of container-raised oak within shelters of 123.6% over unprotected trees after one year. The glasshouse environment alone i.e. under natural daylength, without hormone treatment gave no significant advantage in height growth over the tube environment. Other techniques e.g. application of gibberellic acid or extended daylength which increase height growth of glasshouse trees over tube grown trees will be discussed later. An increase in the number of growth flushes produced (Table 3B.6), also the number of nodes and mean internode length (Tables 3B.9, 3B.10) all contributed to the greater height growth of tube and glasshouse trees.

By October 1983 after only one growing season some tube trees had already grown out of the tops of their tube shelters (height 1.2m), however seedling trees planted in May 1984, also in tubes, made very poor growth in comparison. Seedlings used in 1983 had been grown from seeds of a local source whilst those used in 1984 came from a Dutch seed source and may have had more prolonged or unfavourable storage conditions. The wide distribution of both Q.robur and Q.petraea could be expected to lead to considerable differences between seed origins. There is little experimental evidence, however, of differences between provenances but it does suggest that locally collected seed should be as good as any other (Evans 1984b).

Tube shelters have been shown to increase the growth of many forest species. Tuley (1983) reported that beech did not respond to tubes after one year but height growth was significantly increased after two years. In this study beech seedlings did respond to the tube environment in one season, whilst no significnat increase in height was recorded in oak within tubes in the same season (1984).

The height growth of forest species e.g. Sitka spruce, Corsican

pine can be correlated with various meteorological conditions, the highest correlation coefficients were obtained with maximum air temperature, though other variables (mean air temperature, minimum temperature, depression of wet bulb, wind speed, hours of sun) were also significantly correlated (Ford 1980). In terms of general weather conditions 1984 growing season may not have been as favourable for growth. Mean air temperature and also soil temperature were lower, there was less total shortwave radiation and a reduced number of hours of sunshine. The 1984 season was also drier, though expreimental plots were kept well watered. The effectiveness of the tube shelter in increasing height growth may thus be dependent upon general weather conditions and also the plant material used.

Glasshouse conditions are less dependent upon weather in terms of temperature, even so seedlings grown under glasshouse conditions in 1984 also made poorer growth than those grown in 1983, this suggests that radiation, which was poorer in 1984, may have been the important environmental factor.

There are several problems involved in the analysis of growth in response to the environment, particularly where the environment cannot be controlled. There are problems of sampling frequency and measurement accuracy, the analysis of a growth response is the integrated result of a mixture of effects with both seasonal and daily trends, there are also lags in the response of plants to changes in the environment (Ford 1980), as well as the effects of preconditioning (Kozlowski 1979).

All aspects of temperature environment may be important for growth i.e. total heat sum, maximum temperature, minimum temperature and thermoperiod (Hellmers 1966, Brix 1971). Though various growth parameters may all have different temperature optima (Hinesley 1981). Maximum temperatures were similar in glasshouse and tube environments but night temperatures were consistently higher in the glasshouse.

Temperature exerts its effect on growth by altering rates of many processes e.g. photosynthesis, respiration, cell division and elongation, enzymatic activity, chlorophyll synthesis, water uptake and transpiration (Kozlowski, Winget and Torrie 1962). There may be a lag in response to temperature due in part to the long translocation paths involved in trees. Maximum temperature dependence of growth often occurs under rate-saturating light intensities (Berry and Björkman 1980), though this is unlikely to occur in the tube environment.

Temperature, although obviously an important environmental factor, increasing day temperature in relation to the night temperature (30°C/12°C) to correspond with the greater range in temperature within the tube environment compared with the field had no significant effect on height growth (Figure 5A.1).

There was an increase in height growth when the seedling oak were shaded, the number of nodes produced, the length of shoot produced per flush and mean internode length were also increased (Tables 5B.3, 5B.4). Phares (1971) also noted an increase in the number of flushes produced when red oak was shaded. When seed reserves are exhausted growth becomes totally dependent upon fresh photosynthate. The supply of photosynthate for new growth, be it stem extension or leaf production, is, of course, directly related to the quantity of light, CO_2 etc. available to the existing leaves. Equally important is the "investment" of the fresh assimilate,(use of it for cell wall thickening only would be inversely related to new growth), it is a second determinant, which would affect height growth provided suitable extension sites are available (Grime and Jeffrey 1965).

The past history of radiation of a plant must also affect its response to radiation conditions at any time (Anderson 1971), and thus the effects of different environments may accumulate, though in oak conditions during bud formation may have a greater control on shoot length than those occurring whilst the shoot is expanding, since shoot growth is determined to a large degree by the anatomical stem units present in the unopened buds (Kramer and Kozlowski 1979).

The radiation measurements in the field, tube and glasshouse represent the maximum levels available to the trees, but not necessarily the total radiation available to every leaf on the plant due to mutual shading. In the tube environment the leaves are packed closely together therefore the light available to many leaves may be greatly reduced. Leaf area index (LAI) for tube trees was 33.3 ± 0.8 (September 1983), though in tubes there was also some lateral light.

The spectral composition of the light received, especially by the lower leaves is also important, thus the ratio of red:far-red light under oak vegetation is reduced compared with daylight under all conditions (Morgan and Smith 1981); far-red light enhanced stem growth of oak (Axelsson, Klockare and Sundqvist 1979). However once the tree has emerged from the top of the tube, leaves are experiencing conditions similar to those in the field and therefore different from those within the tube itself. This also affects their longevity, Tuley (1980)

noted that leaves within shelters remained green longer than those in the same tree produced outside the shelter.

Both tube and glasshouse environments appear to increase the 'apical control' (Longman and Coutts 1974) of the oak seedlings. Apical dominance appears to be a spatial response, dependent upon the proximity of main stems and laterals to hormone sources (Field and Jackson 1974). However hormones are not the only factor involved in apical dominance, the nutrient status of a plant also has a marked effect. Young birch seedlings grown under conditions of poor mineral nutrition and low light show inhibition of lateral buds i.e. marked apical dominance (Wareing 1970).

Gibberellic acid application increased height growth of trees significantly in the tube and glasshouse only, with the greatest growth occurring in the glasshouse. Beech seedlings differ from oak in that beech seedlings in both the field and tube responded to application of 50ppm GA_3.

Gibberellic acid was not effective in maintaining growth of oak in the glasshouse in the winter (after breaking dormancy), other treatments are required e.g. photoperiod (Schoeneweiss 1963). The lack of effect of GA_3 on trees in the field may have been due to too low a concentration being used, or the extent to which it was taken up through the thick cuticles of the leaf epidermis, since increasing the concentration did evoke the expected response of increased stem growth. There are, of course, also species differences e.g. in conifers height growth of Pinus strobus was not increased by increasing the concentration of GA_3 used, though seedlings receiving three applications grew for a longer period than those having received only one application (Jensen and Dochinger 1972). Repeated applications however were not beneficial in increasing the effect of gibberellin on growth of greenhouse grown cherry trees (Stuart and Cathey 1961).

Even from the practical point of view it is important to test a wide range of concentrations of growth regulator as when a certain dosage of gibberellin is applied to an intact plant its effective concentration depends on other circumstances e.g. the level of endogenous gibberellin, and its effect can only be exerted in conjunction with other factors such as other endogenous growth substances and metabolites (Low 1975).

Gibberellic acid at 50ppm did cause an increase in growth in the tube and glasshouse environments suggesting that there were other factors limiting the response of oak to applied GA_3 under field

conditions. A plant's response to a growth substance may vary according to physiological or developmental stage, differences in environmental conditions, differences in nutritional status and in absorption and translocation of growth substances (Weaver 1972). It is also possible that the field leaves had thicker cuticles than those of either tube or glasshouse trees. Stuart and Cathey (1961) stated that gibberellin often induces its maximum response when growth conditions are adversely influenced by temperature, nutrition and other environmental factors.

Interestingly gibberellic acid decreased the number of growth flushes but height growth was increased by extending the period of growth, increasing the length of stem produced per flush and also increasing mean internode length. The number of nodes was only increased in the glasshouse environment. Frequently the effect of gibberellin on younger internodes is to increase their length whilst their number remains unchanged (Weaver 1972).

Gibberellin stimulated stem elongation is basically due to stimulation of cell division. However cell division alone does not result in growth so the stimulation of cell division must also be coupled with a normal or enhanced rate of cell elongation (Shininger 1975). One effect of gibberellin is to enhance apical dominance involving the enhancement of auxin effects in other parts of the plant (Paleg 1965).

6.4 Duration of Growth in the FTG-Environments

The use of incandescent lamps to extend photoperiod in the greenhouse did contribute significantly to the increase in height growth and a similar effect was described for Loblolly pine (Pinus taeda) seedlings (Boyer and South 1984). In the glasshouse under 24hour light winter resting buds of oak were not formed whereas trees did become completely dormant in the field and tube environments. This was also the case in the continuous light treatments in these two environments. The minimum light intensity capable of eliciting a photoperiodic response in different species has not been determined with precision (Nitsch 1957b). The lack of response to 24hour light, effective in the glasshouse in preventing the onset of dormancy and promoting the continuation of flushing, in field and tube environments was therefore not due to inadequate light intensity as a similar intensity maintained growth in the glasshouse, but was very probably due to a low temperature effect inducing dormancy (Vince-Prue 1975).

It is well known that a plant can have an absolute photoperiodic

requirement at one temperature but only a quantitative one, or none at all, at another (Vince-Prue and Cockshull 1983, Salisbury 1981). Low temperature may be more important than photoperiod for leaf fall in the field (Vince-Prue 1975), however, leaves were not retained under natural short daylength in the heated glasshouse.

Quercus robur can be induced to make as many as 14 flushes in a 12 month period in the glasshouse under 24hour light (Smith 1977). Plants growing in long days are generally very much taller than those under short days. 24hour light did increase height growth of oak, however there was no significant effect on the number of nodes produced, but there was some increase in internode length, still seen at the start of the second growing season. This may have been mainly due to an effect on glasshouse trees, though the interaction between FTG-environment and light was not significant.

Photoperiod has been shown to bring about quantitative and qualitative changes in gibberellin levels in higher plants (Jones 1973). But extended photoperiod does not always significantly increase early growth e.g. in chestnut oak, northern red oak seedligns (Immel, Rumsey and Carpenter 1978). However combining extended photoperiod with application of GA_3 increased shoot growth, lengthening distance between tops and roots thus overcoming juvenility (Schwabe 1976). However a combination of 24hour light and GA_3 application did not increase the growth of seedling Q.robur compared with 24hour light alone.

6.5 Leaf Production and Growth

In the tube and glasshouse environments there was an increase in total leaf area, both resulting from an increase in individual leaf size but not in the total number of leaves. Field trees had the greatest number of leaves, but the largest leaves were found on glasshouse trees; at the end of 1983 there was however no significant effect on leaf weight per leaf or specific leaf area. By the end of the second season mean leaf weight per leaf and specific leaf area were increased in the glasshouse. Larger leaves in the tube may have been due to higher humidities or temperatures, which also occur in the glasshouse, causing leaves to expand more. Whether this was due to greater cell size or cell number or both was not determined. Higher day/night temperature (30°C/12°C) had no significnat effect on leaf area, nor did shading, to the extent used here, affect the total leaf area or mean leaf area per leaf; however, specific leaf area was increased under the heaviest shade treatment. Exposed sun leaves, (as in the

field), tend to be smaller, thicker and leathery compared with shade leaves (Helms 1976).

Gibberellic acid decreased total leaf area by decreasing the number of leaves with no effect on individual leaf area. This may have been related to more carbohydrate being diverted to increased stem growth. Leaf shape too can be influenced by applied gibberellins, leaves becoming longer and narrower in Q.robur (Longman and Coutts 1974). The reduction in the number of leaves and total leaf area was not related to the concentration of GA_3 used. Repeated applications of GA_3 also had no significant effect on leaf area. Observed growth acceleration in Populus sp. after GA application indirectly caused a promotion of leaf area owing to decreased plastochron (average time interval prior to emergence of a new leaf) and a promotion of leaf enlargement (Rood, Davies and Blake 1984).

6.6 Total Dry Matter Production

The tube environment had no significant effect on total dry weight production compared with field grown plants after the first growing season whereas total dry weight was significantly increased in the glasshouse. Increasing the day/night temperature (30°C/12°C) had no significant effect on dry matter nor did shading over the range employed, though there was some decrease in the heaviest shade (20.5% of daylight) treatment. 24hour light increased dry matter production but only of glasshouse trees. A report on aspen trees states that there was greater productivity in longer photoperiods though the photosynthetic rate itself was not affected by photoperiod (Bate and Canvin 1971). In the present experiments total dry weight was measured only at the end of the growing season; this does not represent the total production quite accurately since there was some loss of dry matter e.g. leaves and fine roots through the season (Jarvis and Leverenz 1981).

There was an increase in potential photosynthesising leaf area in tube and glasshouse trees compared with those in the field, but this led to no increase in dry matter production in the tube, probably due to the bunching of leaves in the tube. Leaf area increases raise total photosynthesis, provided the leaves are dispersed adequately in space to ensure effective interception of solar radiation (Ledig 1976), clearly within the tube the foliage is not adequately spaced. There was a substantial increase in dry matter production in the glasshouse trees and this must be due to an increase in photosynthesis but also

from the increase in the length of the growing season, particularly under 24hour light. Unfortunately it is not known precisely how much of the dry matter increase must be attributed to either. Continuous light could not have contributed more than a small percentage of photosynthetically useful light energy, it does however prolong active green leaf retention. The glasshouse environment increased dry matter production by about 40% compared with the field environment after both the first and second growing seasons. The effect of extended daylength (in the glasshouse) was however small after one season, giving an increase of 8.2% in dry matter production compared with trees under natural daylength, but after two growing seasons there was a marked increase of 65.3% in total dry weight of trees under 24hour light compared with those grown under a natural daylength regime.

Small reductions in light intensity would not necessarily decrease photosynthesis of oak since Q.robur and Q.petraea both reach maximum rate of photosynthesis at relatively low light intensities; rapid photosynthesis can even occur at only 20% of full daylight (Longman and Coutts 1974). Although shoot growth may remain unaffected with shading up to 20% of full daylight root growth is greatly reduced (Longman and Coutts 1974). Presumably when there is a shortage, roots are more affected than shoots as competition between shoot growth (new leaves and stems) and roots for carbohydrate becomes more intense, although the effects of endogenous growth substances, which may be involved in such competition and regulate it indirectly, must also be taken into account (Scott-Russell 1977).

Nelson and Ehlers (1984) showed that the saturating photo flux density was higher for field trees than those grown in the greenhouse the difference being related to the average light levels under which the plants were grown. In Populus sp net photosynthesis (per unit leaf area) was higher in field than in glasshouse trees, however when expressed on a leaf dry weight basis rates were similar (Nelson and Ehlers 1984).

According to Chabot and Lewis (1976) the photosynthetic ability of plants also acclimates to some extent to those temperatures experienced for the major portion of a 24hour period, such that net gas exchange is most favourable at the predominant temperature. The same authors also state photosynthesis and extension growth in red oak are only indirectly related. Thus the decline in growth found above 30°C may well be related to a limiting supply of substrates, since photosynthesis declines rapidly above its 25°C optimum, but at the higher

temperature processes intrinsic to entension growth would also be inhibited (Chabot and Lewis 1976).

Tube trees can experience higher temperatures than in either the glasshouse or field. The failure of tube trees to produce more dry matter than field trees - in spite of more sheltered conditions in the tube - may additionally have been due to increased respiration which has a higher optimum temperature than photosynthesis (Kramer and Kozlowski 1960). Reduced carbohydrate supply would tend to favour stem growth at the expense of the roots (Brouwer 1977). In forest trees (as in many herbaceous species) carbohydrate consumed in respiration may amount to 30-60% of total productivity (Helms 1976). Therefore a greater impact on seedling establishment and survival may be made by decreasing respiratory loss by providing shade than by increasing photosynthetic production (Helms 1976). Respiration rates in Q.robur and Q.petraea may be reduced when plants are grown under shade conditions (Longman and Coutts 1974).

Within a tube shelter trees are greatly protected from the action of wind, this would reduce mixing of air perhaps tending to CO_2 deficiencies as may occur in the dense canopy of forest trees (Helms 1976). Actual measurements however indicated that CO_2 levels in the lower part of the tube were increased through production from the soil, though very low levels of CO_2 were recorded in the upper part of the tube. Nocturnal CO_2 flux density in a forest is a result of two processes, respiration from forest vegetation and respiration of soil microorganisms and the roots (Murphy 1985). CO_2 did accumulate in both tube and glasshouse environments over night, increasing CO_2 supply is of course common practice in the greenhouse industry, it may be used to enhance growth (Tolley and Strain 1984, Milhet and Costes 1984).

In the main experiment gibberellic acid had no significant effect on total dry weight accumulated, nor was there an effect by increasing the concentration or using repeated applications of GA_3. Applied gibberellins can stimulate vegetative growth but not necessarily total yield (dry weight) (Stuart and Cathey 1961). Its major effect is rather to modify dry matter distribution.

6.7 Dry Matter Distribution

In the field environment the majority of growth was in the form of roots, giving a stem:root ratio less than 1. In both the tube and glasshouse environments the stem:root ratio was substantially increased, 2.75 and 1.77 respectively, i.e. a shift towards shoot growth, the effect being particularly marked with the tube environment. Tuley (1985)

had shown that tube shelters increased the dry weight of all components of young oaks (stem, leaves, branch and roots) but especially stems compared with trees grown in mesh tree guards. In another study with Populus clones glasshouse grown plants had low root:stem weight ratios (Nelson and Ehlers 1984).

In both tube and glasshouse environments light intensity is less than in the open air. With shading root growth is greatly reduced (Longman and Coutts 1974). In red oak under low light intensity most of the dry matter is accumulated as stem and leaves (Phares 1971). Not surprisingly therefore, the growth patterns in the tube environment and in the shade were similar. Quercus petraea also responds to shading by increasing height, leaf area, specific leaf area, and by decreasing root weight and root:stem ratio (Jarvis 1964). In fact as no significant change in stem weight was recorded Jarvis (1964) considered the increase in stem length with shading as etiolation. Stem weight of oak was increased as well as root weight decreased also there was no significant effect on specific leaf area.

The total dry weight of beech seedlings was increased in the tube environment with the proportion of dry weight as leaves increased with no significant effect on stem or root dry weight . Although beech is not a species characteristic of shade and reacts favourably to increase in light (0-50%), it can survive under dense cover but growth is slowed right down (Oswald 1981). Less than full daylight reduces total growth (biomass) though height increment may be enhanced (Evans 1984b). Growth of roots is more affected under shading but growth in height only lessens notably under 20% light (Oswald 1981). Logan (1973) stated that in terms of height, dry matter production of root and leaf area growth of beech was greatest at 45% of full daylight. Also the optimum temperature for photosynthesis is near 20°C (Aussenac 1981).

The amount of dry matter accumulated in leaves, stem, roots and flowers account for some of the differences in growth rates at different temperatures (Berry and Raison 1981). One effect of the tube environment was to increase shoot temperature (Table 3A.2) relative to the root temperature. Root growth has generally a lower optimum temperature than shoot growth (Brouwer 1962), thus increasing shoot temperature in relation to root temperature could increase shoot:root ratio provided the shoot temperature does not become supra-optimal (Smith 1977). Higher day/night temperature (30°C/12°C) increased the proportion of dry matter as stem and decreased that of roots. In the glasshouse not only is day temperature increased but also the night

temperature. The temperature of the soil within the containers of glasshouse trees will also tend to equilibriate with glasshouse temperature, (as seen in the growth cabinet experiment), though the effect is greater in smaller pots. Smith (1977) showed that the growth of oak roots was less sensitive to temperature though both are interdependent. Differences in the lag phase between soil and air temperature, which could be shorter in the glasshouse than in the field, may also be important when comparing field experiments with those under controlled conditions (Bierhuizen 1973), but no appropriate data were obtained in the present studies.

It is known that exogenous application of gibberellic acid increases the growth of the shoot at the expense of the roots (Smith and Schwabe 1984). Gibberellic acid increased the stem:root ratio in the tube and glasshouse but not in the field, the proportion of stem was increased but there was no corresponding decrease in root growth. Increased height growth in balsam fir with exogenous GA_3 resulted from an alteration of the normal distribution of photosynthate, with a disproportional amount being concentated in the main stem (Little and Loach 1975).

Twentyfour hour light had no significant effect on stem:root ratio or the distribution of dry matter within the plant after the first growing season. After two seasons there was an increase in the proportion of stem and a decrease in roots in the glasshouse trees only, with no effect in the other two environments. The effect of long days on oak is similar to that of gibberellin application i.e. it increased shoot growth and reduces root growth (Schwabe 1976).

Root growth equally depends on numerous conditions - supply of carbohydrate, water,minerals and hormones, oxygen availability and favourable temperature (Brouwer 1977). Plants which develop extensively branched and deeply penetrating root systems are able to utilise soil water and minerals most effectively (Kramer and Kozlowski 1960). Barr and Pellet (1972) noted that roots produced at low soil temperature were whiter, more succulent, thicker and had fewer lateral roots than those produced at higher temperatures. In the present experiments roots of trees grown in the glasshouse were finer than those of field or tube trees. This may have resulted from the combined effects of temperature, the different growth media, the confinement of the container of glasshouse trees, and perhaps also differences in the watering and feeding regimes.

6.8 Branching Habit

The branching habit is another character which can be greatly modified by the environment. In the glasshouse under 24hour light straight stemmed seedling oak with few side branches can be produced (Schwabe 1976). Glasshouse conditions thus reduced the number of branches, moreover branches tended to be longer than in the other two environments. Field trees had the greatest degree of branching i.e. number primary branches per 10cm stem length and number of secondary branches (Table 3B.12). Boyer and South (1984) suggested that tree form in the glasshouse - seedling Loblolly pine grown in the greenhouse were taller, more slender and less branched than those grown outside - will be modified by a combination of several factors, such as temperature, light quality and quantity and also lack of mechanical stimulation.

Tube trees had a greater total number of branches than field trees but the number per 10cm of main stem was reduced. Further, branches tended to be thin and short and often distorted, particularly where they were pressed against the inner surface of the tube. Tuley (1985) noted that side branches inside the shelter tended to die producing a straight, branch-free stem (1.2m high).

6.9 Shape of Main Stems and Diameter Growth

Tree trunks tend to grow as cylinders below the crown and like a cone within the crown. The shape of the trunks of tube and glasshouse trees were similar, both showed less taper as was also observed in sheltered trees by Tuley (1982b). Hormone as well as carbohydrate supply are involved in determining the potential of the cambium, and there is a fairly extensive literature on this, but the environment at the cambium can modify the response of the cambium to physiological messages from elsewhere (Worrall 1980). In the field wind stress may have triggered hormone reactions that induced more radial growth and less elongation (Grace 1977).

Trees prevented from swaying make less diameter growth than those allowed to sway (Kramer and Kozlowski 1960). Stem diameter was reduced in tube trees, this may represent a serious disadvantage of tube trees as this may make the trees more prone to breaking if not fully supported once the tube is removed. However once the tree had emerged from the top of the tube height growth decreased and stem diameter increased. This is similar to the effect of thinning of plantations when crown width increases and height growth decreases. Changes after

thinning lead to increased production and basipetal flow of carbohydrate and hormonal growth regulators, eventually leading to a more tapered stem (Kramer and Kozlowski 1979).

The reduced light intensity in the tube probably did not affect stem diameter since shading had no significant effect on this character. However higher day/night temperature (30°C/12°C) did increase radial stem growth. In beech 50% of the variation in diameter growth was caused by variation in maximum temperature and soil moisture, relative humidity was the third most improtant factor (Kramer and Kozlowski 1960).

Roussel (work quoted by Le Donssal 1975) found that oaks which had had their stems protected from lateral illumination for 3 years were nearly three times the height of those grown in full lateral light. Roussel hypothesised that lateral light passes through the bark to the secondary meristem destroying or inhibiting auxins thus curbing growth. The length of cells in protected stems was not altered so the additional height was the result of an increase in number of wood cells in a longitudinal direction.

The effect of field, tube and glasshouse environments on wood structure, in particular the number of vessels/mm^2 and vessel diameter were unclear, perhaps due to the small sample size. There was some tendancy for tube trees to have fewer larger vessels. However, both 24hour light and gibberellic acid application decreased the number of vessels/mm^2 and increased vessel size.

Other aspects of wood anatomy e.g. fibres, were not examined in this study. The wood of fast grown Eucalyptus grandis was similar to that of slower grown trees with respect to density and fibre dimensions. However vessels were smaller and less numerous and the ray volume greater in fast grown trees (Bambar, Horne and Graham-Higgs 1982). Fast growth thus appears to have affected the physiologically active cells and not the mechanical cells.

The relative proportion of early- and late- wood in each ring of growth has an improtant effect on the quantity and quality of wood products (Kramer and Kozlowski 1960). Latewood formation is especially improtant because it replaces cavitated large diameter earlywood vessels in ring porous species such as oak (Roger and Hinckley 1979). Within the growth rates normally experienced in Britain there is little likelihood of serious effects on the physical and mechanical properties of the wood due to environmental conditions experienced during the very early growth period (Brazier 1985). Exceptionally

fast growth, with less than four rings per 25mm, can reduce toughness in ring-porous woods, but this reduction is usually small compared with the loss in strength of slowly grown wood, with twenty or more rings per 25mm. Vigouous growth of ring porous wood e.g. oak with a coarser and more uneven texture and greater hardiness is more difficult to machine and is less attractive for finishing processes, but it is stronger and can be more durable (Brazier 1985).

6.10 Practical Aspects

One of the chief problems with growing hardwoods e.g. oak, for timber is the time required before harvesting. Exotic conifers planted in Britain require only 50 years to mature and theoretically yield 18cu.m. of wood per ha. whereas oak may take 150 years to grow and yield only 4-6cu.m. per ha. (Mills 1983).

This study compared the effect on growth of tube shelters and the glasshouse environment, also the effect of additional treatments, in particular extending the photoperiod, and the application of gibberellic acid. Increases in growth that can be obtained under experimental conditons i.e. by increasing light and temperature suggest that the growth of oak under field conditions is below its full potential (Farmer 1975).

Within the forest situation seedlings are at risk from damage by mammals, particularly deer and rabbits, unless protected by an adequate fence. Newly planted seedlings may make poor growth for the first few years, they have to compete with surrounding vegetation e.g. for light and space. Field grown trees also tend to be more branched e.g. than those within tube shelters. Free growth i.e. allowing the crown to develop while suppressing height can increase the diameter of selected trees. Free grown oak trees are usually of low height and to obtain a satisfactory length of clean bole green prunning is essential (Jobling and Pearce 1977).

Tube shelters offer several advantages over growing oak in the field. Tube shelters not only reduce the susceptibility of young plants to predators but also increase height growth. This enables plants to outgrow ground vegetation and become established and free growing sooner. Once the plant has outgrown the shelter, which can occur in only one season, growth in height decreases but the tree still has protection to the lowest part of the stem e.g. from mammal damage or herbicide spray. The shelter itself may also help to support the tree, however should the shelter become damaged or be removed the

tree would require staking. Once the tree has grown out of the tube growth depends upon the ability of the tree to respond to the space available. With tube shelters wider spacing at planting is a possibility due to greater survival and increased growth rate (Lang-Brown 1985), however providing more space for growth does not necessarily produce better quality wood (Brazier 1985). There may be more growth of branches which would require pruning to ensure an adequate length of branch-free stem, wider spaced trees may be more exposed increasing the likelihood of mis-shapen stem, due to the formation of reaction wood. Problems such as shake on felling and splitting on sawing and drying may result (Brazier 1985).

The effects of transpiration are particularly serious to foresters, thousands of seedlings are killed after planting by drought before they are able to produce a new root system large enough to absorb water as rapidly as it is lost (Kramer and Kozlowski 1960). Without the high humidities associated with the tube a tree with decreased root relative to shoot may have reduced ability to survive drought conditions (Kozlowski 1976). It is unlikely that water deficits are experienced by tube trees particularly when the foliage is contained within the tube. Also experimental plants were always well watered and competition from weeds removed. Under forestry conditions competition with surrounding vegetation, particularly grass, has been shown to affect the growth and survival of trees in tubes, both are enhanced where there is good weed control (Davies 1985).

Once trees had grown out of the tops of the tubes some damage occurred to the stems as they rubbed against the edge of the tube shelter. This produces weakness and a possible site of infection. The tubes were also prone to splitting as the crown increased in size. Round shelters would not suffer from splitting, and problems with stem damage can be overcome by covering the sharp edges of the shelter, or by ensuring that the tree cannot move within the tube e.g. using foam rubber.

The glasshouse situation lends itself to easier manipulation of environmental conditions. Farmer (1980) noted that although seedlings grew more when the growing season was extended, for practical purposes this growth was either not required or of doubtful value in certain species e.g. yellow poplar, northern red oak, chestnut oak, given adequate nursery conditions. Rood, Daicos and Blake (1984) state that the silvicultural value of exogenous GA-application as a mechanism for growth acceleration will probably be greatest at times when tree

growth is limited by cultural factors. Also they suggest that it would probably be less costly than supplemental illumination in the greenhouse.

Twentyfour hour light does allow for the production of plant material over the winter months. Dormancy of oak seedlings can be broken with gibberellin, however maintenance of growth in the greenhouse over winter months requires additional procedures (Schoeneweiss 1963). Following the first flush of growth after breaking dormancy the seedligns become quiescent, possibly due to a photoperiodic effect (Schoeneweiss 1963).

The growth of planted seedlings is generally poor until they become established. It would therefore be an advantage to use larger seedlings with more fully developed root systems at the time of planting which may have better initial survival and early growth (Immel, Rumsey and Carpenter 1978). Production of seedlings in the greenhouse may provide such material, though taller seedlings would require staking. Seedlings would also have to be protected from deer and rabbit damage by enclosing in an appropriate fence. Before planting the lower branches of taller glasshouse grown seedlings could be removed to give the clean stem length required for timber production.

Increases in early shoot growth and leaf area investment by increasing temperature could be accomplished with low cost plastic greenhouses over nursery beds (Farmer 1975). Oak seedlings raised for 6 months under continuous light to an average height of 75cm, planted in spring withstood winter frosts. Bud break and growth in the following year were comparable to well established 2 year old plants in the field (Smith 1977).

Lang-Brown (1985) considered the cost of various alternative ways of planting broadleaves. Seedling trees could be planted within a deer and rabbit fence. Within such a fence tube shelters would not be required, thus fairly close Spacing 2mx2m (2000/ha) must be used to account for losses. Weeding would be required for at least 4 years and with growth not as great as within shelters, planting within deer and rabbit fencing is the most expensive method, particularly for areas under 3ha.

With tube shelters the spacing can be 3.5mx3.5m (816/ha). Where there is heavy pressure from cattle, sheep, there may have to be a stock fence. With the advantage of increased height growth and greater survival, together with easier weeding, it is probably cheaper, taking grants into account, and more effective to use shelters instead of a

fence with areas up to 15ha. (Lang-Brown 1985).

To produce larger seedlings within the greenhouse would require additional costs compared with growing a smaller sized transplant. More space would be required since seedlings are kept in the greenhouse for a longer period. There would be higher heating costs, particularly for the production of trees over the winter. Labour costs will be higher and there may be problems with pests and diseases. Glasshouse grown trees had a higher input of chemical pesticides.

The long term effects of accelerating the early growth of oak have yet to be examined. The use of tube shelters is still a relatively new technique in forestry. The effects on wood quality are still unknown. The microclimate within the tube shelter has been examined and the effect of temperature and photoperiod and GA_3 application studied.

Further information is required to elucidate exactly how the tube shelter is acting to increase growth, further examination of the effect of each environmental factor e.g. temperature, light intensity, humidity, CO_2 and also those factors not measured directly e.g. wind. Detailed studies of carbohydrate metabolism, perhaps including the use of C^{14}, and water relation studies may yield useful information. The growth of trees within the tube may also help to increase knowledge of hormonal relationships within trees e.g. through its effects on 'apical control'.

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