AGRONOMIC AND PHYSIOLOGICAL STUDIES ON THE EFFECT OF RSWO411 ON EVENING PRIMROSE.

by

Christopher David Collins

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Wye College
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England.

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ABSTRACT

In three years of trials the effect of the triazole plant growth regulator, RSW0411, on the evening primrose crop was investigated. In first year field trials chemical application post-bolting gave a significant yield increase on a high density direct sown crop. This yield increase was considered to be a consequence of improved light penetration to the more mature, higher yielding, pods lower in the canopy. This theory was supported when no yield increase following chemical application was recorded in a widely spaced transplanted crop, where light was considered not to be limiting. In these initial trials no conclusive evidence was found for an optimum application rate of the PGR and no nitrogen x PGR interaction was observed. RSW0411 was seen to have similar effects on evening primrose as PP333 another triazole plant growth regulator which has been more thoroughly investigated.

In a second year of field trials inconclusive results were obtained. When RSW0411 was applied at a range of post-bolting timings to a high density transplanted crop no yield differences were observed. However, when the chemical was applied to a spring drilled crop non-significant yield increases were recorded. The differences in response to the chemical between the two crops are proposed to result from differences in chemical uptake resulting from the restricted root network of the transplanted crop.

In the final research year a glasshouse trial was undertaken to investigate the effect of RSW0411 on the flowering pattern of the crop; differences had been observed in the two preceeding field years. In this experiment RSW0411 was seen to promote the flowering of evening primrose following application. This produced an increase in pod weight at final harvest, because treated plants had more mature pods. The promotion of flowering was thought to be a result of effect of RSW0411 on gibberellic acid metabolism.

With carbon 14 studies the assimilate partitioning of evening primrose was investigated. Leaves were shown to be the chief sources of assimilate throughout the life cycle. Carbon 14 assimilated before flowering was recovered from the pods at final harvest, emphasising the need for good crop husbandry from an early stage of the season. Some evidence was gathered from these experiments to suggest that there was a repartition of assimilate from the stem to the pods in plants treated with RSW0411.

The implications of the results for the mode of action of RSW0411 on the evening primrose crop and for future agronomic improvements of the crop are discussed.

This thesis is dedicted to Fran Herbert,
a friend I lost too early.

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Thanks also to mom and dad for always being there and not being mean with the readies. Anne also deserves much affection for continually maintaining my humour with her stupidity. Finally thanks to all the friends who make life worth living.

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CHAPTER 1

Literature review

1.1 Literature review

1.1.1 Evening primrose agronomy

Evening primrose *Oenothera spp.* is a combinable break crop that came to the attention of U.K. farmers during the early eighties (Anon,1984). With a gross margin of £670 ha^{-1} compared with £495 ha^{-1} for an average crop of winter wheat for feed (Nix, 1984) the crop offered a chance for diversification with a good financial return. Today the financial advantage is less attractive, but still significant (Evening primrose £550 ha^{-1}, winter wheat for feed £430 ha^{-1}, winter wheat for milling, £500 ha^{-1}) (Nix, 1989). The crop is a rich source of gamma linolenic acid (G.L.A.), c. 12.5% of the oil by volume, which has been promoted for its relief from the symptoms of such diverse conditions as atopic eczema, pre-menstral tension, alcohol withdrawl and multiple sclerosis (Graham, 1984). However, the National Health Service has not granted a licence for the use of evening primrose oil in the treatment of any of these conditions.

Evening primrose is in the family Onagraceae and is a member of the genus *Oenothera*. Present agricultural cultivars resemble *O. biennis*, L. or *O. erythrosepela*, Borbas. The plant is an annual to perennial herb with spirally arranged leaves that terminate in a long, leafy flowering spike. Flowers have four yellow, overlapping petals and usually open in the evening and last for one or two days. The pod is fused to the stem and has four loculi containing seed. These seeds are small, the one thousand seed weight is only 0.4g.

Little academic work exists on the agronomy of the evening primrose crop with most of the information coming from the farming press, fact sheets from oil companies and seed merchants. This work has been reviewed by Dodd (1988) and only a brief synopsis is given here. The crop can be either direct sown or transplanted. Direct sowing is best carried out between late July and early August into a seedbed with a fine tilth. If the seed bed is cloddy the very small seeds are unable to establish a good contact with the soil which is vital for the uptake of water and hence germination. The seedbed at the optimum time for sowing is often dry, and therefore difficult to prepare, which is probably the reason for the many reported crop failures (Anon, 1985a). Sowing in the wetter spring and autumn is not viable because the soil temperatures are too low. Hayward (1985) using *O. spp.* cv. Traditional, found germination dropped from 74% to 59% when soil temperature was reduced from 20°C to 15°C in a controlled growth room experiment.

Once established the crop forms a rosette and it overwinters in this condition. Because of this growth habit the crop is susceptible to weed competition until bolting occurs (Dodd, 1988). Bolting is the processes of rapid stem extension that occurs in the spring, and is an equivalent process to jointing in cereals. Bolting is induced by cold and long days

(Vince-Prue, 1975), although Zeevart (1978) found the cold requirement could be overcome by the exogenous application of gibberellic acid. In both summer sown and autumn transplanted crops bolting takes place in the first week of May. This would suggest a daylength requirement of approximately 15 hrs.. For its cold requirement to be satisfied the plant needs temperatures of below 10°C (personal data). Spring transplanted crops bolt later; a crop transplanted in mid-May bolted in late June.

Flowering commences five to six weeks after bolting and lasts for up to six weeks; sometimes a second short flowering period has been observed in late September. The flowers are usually self fertilised and this often occurs before the flower has opened. The ovules, which are situated at the base of the flower stalk, swell to form the pod which is then allowed to mature.

Sidestem extension is obviously dependent upon plant density. In the work here it was noted that at lower densities (5 plants m^{-2}) sidestems extended from the base of the stem. In the higher densities (> 60 plants m^{-2}) sidestems extended from just below the flowering spike and their extension coincided with the start of flower production.

When pods in the middle of the main flowering spike start to dry and the seed within them becomes dark brown, the crop is either swathed or desiccated. This usually takes place in mid-September with crops established in the preceding year, with combining taking place a fortnight or so later. With spring sown crops this process is delayed. In one report (Howie, 1987) a spring established crop was not combined until Christmas week.

The work of Dodd (1988) found no conclusive advantages of desiccation over swathing. In one season, which had a warm and wet autumn, the crop in swath was easily re-wetted compared to the upright desiccated crop. This lead to the rotting of the swathed plants and subsequent loss of yield. In the following season, which had a drier autumn, there were no yield differences between desiccated and swathed treatments. Seed from the desiccated crop, however, had a very high moisture content, because of the higher moisture content (80%) of the uncut stems. This would increase the drying costs of a desiccated crop.

Agrochemical inputs to the crop are low with 40 kg N ha^{-1} providing adequate nutrition when P and K are kept at maintenance levels (Efamol, 1986). Early reports (Anon, 1984) suggested higher nitrogen levels only encouraged vegetative growth without increasing seed yield and the research work of Dodd (1988) failed to propose a more definite recommendation for nitrogen application.

The most common herbicide programme for use in the evening primrose crop, is the incorporation of trifluralin pre-drilling with bentazone post-emergence (Anon, 1985b). No specific timing has been recommended for bentazone, but post-bolting applications are unnecessary because the crop is then sufficiently competitive to smother weeds and

bentazone temporarily checks this growth (Dodd, 1988). The crop is relatively disease free although powdery mildew (*Oidium spp.*) and a condition resembling virus yellows have been observed, the former preventing production in the western U.S.A. (Walker, 1985). A condition referred to as 'stem stunt' which kills the mainstem apex promoting the growth of side shoots which may themselves become 'stunted' later, has also been observed. No data are available on the causal agents of the virus yellows and stem stunt.

1.1.2 The need for crop manipulation.

The crop was chosen for growth regulator studies for several reasons:

It is very tall (upto 1.5 m) and previous studies had shown it to be susceptible to lodging. The stem shortening properties of the anti-gibberellin plant growth regulators may combat this problem.

The breeding programme is relatively new and the use of plant growth regulators may give a shorter route to a desirable plant structure.

The plants physiology has not been previously investigated and plant growth regulators will enable some aspects of this to be investigated, most notably alterations resulting from a temporary interference with GA metabolism.

1.1.3 The Triazoles

The triazoles are a new group of compounds showing promise as plant growth regulators. Chemicals from the triazole group are widely used in agriculture as fungicides and plant growth regulators (PGR). Some of the PGR's have been shown to have fungicidal activity (Fletcher, Hofstra and Gao, 1986; Froggat, Thomas and Batch, 1982; Luib, Kohle, Hoppner and Rademacher, 1987). Lenton (1987) in his review of triazoles discussed the similarities between the fungicides and PGR's of this group. He described the PGR's as 'racemates' (consisting of a mixture of dextrorotatory and laevorotatory isomers), the enantiomers of which split into those with predominantly plant growth regulatory activity, (S) enantiomers, and those with fungicidal activity, (R) enantiomers (Fig. 1.1.). Enantiomers are optical isomers, one enantiomer being the mirror image of the other. Usually they contain a carbon atom bearing four different substituents, this is known as the chiral centre. The enantiomers for both triapenthenol (Lurssen, 1987) and paclobutrazol (Sugavanam, 1984) have been described. Paclobutrazol is in fact a diasteroisomer having two chiral centres.

The plant growth regulatory activity of these compounds derives from their ability to block the pathway for gibberellin (GA) biosynthesis. More specifically they fill the binding site of ent-kaurene oxidase preventing it reacting with the normal substrate, thus blocking the transformation of ent-kaurene to ent-kauronic acid (Lenton, 1987). Several other groups of regulators have been shown to act at this site (Fig. 1.2).

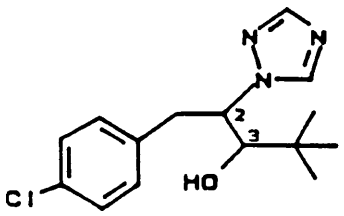
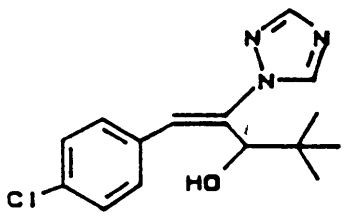
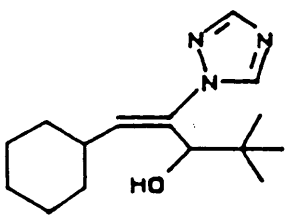
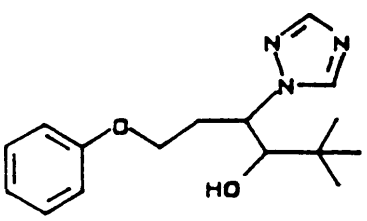
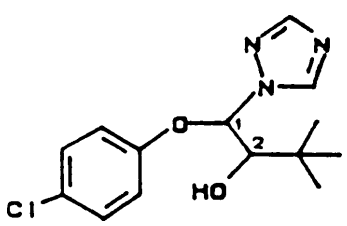
Structure	Common name and manufacturer	Stereoisomers
	Paclobutrazol (PP 333) ICI	(2*RS*,3*RS*)
	Uniconazol (S 3307) (XE 1019) Sumitomo	*RS*-*E*
	Triapenthenol (RSW 0411) Bayer AG	*RS*-*E*
	——— (BAS 111) BASF	Not known
	Triadimenol Bayer AG	80%(1*RS*,2*SR*) 20%(1*RS*,2*RS*)

Figure 1.1 - Structures of some of the recently developed triazole plant growth retardants and the fungicide triadimenol, from Lenton (1987).

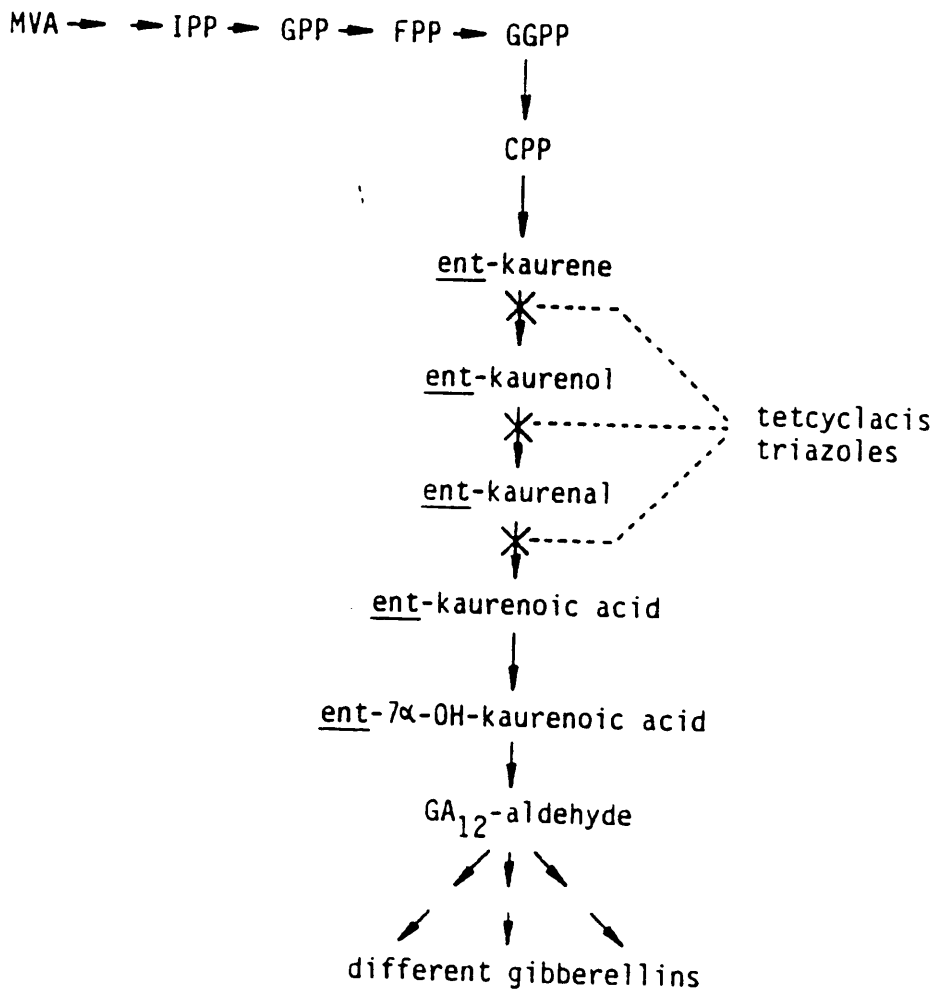


Figure 1.2 - Site of inhibition of GA synthesis taken from Rademacher, Fritsch, Graebe, Sauter and Jung (1987). (MVA = mevalonic acid, IPP = isopentenyl pyrophosphate, GPP = geranyl PP, FPP = farnesyl PP, GGPP = geranylgeranyl PP, CPP = copalyl PP)

The movement of triazoles has been the subject of much work. Sterret (1985) followed the movement of 14-C paclobutrazol using pressure injection into *Malus domestica*, only 23% of 14-C activity was in the shoot displaying growth inhibition. Quinlan and Richardson (1986), also using labelled paclobutrazol on apple, found acropetal movement when applied to young stem internodes and, to a lesser extent, from the youngest unrolled leaf, but none from mature leaves. Wang, Sun and Faust (1986) dipped mature leaves of apple in a solution of paclobutrazol with a surfactant, following gas chromatography they found no paclobutrazol in the stem or roots. Foliar applications of triazoles have shown differential effects in monocotyledons and dicotyledons. Lurssen and Reiser (1987) found growth inhibition in dicotyledons following either foliar or root application of triapenthenol, whereas monocotyledons were only strongly retarded by root applications. These results can be accounted for by the acropetal transport of triazoles in the transpiration stream via the xylem which has been reported by several workers (Lever, 1986; Richardson and Quinlan, 1986; Shearing and Batch, 1979). Foliar applications on monocotyledons do not therefore reach the growing apices as they are positioned in the leaf bases.

Lever (1986), working with paclobutrazol on apple, suggested that a pool of growth retardant was available in the vascular system behind the apex and that this reservoir was better maintained from root and stem applications, there being no reserve from foliar applications. This reservoir theory was supported by the ability of triazole compounds to be vascularly bound and the work of Sterret (1985), who working with labelled compound, found the 14-C activity after 27 days co-chromatographed with paclobutrazol. These factors suggest there was very little metabolism of the compound.

Jaggard, Lawrence and Biscoe (1982) recorded a reduction in cell division and cell elongation when plant cells grown in a suspension culture were bathed in a medium containing 20 $\mu g\ ml^{-1}$ of paclobutrazol, this effect was also recorded by Shearing and Batch (1982). These findings are consistent with the observed morphological effects of triazole applications discussed below.

The most profound effect of these chemicals is the reduction in plant height with small doses, compared with previous PGR's such as chlormequat, causing large reductions in plant height (Menhennett, 1984). Another advantage of the triazoles is that even when used at high rates they rarely cause severe phytotoxicity, although there have been reports of leaf curl (Davis and Sankhla, 1987) and an interference with gravitropic responses at higher concentrations (Forster, Buchanauer and Grossman, 1980). The reduction in plant height is usually observed as a result of decreased internode length (Wood, 1984; Wample and Culver, 1983; Steffens, Byun and Wang, 1985). Other morphological changes recorded following triazole application include reduced stem weight (Wample and Culver, 1983; Steffens *et al.*,

1985; Bausher and Yellonsky,1986), and reduced leaf area (Steffens *et al.*, 1985; Sankhla, Davis, Upadhyaya, Sankhla, Walser and Smith, 1985; Wood, 1984; Jaggard *et al.*, 1982; Lurssen and Reiser, 1985). The reduction in leaf area has often been recorded without a concomitant reduction in leaf weight thus giving rise to a higher specific leaf weight in treated plants. The number of leaves was unaffected unless high concentrations were used in which case it was reduced (Sankhla *et al.*, 1985; Braun and Garth, 1986), leaf retention has also been observed (Child, Butler, Sims, Johnson and Thorn , 1987). Iwahori and Tominga (1986) working with kumquat (*Fortunella crassifolia*) and Lamont (1986) working with wax flowers (*Chamalaucium uncinatum*, Schauer.) found no effect of triazoles on shoot number, but Child *et al.* (1987) and Hack and Lembrich, (1985) working with oilseed rape (*Brassica napus*) found significant increases. Such increases have been found with other anti-gibberellin plant growth regulators (Koranteng and Mathews, 1982). Cartwright and Waddington (1982) and Hampton and Hebblethwaite (1985a), working with spring barley (*Hordeum vulgare*) and a *Lolium perenne* seed crop respectively, observed an increased number of fertile tillers as a result of reduced apical dominance. In treated plants the reduction in apical dominance provided more assimilate to the tillers of a lower hierachy.

The reversibility of the effects of triazole PGR's by GA is not conclusive. Some workers found that application of GA completely reversed the effect of the regulator (Dalziel and Lawrence, 1984; Rademacher, Jung, Graebe and Schwenen 1984; Wample and Culver, 1983; Jung, Luib, Sauter, Zeech and Rademacher, 1987). Lurssen and Reiser (1985), however, found this reversal incomplete and ascribed their results to the effect of triapenthenol on sterol biosynthesis. The effect on sterol biosynthesis is a product of the fungicidal properties of the triazole PGR's. Grossman, Nitsche, Sauerbury and Jung (1985) suggested the interference with sterol biosynthesis reduced cell extension at lower concentrations and cell division at higher concentrations.

A dark green colour is often observed on crops following application of these chemicals. Jaggard *et al.* (1982) thought this was a result of increased chlorophyll content. Wample and Culver (1983) and Sankhla *et al.* (1985) also found an increase in chlorophyll content by fresh weight. Dalziel and Lawrence (1984) proposed that this increase came from two factors; an expansion of the mesophyll, more notably the pallisade mesophyll, making the leaves thicker and an increase in the leaves chlorophyll content per unit area. It is not known if this is a biochemical or a 'concentration' effect.

Triazole PGR's have often been associated with reduced water consumption (Lurssen and Reiser, 1987; Lurssen, 1987; Dalziel and Lawrence, 1984). Fletcher and Nath (1984) found soil applied triademefon increased yields of *Glycine max* and *Pisum sativum* under drought conditions in a controlled growth room. Using the same chemical on *Phaseolus*

vulgaris, Asare-Boamah, Hofstra, Fletcher and Dumbroff (1986) observed a reduced transpiration and an increase in abscisic acid (ABA) concentration in stressed and non-stressed treated plants. Lurssen (1987) proposed triapenthenol was increasing the ABA concentration, however, working with paclobutrazol Norman, Bennet, Poling, Maier and Nelson (1986) found a reduction in ABA concentration. Dalziel and Lawrence (1984) concluded that such reduced water consumption was primarily a consequence of reduced leaf area, but Lurssen and Reiser (1987) found reduced water consumption per unit leaf area. Expressing these results per unit leaf weight may be more meaningful. Wample and Culver (1983) also found reduced water consumption per plant with paclobutrazol when applied to sunflowers (*Helianthus annuus*), but because there was no effect on leaf diffusive resistance they concluded that the reduced water consumption was a product of reduced leaf area. They therefore proposed that paclobutrazol be sprayed to conserve moisture only when the biomass was unimportant, because of the chemical's effect on shoot weight, or when the leaf area index was below 2, because once the crop canopy was closed paclobutrazol would not reduce water use as the evapotranspiration per unit area was not reduced by the chemical.

Izumi, Nakagawa, Kobayashi, Oshio, Sakurai and Takahashi (1988) investigating uniconazole-P, found no effects on ABA concentration, but did observe increases in several cytokinins, and proposed that this may have been the reason for their previous observations of increased flowering in woody plants and changes in sex expression in cucurbit (*Cucurbita maxima*)(Oshio and Izumi, 1986). Cytokinins have been reported to act positively in flower bud formation (Zeevaart, 1978). Gibberellins have, however, inhibited flowering in woody angiosperms and promoted male tendency in cucurbit (Pharis and King, 1985).

One of the reservations concerning widespread use of the triazoles is their persistency in the soil. Lever (1986) reported the soil persistency of paclobutrazol to be of the order of 3-12 months, whereas Hack and Lembrich (1985) found no effect on crops grown five months after the application of RSW0411. This would not, however, be a problem in continuous cereals.

1.1.4 Field trials

In field trials triazoles have often given yield increases (Child, Arnold, Hislop, Huband and Stinchcombe, 1985; Child *et al.*, 1987; Jung *et al.*, 1987; Hack and Lembrich, 1985; Froggat *et al.*, 1982). Froggat *et al.*, (1982) applied paclobutrazol to winter wheat and found yield increases that were positively correlated with the degree of lodging control afforded by the chemical, however, only small increases in yield were recorded in the absence of lodging. Scarisbrick, Addo-quaye, Daniels and Mahamud (1985) recorded yield increases of 16.9% in oilseed rape following application of paclobutrazol in the early winter. Using labelled carbon these results were related to increased assimilation in, and assimilate movement to, the upper

canopy (Addo-Quaye, Daniels and Scarisbrick, 1985), but they were not repeated in proceeding years. Scarisbrick *et al.* (1985) noticed that the dense canopy produced by spring application of paclobutrazol, because of reduced branch lengths, increased fungal attack and late spring application caused abscission of immature pods. Hampton and Hebblethwaite (1985a) found increases in yield for grass seed production following application of paclobutrazol. This was primarily due to lodging control but these workers also recorded increased root production throughout the profile and an increase in leaf area duration. Work with labelled CO_2, (Hampton and Hebblethwaite, 1985b) found increased assimilate demand by the ear in treated plants. These plants had more seeds per spikelet which increased the sink strength of the ear.

Jung *et al.* (1987) working with BAS111000W, found 11% yield increases in barley, and 15% in oilseed rape. The increases in barley yields were principally a result of lodging control. For oilseed rape these workers suggested a multifactorial process in which chemical application resulted in a more upright canopy less susceptible to lodging with improved light penetration, the delayed senescence of older leaves increasing photoproductivity and stimulation of root growth giving better utilization of water and nutrients. This lack of specificity of effect induces some cynicism in the reader.

Hack and Lembrich (1985) using RSW0411 at 500-750 g a.i. ha^{-1}, recorded yield increases in oilseed rape, rice and field bean. The chemical decreased plant height in all crops. This conferred lodging resistance which was the chief factor in the significant increase in rice yields when the chemical was applied at the two node stage. With beans sprayed at flowering treated plants gave increased yield because of increased numbers of pods. Application to oilseed rape when the crop was 30cm high increased the number of side branches and the total number of pods which resulted in a yield increase of over 1 t ha^{-1} in one trial year and 0.4 t ha^{-1} in another. Child *et al.* (1985) working with BAS111000W and RSW0411 on oilseed rape found 20-30% increases in yield with spray application at bolting, flowering or branch extension; yield increases were lower in those plots receiving a full fungicide programme, which suggests some of the yield increase results from the fungicidal affect of the chemical. These workers also compared spray methods; a coarse spray in a large volume compared to a fine spray electrostatically charged, but found no treatment differences. Child *et al.* (1987) found reduced stem height and branch lengths following RSW0411 application. The variable affected was extending at the time of application. As a consequence of this early treatments gave a dense canopy and later treatments a more open canopy. This is supported by the data of Scarisbrick *et al.* (1985) and Hack and Lembrich (1985). Child *et al.* (1987) recorded a yield increase in oilseed rape associated with

treatment. However, in this experiment combining was delayed and there were large losses due to pod shatter. Such conditions would favour the treated plants because of their delayed senescence and higher number of pods on later formed branches.

CHAPTER 2

Field trials 1985/6.

2.1. General introduction

Hack and Lembrich (1985) had found applications of RSW0411 on oilseed rape before stem extension produced the largest yield increases, but Child *et al.* (1987), also working with oilseed rape, obtained yield increases with applications as late as branch extension. The results of Hack and Lembrich (1985) had also proposed the recommended dose of 700g ha^{-1} which had been recommended by Bayer at the start of these trials (Bluett, pers. comm.) and has been used by subsequent workers (Child *et al.*, 1987; Bolton and Adam, 1987).

As a result of the lodging control conferred by plant growth regulators they have been used to increase yield by enabling increased nitrogen applications (Herbert, 1983). In field trials, evening primrose had not given any significant yield response to nitrogen (Dodd, pers. comm.), but these crops had lodged. Kachi and Hirose (1983) reported that a critical plant size was required for the bolting of evening primrose, and that plant size was increased by nitrogen application. Thus in the first year a wide range of trials were undertaken to investigate the effect of RSW0411 and nitrogen on aspects of the growth and development of evening primrose.

Experiment 1	The effect of application date of RSW0411 on a sown crop.
Experiment 2	The effect of application date on a transplanted crop.
Experiment 3	The effect of concentration of RSW0411 on a sown crop
Experiment 4	The nitrogen/RSW0411/nitrogen timing interaction.
Experiment 5	The effect of application date of PP333 on a sown crop.

These trials were designed to provide information on the optimum timing of application and application rate of RSW0411 on evening primrose. In these preliminary trials the physiological differences between sown and transplanted crops could also be investigated through their response to RSW0411.

Autumn nitrogen was specifically varied in the nitrogen trial as it was hoped that this would produce a larger overwintering rosette which would then bolt earlier in the spring.

Experiment 5 was included to compare paclobutrazol (PP333) another triazole PGR, with RSW0411. The reason for this was there is a much larger data bank on PP333, which would then be available for comparison with any results obtained here.

2.1.1 The effect of application date of RSW0411 on a sown crop (Experiment 1).

2.1.1.1 Materials and methods

The trial was carried out at Wye College on a brick earth soil (pH 7.8). The site had been ploughed after the removal of the previous horticultural crop and Treflan (480 g l^{-1} trifluralin, Elanco) was applied at the rate of 3l ha^{-1}, followed by discing and harrowing. On 18/7/85 the field was drilled with evening primrose, cv.Paul (Efamol)[1], at 3.5 kg ha^{-1}, using a Massey Ferguson cereal drill, with chicknuts added to the seed hopper for bulk. The site was then consolidated with a Cambridge roll. Basagran (480 g l^{-1} bentazone, BASF) was applied at 3 l ha^{-1} on 21/10/85 and 40 kg ha^{-1} N (Nitram 34.5% N) was broadcast by hand on 9/5/86.

RSW0411 (70% wettable powder, Bayer) was sprayed on five dates (Table 2.1), by a CO_2 pressurised knapsack sprayer at 2.0 bars using a tee-jet flat fan SS8002 nozzle at 700 g ha^{-1} (480 g a.i.) in 222 l ha^{-1} H_2O. T4 was a split application with 500 g ha^{-1} applied at each occasion. Bolting is defined as the time when stem elongation begins.

A complete, all treatments plus control, randomised block design was used, with four blocks. Each plot (treatment) was 12 x 3 m, with a plant density between 80 - 160 plants m^{-2}, because of variable establishment. The crop was established before the arrival of the experimenter to Wye College with two passes of the cereal drill at right angles to one another, so it is not possible to provide information on row widths and numbers. This is the case for all sown crops in this season. Sampling details are given in Table 2.2.

Sampling proceeded stepwise up the plot to maintain a uniform area for combine yield assessment (10m x 2.5m). At S1 two samples of 0.25 m^{-2} were taken from each plot to obtain an accurate measure of the background variation, but this was very time consuming and only one sample per plot was taken thereafter. All plants in the sample were analysed at S1, S2 and S3, at S4 a ten plant sub-sample was taken. Samples were dissected into their component parts in the laboratory, these were then dried for 48 hrs at 80°C. On 4/6 (S1a) the height of four randomly selected plants per replicate were measured in the field.

All recorded component numbers and component weights are expressed per plant. The term 'yield ratio' is defined as the total pod weight divided by the total plant weight. In a small experiment it was established that seed weight was c.50% of pod weight regardless of treatment. Therefore to arrive at an approximate harvest index the yield ratio should be divided by two.

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1 This variety was used in all subsequent experiments

Date	reference	growth stage	% ground cover *
2/4	T1	12 cm rosette	40
23/4	T2	12 cm rosette	40
12/5	T3	10 cm tall	75
2/5 + 20/5	T4	at bolting and 20 cm tall	60 and 100
3/6	T5	50 cm tall	100

* assessed by eye.

Table 2.1 - Application dates of RSW0411

Sample	Date	Variable
$S1_y$	26/5	plant density plant height number of mainstem leaves mainstem weight mainstem leaf weight
$S2_y$	30/6	plant density plant height number of mainstem leaves number of mainstem flower buds mainstem weight mainstem leaf weight sidestem weight
$S3_y$	20/8	plant density plant height number of mainstem flower buds number of sidestems number of mainstem pods number of sidestem pods mainstem weight sidestem weight
$S4_z$	18/9	plant density plant height number of sidestems number of mainstem pods number of sidestem pods mainstem weight sidestem weight mainstem pod weight sidestem pod weight

y - each sample was a 0.25 m^{-2} quadrat.
z - ten plant sub-sample taken from quadrat.

Table 2.2 - Measurements taken at each sample.

On 19/9/86 the crop was desiccated with Reglone (200 g l^{-1} diquat, I.C.I.) @ 2 l ha^{-1} in 450 l ha^{-1} H_2O, with 0.5 l cittowet, using 10.F.80 royal blue Lurmark tips @ 1.5 bars, when those pods in the middle of the mainstem were brown and mature, desiccation took place at this stage in all subsequent experiments. A double pass was used to improve penetration and crop cover. Plots were harvested on 29/9/86, using a Deutz plot combine with the air flow shut down and the concave at the rapeseed setting. Harvested plot yields were converted to t ha^{-1} dry weight of seed.

Covariance analysis was used on all data with density as the covariate.

'Covariance analysis operates on the premise that the various biological features of an experimental plot do not behave independently, but are often functionally related to each other, the analysis of covariance simultaneously examines the variances and covariances among selected variables such that the treatment effect on the character of primary interest is more accurately characterised than by the analysis of variance only.' (Gomez and Gomez, 1983)

Covariance analysis has three important uses:

1. To control experimental error and adjust treatment means.
2. To estimate missing data
3. To aid the interpretation of experimental results.

Density showed no significant differences between treatments, but did show a very wide range of values eg. at S1 the range was 60 => 300 plants m^{-2} (mean = 118 plants m^{-2}). For this experiment covariance analysis was employed for use number 1.

At S1 the efficiency of the covariance analysis was below 100% giving a worse description of the data for height and number of leaves than the standard ANOVA. For other variables covariance analysis improved the efficiency (Appendix 1). For the proceeding samples, the use of covariance analysis was valid for all components.

In all tables * and **, refer to the significance of the F-value at the 5% and 1% levels respectively. Where LSD's have been calculated without a significant treatment effect, such calculations should be ignored. Those LSD's calculated following a significant F-value are expressed at the 5% level. The LSD is calculated as the product of the standard error of the mean square and the tabular t-value using the error degrees of freedom.

2.1.1.2 Results

2.1.1.2.1 Plant height

Plant height was significantly reduced by treatment ($p<0.05$) (Table 2.3). Height differences were most pronounced in those samples taken soon after spraying, but were retained until S4. At S4 these differences were no longer significant, but the difference between the control and T4, and the control and T5 was greater than the LSD. No lodging was observed in any of the treatments.

2.1.1.2.2 Component numbers

Plants treated at T1 had a greater number of leaves ($p<0.05$) (Table 2.3), than the control at S1, but later treatments had fewer leaves ($p<0.05$). However, by S2 these later treated plants also had more leaves than the control, but these differences were not significant.

Flowering started on 1/6. The number of flower buds was increased by treatment at S2, although this was only significant for T5. This increase in flower bud numbers resulted in an increase in the number of mainstem pods at S3, which produced a highly significant ($p<0.01$) orthogonal contrast between treated plants and the control. Flowering was finishing at S3, hence the lower number of flowers and the increased CV%, with some plants flowering and others not. This variability could account for the lack of treatment differences.

The increase in total pods at S3 for T4 should be treated with caution, because of the large sidestem pod value of this treatment. At S4 flowering had finished and so the total number of pods recorded here would be those at final harvest, as subsequent pod abscission was not observed. There were no significant differences in the number of pods at S4.

The number of sidestems with the exception of T2 declined between S3 and S4. This variable was unaffected by treatment.

2.1.1.2.3 Component weights

Leaf dry weight followed the same pattern as number of leaves, later treatments were lighter at S1, but at S2 all treatments were heavier than the control (Table 2.4). When an orthog n l contrast was carried out between treated plants and the control for leaf weight at S2 it was highly significant ($p<0.01$). Mainstem dry weight increased from S1 to S4. Mainstem dry weight was significantly reduced by later treatments at S1 ($p<0.05$), but at later samples these differences disappeared. Sidestem dry weight was increased by T2 and

Component	Sample	Spray timing						lsd	sig.	CV%
		C	T1	T2	T3	T4	T5			
plant height (cm)	S1	29.8	28.2	24.0	21.8	18.4	--	2.85	**	12.7
	S1a	66.8	64.8	60.2	57.7	51.6	65.8	4.63	**	11.1
	S2	105.3	102.5	105.3	98.9	95.1	96.6	6.37	*	4.2
	S3	131.9	135.1	130.6	126.7	122.4	120.6	9.30	*	4.8
	S4	151.4	148.2	146.1	147.4	140.4	141.9	9.10	ns	4.2
mainstem leaves	S1	17.7	18.9	16.1	16.5	16.1	--	0.12	*	15.5
	S2	27.3	30.5	30.3	31.4	29.8	32.3	3.53	ns	7.6
mainstem flowerbuds	S2	3.11	3.48	3.88	3.85	3.96	5.58	1.24	*	20.2
	S3	0.33	0.45	0.43	0.24	0.50	0.34	0.29	ns	47.9
mainstem pods	S3	15.3	18.9	18.4	19.6	20.2	19.2	4.14	ns	14.0
	S4	28.1	25.8	27.1	28.1	30.0	33.1	9.18	ns	20.4
sidestem pods	S3	4.6	4.3	1.5	1.3	11.1	5.1	3.29	ns	95.3
	S4	7.5	4.9	8.0	3.9	6.7	5.0	6.83	ns	72.5
total pods	S3	19.9	23.2	19.9	20.9	31.3	24.3	8.08	*	21.8
	S4	35.9	30.7	35.1	32.0	36.7	38.1	11.50	ns	21.2
sidestems	S3	1.99	1.53	1.40	1.86	3.26	2.47	1.56	ns	47.6
	S4	1.64	1.46	2.29	0.86	1.61	1.57	1.57	ns	64.1

Table 2.3 - The effect of application time of RSW0411 on component numbers per plant.

Component	Sample	Spray timing						lsd	sig.	CV%
		C	T1	T2	T3	T4	T5			
mainstem	S1	1.71	1.76	1.45	1.53	1.41	--	0.31	ns	18.9
leaf	S2	1.88	2.33	2.20	2.19	2.14	2.37	0.48	ns	14.2
mainstem	S1	0.98	1.11	0.71	0.67	0.58	--	0.19	*	22.7
	S2y	5.43	6.60	6.48	5.67	5.10	6.17	1.40	ns	15.2
	S3	11.1	11.4	9.90	10.8	11.4	9.10	3.10	ns	18.6
	S4	17.1	14.3	15.1	13.5	14.9	16.4	4.50	ns	19.1
sidestem	S2	0.13	0.18	0.34	0.17	0.17	0.24	0.11	**	35.1
	S3	1.05	0.88	0.38	0.53	2.27	1.29	1.44	ns	84.7
	S4	5.79	4.47	6.97	2.94	6.11	4.16	5.52	ns	69.6
mainstem pods	S4	4.55	3.97	3.95	4.15	4.56	5.16	1.52	ns	22.1
sidestem pods	S4	0.95	0.74	0.90	0.50	0.74	0.58	0.91	ns	79.2
total pods	S4	5.50	4.71	4.85	4.65	5.30	5.74	1.66	ns	20.7
total	S1	2.70	2.77	2.17	2.20	1.99	--	0.47	*	19.4
	S2	7.43	9.10	9.02	8.03	7.41	8.78	1.91	ns	14.7
	S3	12.2	12.3	10.3	11.4	13.7	10.5	4.10	ns	22.2
	S4	22.9	18.0	22.1	16.4	20.0	20.6	6.21	ns	20.5

y - From S2 the plant was divided into mainstem and sidestems.
Mainstem weight and sidestem weight include their respective pod weights

Table 2.4 - The effect of application time of RSW0411 on component dry weight
All weights are expressed as g plant $^{-1}$.

T5 at S2, but these increases were not maintained. Despite the drop in the number of sidestems between S3 and S4 sidestem dry weight increased in this period. There were no treatment effects on pod weights.

The differences recorded in component weights at S1 were reflected in the total weights, where T2, T3 and T4 were lighter than the control and T1 ($p<0.05$). Total plant dry weight was significantly reduced at S1 ($p<0.05$) by the later spray applications, but these differences were not shown at subsequent samples. Plant dry weight increased most rapidly between bolting and S2 (0.16 g plant^{-1} day^{-1}). It continued to increase between S2 and S4, but at a lower rate (0.06 g plant^{-1} day^{-1}).

2.1.1.2.4 Yield

Final yield data demonstrated significant increases in seed yield ($p<0.05$). T3, T4, T5 were all greater than the control (Table 2.5). Yield ratio (pod dry weight/total dry weight) showed a similar pattern to that of yield, later treatments (T3, T4 and T5) being significantly greater ($p<0.05$) than the control.

Component	Spray timing						lsd	sig.	CV%
	C	T1	T2	T3	T4	T5			
Yield	0.912	0.918	0.904	1.032	1.018	1.024	0.06	*	7.5
Yield ratio	0.227	0.231	0.225	0.247	0.246	0.247	0.01	*	3.9

$$Yield ratio = \frac{total pod weight}{total plant weight}$$

From data at S4

Table 2.5 - The effect of application time of RSW0411 on seed yield (t ha^{-1}) and yield ratio.

2.1.1.3. Discussion

In previous studies with other crops Hack and Lembrich (1985) have shown a reduction in height with RSW0411, and this was supported by the results here. The decreases in the number of leaves and stem weights of T2, T3 and T4 at sample 1 were most likely a consequence of reduced plant height, but these differences were not found at subsequent harvests. The numerical increase in leaf number at S2 may have been due to leaf retention. Child *et al.* (1987) had also observed this phenomenon when working with RSW0411 on oilseed rape.

Sidestem dry weight was increased by T2 and T5 at S2. Such differences disappeared at later samples. Sidestem number was unaffected by treatment. Iwahori and Tominga (1986) and Lamont (1986) also found little effect on sidestem number when they applied paclobutrazol to kumquat and wax flowers respectively. At S2 several large values for sidestem weight were recorded for T2 and T5, even though the plant density of the samples was not significantly different. In each case the sample was comprised of several large plants with large sidestems, plus a number of smaller plants without sidestems. Covariance analysis, with density as the covariate, would not account for this type of variability, this may also have been the reason for the large sidestem pod value for T4 at sample 3 and was the reason for the high CV's associated with sidestem measurements throughout the season.

Between S3 and S4 sidestem dry weight increased despite a decrease in the number of sidestems. The reason for this apparent conflict was the die back of the smaller sidestems in the unfavourable positions lower in the canopy and the continued growth of those larger ones in the upper canopy.

A numerical increase in the number of flower buds was associated with treatment at S2. By S3 these differences had disappeared, but at this time flowering was finishing (grand mean for flower buds at S3 = 0.384, i.e. less than one flower bud per plant). The increased number of mainstem pods for treated plants at S3 was probably a result of the greater number of flower buds on these plants at S2. At S4 only T4 and T5 had a greater number of mainstem pods than the control, but these differences were not significant.

Sidestem pods at S4 comprised of 20% of the total pod weight. Such pods would be less mature, and hence have a higher moisture content, than those of the mainstem due to their later development, so the contribution to seed yield is likely to be less than 20% .

Yield increases were shown by the later timings. However, the increased production of flower buds of these treatments at S2 may not be be the reason for this increase as there was no significant increase in mainstem pod weight or pod number in these treatments at S4. It is

possible that the pods of these later treatments may have been more mature, as these later treatments had increased numbers of pods at S3. Such advanced maturity would not be reflected in pod weight, because the older pods and seeds were starting to dry at S4.

The yield ratios of T3, T4 and T5 were significantly different from the control and showed a similar pattern to yield (Table 2.5). These two variables also had a low CV (7.5% and 3.9% respectively). On a plot scale it is proposed that there were significant differences in total pod weight but that these were masked by the variability associated with subsamples (N.B. Pod weight was recorded only at S4, ie 10 plant sample, CV = 22%).

Child *et al.* (1987) found increased yield following the application of BAS0411 to oilseed rape. This was a result of an alteration in the canopy structure of the crop. The later sprays shortened the late formed top branches, without reducing numbers of pods on them. This gave better light penetration through the canopy to earlier formed pods increasing their photosynthetic rate compared to control and early sprayed treatments, leading to increased seed weight. It is suggested that the same process is occurring in this experiment and this would be supported by the increased yield ratios discussed above. Advanced pod maturity as a consequence of a different pattern of flower production may or may not be part of this process.

2.1.2 Effect of appplication date of RSW0411 on a transplanted crop (Experiment 2).

2.1.2.1 Materials and methods

On 1/8/85 seed was scattered onto a firm compost (5 shovels of grit + 1 bale of peat +1 bag bio seed mix additive) in Plantpak seed trays, a thin layer of compost was then sieved on top of them. Trays were watered and placed in a glasshouse cubicle (set at 20°C day, 17°C night). At the cotyledon stage, 4/9/85, these plants were transplanted into 4.5 cm Jiffy pots containing potting compost (8 shovels of grit + 1 bale of peat + 1 bag Bio potting compost mix additive). When plants were approximately at the 15 cm rosette stage (10/10/85), they were transplanted by hand into the field to give a stand of 5 plants m^{-2}.

Basagran was applied at 3 l ha^{-1} on 14/4/86, however this had little effect, so blocks 1 and 2 were hoed on 4/6/86. Nitrogen (Nitram, 34.5% N), 40 kgN ha^{-1}, was broadcast by hand on 10/4/86.

The spray programme for RSW0411 was similar to experiment 1 (section 2.1.1.1), with application taking place upon the same dates; although the rosette size of the crop in this experiment was greater at T1 and T2. A randomised complete block design with four blocks was used. Each plot (treatment) was 12 x 3m, with 7 rows per plot with a row width of 40cm. One sample was taken mid-season on 29/7/86, using five randomly selected plants from each plot. Plots were desiccated as before and combined on 3/10/86.

2.1.2.2 Results

The chemical had very little effect on plant height (Table 2.6). As no lodging was observed in any of the treatments any lodging resistance conferred by the chemical could not be assessed. The number and weight of sidestems and the number of sidestem pods were also unaffected by treatment. The numbers of mainstem flowers showed no treatment effects, but the number of mainstem pods did appear to be improved by treatment. However, an orthogonal contrast of treated plants against the control did not improve the significance of this result. Other variables measured displayed no trends or differences.

Final seed yield was also unaffected by treatment. No differences in block yields were recorded, despite the differences in the weed control programme between the blocks.

Component	Spray timing						lsd	sig.	CV%
	C	T1	T2	T3	T4	T5			
plant height (cm)	134.0	133.7	128.7	137.2	136.3	132.0	7.33	ns	3.5
sidestem number	22.9	24.8	21.5	23.1	19.6	23.8	4.77	ns	14.2
mainstem flower bud number	12.0	8.1	14.3	11.3	15.3	13.6	7.79	ns	41.7
mainstem pod number	7.52	9.49	9.93	9.96	8.30	10.25	4.88	ns	34.5
mainstem weight	53.7	58.7	43.7	60.7	57.8	56.1	15.0	ns	17.0
sidestem pod number	180.4	186.1	171.1	174.9	177.8	196.9	65.2	ns	23.0
secondary sidestem number	34.9	32.6	21.5	33.2	21.2	18.4	14.1	ns	33.4
sidestem weight	132.8	133.4	93.7	126.7	100.2	135.6	57.0	ns	30.1
total pod number	187.9	195.6	181.7	184.8	186.1	207.2	62.9	ns	21.5
seed yield (t/ha^{-1})	0.59	0.59	0.68	0.54	0.62	0.63	0.10	ns	11.5

Table 2.6 - Effect of application time of RSW0411 on plant components (numbers are total per plant, weights total g per plant) at a mid-season sample and final seed yield.

2.1.2.3 Discussion

One of the notable features of the results in this experiment were the lower CV's associated with the sidestem variables, conversely the CV's for mainstem variables increased compared with experiment 1. The lower sidestem variables CV's are the result of having a fixed density and the increased CV's for mainstem variables a consequence of only sampling five plants from each plot. Overall however, RSW0411 had very little effect on the transplanted crop.

In experiment 1 it was suggested that the yield increase was a result of changed canopy structure, allowing better light penetration to the pods. The transplants had a much more open structure because of the lower plant density (5 plants m^{-2} c.f. 100 plants m^{-2} with the direct drilled crop), with several of the sidestems coming from the base of the plant. Pods were not visibly shaded and no increase in light penetration would be achieved by shortening the sidestems as light was not limiting in the canopy.

The yield of the transplanted crop was upto 0.5 t ha^{-1} less than the drilled crop. This could be a result of the lower plant density. Dodd (1988) when experimenting with density wheels found a reduced pod weight m^{-2} when populations were below 15 plants m^{-2} in one year and below 30 plants m^{-2} in another. The density of this crop was below both these values.

It is therefore concluded that RSW0411 produces a yield increase where it can improve the light penetration to the reproductive structures. It cannot achieve this in a widely spaced transplanted crop. The wide spacing also reduces seed yield, but to increase the density would increase labour costs which would probably not be offset by the any yield increase. Commercially the transplanted crop is therefore best employed where its shorter growing season fits in with the management system. It may, however, have a role to play in reducing the variability of future experiments.

2.1.3 Effect of concentration of RSW0411 on a sown crop (Experiment 3).

2.1.3.1 Materials and methods

The crop was established and received the same inputs as in experiment 1 (section 2.1.1.1).

RSW0411 was sprayed on two dates, 2/4/86 (T1) when plants were at the rosette stage, and 2/5/86 (T2), when plants were just bolting. Three concentrations; 350 g ha^{-1}, 700 g ha^{-1} and 1000 g ha^{-1} were applied at each date. Thus a 2 x 4 factorial design was created with four blocks. The spray was applied @2.0 bars using a tee-jet flat fan SS8002 nozzle in 220 l H_2O ha^{-1}. Plot size was 12m x 2m.

Height measurements were taken for four randomly selected plants in each plot on the following dates; S1 (6/6/86), S2 (28/7/86) and S3 (9/9/86).

The crop was desiccated as before (section 2.2.1) and plots were combined on 4/10/86.

2.1.3.2 Results

Height at S1 was significantly reduced ($p<0.01$) by the high concentrations. At S2 and S3 no significant differences were observed, but shorter plants were associated with the higher concentrations of RSW0411 (Table 2.7). Timing of chemical application had no effect on measured variables. No lodging was observed in any of the treatments so any lodging resistance conferred by RSW0411 could not be assessed.

Yield was not significantly affected by chemical concentration, however a numerical decrease in yield was associated with treatment (Table 2.8).

sample	timing	Application rate g ha^{-1}				lsd_a	lsd_b	sig.	CV%
		0	350	700	1000				
S1	T1	66.4	64.8	60.2	57.7	4.2	4.7	**	1.2
	T2	67.1	65.7	51.6	63.8				
S2	T1	128.6	123.6	127.6	124.4	8.7	9.4	ns	1.7
	T2	128.5	128.3	119.6	117.1				
S3	T1	148.7	150.4	149.6	144.1	9.3	10.5	ns	0.9
	T2	149.2	152.6	146.3	141.5				

a - lsd comparing all treatments.
b - lsd comparing treatments at the same timing.

Table 2.7 - Effect of application rate and timing of RSW0411 on plant height (cm).

	Application rate g ha^{-1}				lsd	sig.	CV%
	0	350	700	1000			
Yield	0.86	0.79	0.79	0.76	0.09	ns	10.6

Table 2.8 - Effect of spray concentration of RSW0411 on seed yield (t/ha^{-1}).

2.1.3.3 Discussion

The lack of a permanent significant reduction in plant height was not expected considering the high concentrations that were used in this trial (upto 1000 g ha^{-1}). However, in experiment 1 (section 2.1.1.2.1) significance was also lost at later samples, despite more recordings being taken per plot (approximately 25). The numerical decrease in seed yield associated with treatment contrasts with the increase that was observed in experiment 1. The sprays here were applied earlier than for experiment 1 (T3 = 12/5 T5 = 3/6), in which these later sprays increased yield. Therefore such differences may be accounted for by inopportune application of the chemical in this instance.

Although no optimum concentration can be recommended from these results, the higher concentrations of RSW0411 did reduce plant height. Therefore it is suggested that these concentrations would alter plant structure. An application rate of 700 g ha^{-1} has been recommended for other crops (Hack and Lembrich, 1985). Therefore to avoid phytotoxicity and the increased cost of the chemical that would occur with the 1000 g ha^{-1} and higher application rates, it is proposed that future experiments use the 700 g ha^{-1} concentration.

2.1.4 Effect of RSW0411, nitrogen and timing of nitrogen (Experiment 4).

2.1.4.1 Materials and methods.

The site was cultivated and received the same herbicide programme as in experiment 1 (section 2.2.1). There were four nitrogen levels; 0 kgN ha^{-1}, 20 kgN ha^{-1}, 40 kgN ha^{-1} and 80 kgN ha^{-1}. The nitrogen (Nitram, 34.5% N) was broadcast by hand on three dates; 4/9/85 (D1), 18/9/85 (D2) and 2/10/85 (D3) to give a 4 x 3 factorial experiment of a complete randomised block design with three blocks. Covariance analysis was used for data at S1 and S2 with density as the covariate, however, at S3 and S4 there were significant treatment effects on density which prevented its use as a covariate.

In the spring all plots received a top dressing of 40 kgN ha^{-1}, with the time interval between treatments maintained. The first application was on 17/3/86. Plants were in the rosette stage for both the autumn and spring applications.

RSW0411 was applied on 12/5/86, when plants had just begun to bolt, using a compressed air knapsack sprayer @ 2.0 bars using tee jet flat fan F80 nozzles at 700 g ha^{-1} in 222 l ha^{-1} H_2O. A split plot design was thus created.

Four samples (0.25 m^{-2}) were taken through the season; S1 (8/5/86), S2 (10/6/86), S3 (14/8/86) and S4 (12/9/86).

Main plot size was 2m x 4m. Sampling proceeded step wise up the plot to maximise the area for combine yield assessment. At S1 the growth regulator had not been sprayed so the data were analysed as a 4 x 3 factorial design. At S1, S2 and S3 all plants in the sample were examined, but at S4 due to the limits of time a ten plant sub-sample was taken. A more detailed growth analysis was undertaken of the plots receiving autumn application of 80 kgN ha^{-1} and 0 kgN ha^{-1}. At S3 the 20 kgN ha^{-1} and 40 kgN ha^{-1} treatments were subdivided into mainstem and sidestems and dry weights of these components taken, the number of sidestems was also recorded. At S2 and S4 only the total sample weight of these treatments was recorded (Table 2.9).

The crop was desiccated as before and all plots combined on 4/10/86 using a Hege 125B plot combine.

sample	date	variable	sample description
S1	8/5	plant density shoot weight root weight	A
S2	10/6	total sample weight plant density number of leaves plant height leaf weight stem weight	A B
S3	14/8	plant density plant height number of sidestems sidestem weight mainstem weight number of mainstem pods number of sidestem pods total number of pods	A B
S4	12/9	total sample weight plant density plant height number of sidestems number of mainstem pods number of sidestem pods mainstem weight sidestem weight mainstem pod weight sidestem pod weight	A B

All plants from the sample were analysed except for S4 B, where a ten plant sub-sample was used.

A - all treatments sampled.

B - all timings and growth regulator treatments of 0 and 80 kgN ha^{-1} sampled.

Table 2.9 - Component measurements taken at each sample.

2.1.4.2 Results

2.1.4.2.1 Plant height

Plants had not bolted by S1, but by S2 plots sprayed with RSW0411 were significantly shorter than the control ($p<0.05$). The growth regulator treated plants were still shorter at S3, but the difference was no longer significant, and this trend was maintained at S4 (Table 2.10). Nitrogen and timing of nitrogen had no effect on height or time of bolting. ~~Timing of chemical application had no effect on measured variables~~. No lodging was observed in any of the treatments so any lodging resistance conferred by RSW0411 could not be assessed.

2.1.4.2.2 Component numbers

Leaf number was only measured at S2 when the nitrogen x PGR interaction was significant 80 kgN - > 80 kgN + ($p<0.05$) (Table 2.17). The number of mainstem pods was unaffected by treatments. Numbers of sidestem pods and the number of sidestems gave a significant ($p<0.01$) interaction between nitrogen and timing at S3 (Table 2.11). The differences in the number of sidestem pods increased the total number of pods (Table 2.15). The number of flower buds was significantly reduced by the later timing of nitrogen at S3 ($p<0.05$) (Table 2.12). The number of sidestems generally declined between S3 and S4 (Grand mean S3 = 3.78, S4 = 2.76). This decline appeared to be less rapid for growth regulator treated plants (Table 2.13). The increased number of sidestems for PGR treated plants at S4 increased other sidestem variables (Table 2.13). However, it should be noted that the number of stunted plants was also increased by PGR treatment (Table 2.13).

2.1.4.2.3 Component weights

The root weight of those roots that could be retrieved was measured at S1 when no treatment differences were found (Table 2.16 and Table 2.18). Leaf weight showed no differences between treatments at S2 and was not measured thereafter. Sidestem weight was unaffected by treatment at S3, but at S4 growth regulator treated plots had significantly ($p<0.01$) heavier side stem weights compared to untreated plots (Table 2.13) and heavier sidestem pod weights ($p<0.01$). At S3 significant nitrogen x timing interactions were recorded for mainstem weight, sidestem weight and total weight (Table 2.16). Total pod weight and mainstem pod weight per plant did not differ significantly between treatments.

2.1.4.2.4 Yield

Nitrogen gave a numerical increase in yield with increasing application rate. D2 gave a significant increase in yield ($p<0.05$) compared with D1 (Table 2.14). Application of

Sample	Growth regulator		lsd	sig.	CV%
	+	-			
S2	45.10	55.49	2.63	*	6.8
S3	132.10	135.90	5.87	ns	8.9
S4	152.31	154.87	7.21	ns	7.2

Table 2.10 -Effect of RSW0411 on plant height (cm).

Sample	Nitrogen	Timing of nitrogen			lsd	sig.	CV%
		D1	D2	D3			
S3	0(40)	19.7	8.6	5.1	7.00	**	94.7
	80(40)	9.5	14.2	12.1			
S4	0(40)	10.8	11.0	12.6	11.9	ns	68.5
	80(40)	12.7	6.8	16.2			

Table 2.11 - Effect of nitrogen (kgN ha^{-1}) and its timing on number of sidestem pods per plant.

Sample	Timing of nitrogen			lsd	sig.	CV%
	D1	D2	D3			
S3	3.85	3.35	2.32	0.83	*	27.6

Table 2.12 - Effect of nitrogen timing on number of flower buds per plant.

Component	Sample	RSW0411			sig.	CV%
		+	-	lsd		
sidestem number	S3	3.29	3.91	1.04	ns	48.3
	S4	3.28	2.24	0.85	ns	51.9
sidestem pod number	S3	11.2	11.9	7.9	ns	94.7
	S4	16.1	7.3	5.8	**	68.5
sidestem weight	S3	7.17	2.35	2.4	ns	35.9
	S4	1.69	0.75	5.4	**	60.7
sidestem pod weight	S4	1.61	0.80	7.5	*	84.4
density	S4	88.0	104.4	14.4	ns	20.9
stunt	S4	17.8	7.8	0.07	**	72.6

Table 2.13 - Effect of RSW0411 on sidestem variables, density and stunt.(weights are g per plant, density plants m^{-2}, stunt expressed as percentage of total plants, numbers are total per plant)

	Autumn nitrogen kgN ha^{-1}				lsd	sig.	CV%
	0	20	40	80			
Yield	0.74	0.73	0.74	0.78	0.08	ns	19.5

	Application time			lsd	sig.	CV%
	D1	D2	D3			
Yield	0.72	0.80	0.73	0.07	*	19.5

	RSW0411		lsd	sig.	CV%
	+	-			
Yield	0.74	0.76	0.08	ns	19.5

Autumn nitrogen	RSW0411		lsd_a	lsd_b	sig.	CV%
	+	-				
0	0.71	0.78	0.13	0.14	*	19.5
20	0.82	0.65				
40	0.75	0.75				
80	0.70	0.86				

a - lsd between treatments, except

b - lsd at same level of nitrogen

Table 2.14 -Effect of nitrogen and RSW0411 on final seed yield (t ha^{-1}).

Component	Sample	Application time						lsd	sig	CV%
		D1		D2		D3				
		0	80	0	80	0	80			
plant density (m^{-2})	S1	118.8	122.8	130.8	77.2	145.2	104.0	86.8	ns	41.3
	S2	129.2	146.8	128.0	154.0	166.0	118.0	49.2	ns	24.3
	S3	84.8	100.0	104.0	88.0	150.8	109.2	36.8	ns	27.0
	S4	90.8	96.8	93.2	97.2	122.0	78.0	26.0	*	20.9
plant height (cm)	S2	50.3	55.2	51.1	47.7	48.9	48.6	7.6	ns	6.8
	S3	136.2	135.7	136.4	136.3	126.8	134.6	14.4	ns	9.0
	S4	150.3	153.2	148.9	151.0	152.3	148.8	16.5	ns	10.3
mainstem leaf	S2	18.7	20.1	20.2	18.4	19.1	19.6	2.1	ns	7.2
mainstem flower buds	S3	3.90	3.79	3.18	3.50	2.36	2.31	0.87	ns	30.0
mainstem pods	S3	15.8	14.6	17.4	17.4	14.3	12.7	6.5	ns	23.4
	S4	22.8	23.7	22.2	19.1	20.1	23.0	9.9	ns	32.4
sidestem pods	S3	19.7	9.5	8.6	14.2	5.1	12.1	7.1	**	94.7
	S4	10.8	12.7	11.0	6.8	12.6	16.2	11.9	ns	68.5
total pods	S3	35.4	24.0	26.1	31.6	19.3	24.9	7.8	*	45.4
	S4	33.6	36.4	33.2	26.0	32.7	39.2	10.1	ns	31.4

Table 2.15 - Effect of nitrogen and timing of nitrogen on component numbers per plant.

Component	Sample	Application time						lsd	sig	CV%
		D1		D2		D3				
		0	80	0	80	0	80			
root	S1	0.31	0.35	0.29	0.30	0.32	0.39	0.12	ns	21.8
mainstem	S1	1.95	1.94	1.76	1.68	1.82	2.41	0.77	ns	23.2
	S2	2.17	2.31	1.94	1.86	2.01	2.41	0.50	ns	25.5
	S3	13.3	10.0	12.2	12.8	9.1	11.0	3.58	*	29.6
	S4	17.9	17.8	17.2	14.4	15.0	19.1	5.12	ns	23.8
leaf	S2	1.74	1.73	1.68	1.75	1.79	2.18	0.39	ns	17.6
sidestem	S3	3.02	1.72	2.00	3.02	1.26	2.59	1.71	*	83.7
	S4	3.45	3.89	3.00	2.03	3.96	4.22	3.23	ns	71.9
mainstem pod	S4	3.35	3.24	3.28	2.66	2.83	3.52	1.56	ns	39.3
sidestem pod	S4	1.17	1.37	0.99	0.67	1.40	1.64	1.34	ns	39.3
total pod	S4	4.51	4.61	4.27	3.33	4.23	5.16	1.35	ns	39.0
total	S1	1.95	1.94	1.76	1.68	1.82	2.41	0.77	ns	23.2
	S2	4.06	4.05	3.62	3.63	3.84	4.57	0.85	ns	20.0
	S3	16.2	11.7	14.2	15.8	10.3	13.6	4.7	*	35.9
	S4	21.4	21.7	20.2	16.4	19.0	23.3	6.5	ns	26.5

Table 2.16 - Effect of nitrogen and timing of nitrogen on component weights. (weights are in g per plant, mainstem weight sidestem weight are inclusive of their respective pod weights).

Component	Sample	0		80		lsd_a	lsd_b	sig	CV%
		+	-	+	-				
plant	S1	131.6		101.2		49.2	--	ns	41.3
density (m^{-2})	S2	142.4	140.0	151.2	128.0	37.6	35.2	ns	24.3
	S3	108.8	117.2	99.2	99.2	29.2	29.2	ns	27.0
	S4	97.2	106.4	78.8	102.8	20.8	20.4	ns	20.9
plant height (cm)	S2	46.5	53.8	43.8	57.2	4.9	3.7	ns	6.8
	S3	130.8	136.2	131.2	137.5	11.5	12.0	ns	8.9
	S4	148.6	152.9	150.1	153.1	13.1	14.0	ns	10.3
mainstem leaves	S3	19.5	19.2	18.4	20.3	1.5	1.4	*	22.1
sidestems	S3	3.29	4.20	3.23	3.92	1.21	1.32	ns	36.5
	S4	3.27	2.41	3.29	2.08	1.45	1.47	ns	51.9
mainstem flower buds	S4	3.07	3.23	2.86	3.53	0.85	0.98	ns	30.0
mainstem pods	S3	15.3	16.4	13.3	16.5	4.48	3.69	ns	23.4
	S4	23.4	20.9	21.7	22.1	7.60	7.25	ns	32.4
sidestem pods	S3	10.6	11.7	11.7	12.2	8.87	11.23	ns	94.7
	S4	15.0	8.0	17.1	6.7	8.89	8.24	ns	68.5
total pods	S3	25.9	28.0	25.0	28.6	9.87	12.56	ns	45.4
	S4	37.4	28.9	38.8	28.9	9.57	10.83	ns	31.4

a - lsd for comparing treatment means
b - lsd for comparing treatment means at the same level of nitrogen

Table 2.17 - Effect of nitrogen and RSW0411 on component numbers per plant.

Component	Sample	0		80		lsd_a	lsd_b	sig	CV%
		+	-	+	-				
root	S1	0.31		0.35		0.07	--	ns	21.8
mainstem	S1	1.84		2.01		0.45	--	ns	23.2
	S2	2.04	2.04	1.88	2.51	0.45	0.57	ns	25.5
	S3	11.5	11.4	10.7	11.8	3.1	3.4	ns	27.5
	S4	13.8	13.3	14.3	13.2	3.4	3.3	ns	23.8
leaf	S2	1.85	1.63	1.79	1.98	0.32	0.34	ns	17.6
sidestem	S3	2.30	1.89	2.38	2.50	1.68	1.94	ns	83.7
	S4	2.89	1.67	3.55	1.42	1.84	1.76	ns	71.9
mainstem pod	S4	3.04	3.27	3.16	3.12	1.25	1.27	ns	39.3
sidestem pod	S4	1.46	0.90	1.76	0.70	1.07	1.04	ns	84.4
total pod	S4	4.50	4.18	4.91	3.82	1.45	1.74	ns	39.0
total	S1	1.84		2.01		0.45	--	ns	23.2
	S2	3.99	3.69	3.66	4.51	0.75	0.84	ns	20.0
	S3	13.8	13.3	13.1	14.3	4.4	5.0	ns	35.9
	S4	16.7	14.9	17.9	14.6	4.1	4.3	ns	26.5

a - lsd for comparing treatment means
b - lsd for comparing treatment means at the same level of nitrogen

Table 2.18 - Effect of nitrogen and RSW0411 on component weights (g plant^{-1}).

RSW0411 produced a non-significant reduction in yield. The nitrogen x pgr interaction was also significant ($p<0.05$). The application of RSW0411 increased yield at the 20 kgN ha^{-1} application rate, but depressed yield at the 0 and 80 kgN ha^{-1} application rate. These later results show the difficulty in interpreting interactions.

2.1.4.3 Discussion

Plant height was significantly reduced by application of RSW0411 at the earlier samples, but significance was lost as the plant compensated later in the season. This finding is in agreement with the previous experimental results in this chapter. Scarisbrick *et al.* (1985) had also observed compensation when PP333 was applied to oilseed rape. Nitrogen had little effect on plant height. This finding is consistent with that of Dodd (1988) who found only a temporary difference in height, when investigating the effect of spring applied nitrogen.

Many of the differences that were reported in the results section can be related to population differences within the quadrat. These differences arose from the use of a cereal drill, which is not adapted for use with such a small seed as evening primrose, and the heavy weed infestation in the autumn following drilling. Some plants were also killed by septoria over the winter. This density effect was highlighted at S3 and S4, because treatment differences in density prevented the use of covariance analysis. The profound effect of density is illustrated by the highly significant regression analysis of number of sidestems against density (Appendix 2). When the results of Table 2.11 are viewed in conjunction with Table 2.15 the sidestem values can be seen to result from density differences between 0 kgN ha^{-1} D3 and 80 kgN ha^{-1} D3 at S3 and S4. At S2 the difference between these treatments was only slightly smaller than the LSD. Also no trends could be seen between treatments for density, only that the 0 kgN ha^{-1} D3 was more dense than other treatments. It therefore seems likely that these differences were not a result of treatment, but existed before the experiment was imposed (see Appendix 3).

The results of PGR application on sidestem variables at S4 are also products of density differences combined with an increase in stem stunt. Stunted plants promote the growth of sidestems as the plant compensates for the loss of the mainstem apex. At the same time the density of PGR treated plants declined from S3 to S4 especially in the 80 kgN ha^{-1} plus RSW0411 treatment (Table 2.17). Any plant death associated with treatment would be expected at S2 soon after spraying, or at the latest at S3. It seems therefore that most of the differences observed in sidestem variables as a result of treatment are in fact a result of the variable density within the trial site.

The variable density between treatments may also account for the reduction in the number of mainstem flower buds. In studies with wheat the number of floret primordia on the mainstem declined with increasing density (Zhen-Wen, Van-Sanford and Egli, 1988).

From the results it is suggested that the crop was unable to efficiently utilize autumn nitrogen. Any component differences were not maintained from one sample to the next. Even total plant weights and total sample weights were unaffected by autumn nitrogen application. Timing D2 did increase final seed yield ($p<0.05$), but there was no evidence from the samples to explain this. In fact at S4, D2 had the lowest pod weights of all the timings. However, it should be noted that at S4 only the 0 and 80 kgN ha^{-1} treatments were measured. It could therefore be possible that the 20 and 40 kgN ha^{-1} nitrogen levels were higher yielding for D2 than for other timings. Even if this were the case the result seems an anomaly as nitrogen itself did not produce a significant yield increase. The problems of interpreting the yield data can be seen from the results for the nitrogen PGR interaction in Table 2.14.

These findings are analagous to results recorded for oilseed rape and wheat. M.A.F.F. (1985) recommended 200 Kg N ha^{-1} for winter rape with all applied before spring growth on heavy soils and a fifty/fifty split on light soils. Winter wheat has also been shown not to require autumn nitrogen (Widdowson, Penny, Derby and Bird, 1984) and this crop has a total recommendation of 250 kgN ha^{-1} depending on the soil type and soil nitrogen index. It is possible that the autumn application here was too late and the crop was unable to use the nitrogen, which was then leached before spring. This may also be the reason that no plant height differences were associated with nitrogen application. A spring no nitrogen treatment would have been a useful addition to the experiment to investigate any leaching effect.

Kachi and Hirose (1983) found an increase in biological yield with nitrogen application on evening primrose (*O. erythrosepala*). However, these workers were investigating a dune system. Dodd (1988) found increases in biological yield when nitrogen was applied to transplanted crops, with restricted root systems, and an increase in seed yield with a late nitrogen application to a high density crop. From these results it would appear that a positive response to nitrogen application in evening primrose is only observed in conditions of low nitrogen availability. The nitrogen levels in the soil were probably too high to observe any nitrogen response.

As a consequence of these results growth regulator application rarely interacted with nitrogen application and where it did effects were not sustained. Application of RSW0411 did increase sidestem pod weight and sidestem weight at S4 dramatically. This was a result of the growth regulator treated plots having a lower density and an increased incidence of stunt at S4. RSW0411 decreased plant height as found in previous experiments. This height reduction was significant at the harvest directly after application, but was not significant thereafter. This finding is also in agreement with previous results.

2.1.5 The effect of application date of PP333 on a sown crop (Experiment 5).

2.1.5.1 Materials and methods

Site preparation, herbicide programme and N application were as for experiment 1 (section 2.1.1.1).

PP333 was sprayed on five dates using a compressed air knapsack sprayer @ 2 bars, using tee-jet flat fan F80 nozzles at 187 g ha^{-1} in 225 l ha^{-1} H_2O [2]. T3 was a split application with 125 g ha^{-1} sprayed on each occasion (Table 2.19).

A randomised complete block design was used with four blocks. The height of four randomly selected plants in each replicate was measured on 24/6/86 (S1a) and three samples were taken (Table 2.20). A sample included all plants within a 0.25 m^2 quadrat.

Plot size was 2m x 5m and sampling was stepwise up the plot as in previous experiments. All plants in a sample were analysed and blocks were completely sampled. At S3 a ten plant sub-sample was taken because of the limits of time.

The crop was desiccated as before and harvested using a Hege 125B plot combine on 8/10/86. The area combined was 5m x 2m, allowance being made for sampled areas.

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2 This concentration was suggested following preliminary experiments on evening primrose at I.C.I. (T. Jones, pers. comm.).

date	ref.	growth stage	%ground cover
3/4	T1	12cm rosette	40
17/4	T2	12cm rosette	40
17/4 + 28/5	T3	12cm rosette/ 35cm tall	40/100
7/5	T4	10cm tall	80
28/5	T5	35cm tall	100

Table 2.19 - Application dates of PP333.

Sample	Date	Crop condition
S1	4/6	bolting rapidly, flower buds visible
S2	27/8	flowering coming to a close, maturing pods
S3	24/9	flowering finished, lower pods brown and beginning to shatter

Table 2.20 - Sampling details of experiment 5.

2.1.5.2 Results

2.1.5.2.1 Plant height

Significant differences in plant height were recorded at samples 1,2 and 3. Sample 1a was not significant, which is suggested to be a consequence of the lower number of plants in each replicate. T3 the split timing produced the largest reduction in plant height followed by T4 and T5. No lodging was observed in any of these treatments, so any lodging resistance conferred by PP333 could not be assessed.

2.1.5.2.2 Component numbers

The number of leaves was only measured at S1, when there was a slight, but non-significant increase in the number of leaves on plants of the later sprays compared to those of the control (Table 2.21). The number of sidestems was not affected by treatment at S1, but at S2 the number of sidestems was increased by treatment at T3 and reduced by treatment at T5 compared to the control. The number of mainstem pods was significantly reduced ($p<0.01$) by the later sprays (Table 2.21) and this was reflected in the significant difference in the total number of pods at this sample. The production of sidestem pods was faster than that of mainstem pods in all treatments between S2 and S3. The number of sidestem pods appeared to be correlated to the number of sidestems, those treatments with more sidestems had more sidestem pods. At S3 there were no differences in the number of pods between treatments.

2.1.5.2.3 Component weights

At S1 the mainstem weights of the earlier sprayed treatments were lighter, although not significantly, than the control (Table 2.22). Mainstem weight was significantly affected by treatment at S2, with T4 and T5 being lighter than the control ($p<0.01$). Only T4 was noticeably lighter than the control at S3, but this was not significant. Although all treated plants were lighter than the control an orthogonal contrast of treated v. control was not significant. Sidestem weight was unaffected by treatment. Pod weights of individual treatments were in the same ranking order as the number of pods recorded for those treatments at S3 (Table 2.21) and average pod weight was unaffected by treatment.

2.1.5.2.4 Yield

All plants had a higher yield ratio than the control (Table 2.23), an orthogonal contrast of treated plants v. control was significant ($p<0.05$). Yield was not effected by treatment, although most treated plots showed improved yields.

Component	Sample	Spray timing						lsd	sig.	CV%
		C	T1	T2	T3	T4	T5			
height	S1	67.5	56.5	57.0	54.0	55.8	55.4	5.12	**	5.9
	S1a	82.5	73.9	75.2	75.0	82.4	82.4	13.79	ns	1.9
	S2	137.9	139.8	120.5	119.4	126.7	126.7	13.08	*	6.7
	S3	155.6	154.2	141.7	140.3	143.4	143.4	12.35	*	5.4
mainstem leaf	S1	24.7	24.5	24.7	27.1	25.8	25.3	2.61	ns	8.2
sidestems	S1	0.61	0.81	0.45	0.93	0.87	--	0.83	ns	71.4
	S2	3.19	3.64	3.40	4.68	2.87	2.27	1.09	*	20.7
	S3	2.37	2.69	1.48	1.42	2.54	2.28	1.19	ns	44.3
mainstem pods	S2	22.2	25.9	21.5	22.9	16.4	16.8	3.3	**	10.0
	S3	27.1	28.0	28.3	30.7	23.9	27.9	8.6	ns	20.0
sidestem pods	S2	0.51	0.49	0.64	0.94	0.71	0.32	0.5	ns	51.1
	S3	11.0	12.9	9.9	6.4	12.1	13.2	8.9	ns	52.5
total pods	S2	22.7	26.4	22.1	23.8	17.1	17.1	3.4	**	10.1
	S3	38.2	40.9	38.3	37.2	36.0	41.1	10.4	ns	17.2

Table 2.21 - Effect of time of application of PP333 on component numbers. (height cm, numbers are per plant).

Component	Sample	Spray timing						lsd	sig.	CV%
		C	T1	T2	T3	T4	T5			
mainstem	S1	7.75	5.80	6.69	6.91	7.53	7.06	2.42	ns	32.8
	S2	13.8	15.2	13.1	15.3	11.2	10.3	2.37	**	11.5
	S3	16.1	16.0	14.7	15.7	13.3	16.0	3.28	ns	13.8
sidestem pods	S3	1.10	1.38	1.06	0.62	1.25	1.37	1.12	ns	63.2
mainstem pods	S3	3.98	3.96	3.83	4.40	3.40	4.06	1.29	ns	20.9
total pods	S3	5.09	5.34	4.89	5.02	4.65	5.42	1.41	ns	17.8

Table 2.22 - Effect of application time of PP333 on component weights (g per plant).

Component	Spray timing						lsd	sig.	CV%
	C	T1	T2	T3	T4	T5			
Yield ratio *	0.38	0.40	0.41	0.41	0.42	0.41	0.04	ns	5.9
Yield (t ha^{-1})	0.87	0.89	0.98	0.86	0.98	0.91	0.14	ns	9.9

* Calculated from data at sample 3.

Table 2.23 -The effect of application time of PP333 on yield and yield ratio.

2.1.5.3 Discussion

The reduction in the mainstem weight by PP333 has been observed before (Steffens *et al.*, 1985 and Bausher and Yellonsky, 1986). Bausher and Yellonsky (1986) were working with potted apple plants, still found differences after five months. In the work described here it would appear that the plants overcame some of the chemical retardation as suggested by the results for plant height and mainstem weight. The significant increase in the number of sidestems for T3 at S2 was not observed at S3. In fact at S3, T3 had the lowest number of sidestems. This would suggest that the significant result at S2 was an anomaly created by sampling variation.

The lower pod numbers of the later treatments at S2 were probably a result of the retardation of these plants as illustrated by the mainstem weight. By S3 these differences had disappeared. Despite this delayed development, seed yield of treated plants was unaffected. In fact a numerical increase in seed yield was shown by the later treatments. Seed moisture was not significantly affected by treatment (Appendix 4) suggesting that the seed development itself was not retarded.

These results are comparable to those found in experiment 1 with RSW0411. Both chemicals caused an initial height reduction, an increase in leaf retention and yield increases with later sprays. It is suggested therefore that the two chemicals have a similar effect on the evening primrose crop.

2.2 General Discussion

From these preliminary experiments several conclusions can be drawn. Later, post bolting, sprays are the ones most likely to increase seed yield and this is thought to be as a result of increased light penetration to the mainstem pods. This hypothesis was supported by the absence of treatment effects in the transplanted crop where light was not a limiting factor, because of the much lower density of this crop. The application rate suggested by Bayer was supported by the results here. However, a note of caution should be taken as in the concentration experiment yield was depressed by PGR application as it was in experiment 4. Perhaps further experiments should be undertaken with application rate using later timings. Autumn nitrogen application did not affect yield. The most probable reason for this is that the plants were not in a phase of rapid growth following its application. Application in the summer of sowing is also unlikely to have an effect as it is more likely to promote the faster growing weeds. Thus it is suggested that in future experiments 40 kgN ha^{-1} is applied just prior to bolting when it is readily available to the plant in its fastest growth period. PP333 affected the evening primrose crop in much the same way as RSW0411.

By far the greatest problem with these experiments were the large CV's that were recorded especially with sidestem variables. This is particularly frustrating as it is the shortening of sidestems by the chemical which is the basis of the theory supporting the yield increase in experiment 1. Sidestem pod weight per unit of sidestem weight was not increased by treatment, neither was the sidestem weight to total weight ratio. It is therefore unlikely that yield increases were a result of increases in the number of reproductive sidestems or the repartition of assimilate from mainstem to sidestem as a result of applying RSW0411, as had been found by Hampton and Hebblethwaite (1985a) using PP333 on a ryegrass seed crop.

The CV's of sidestems were reduced when a fixed density was imposed upon the crop by using transplants and this may be the way forward in terms of the research of this project. The reduction in CV would then allow the measurement of such factors as sidestem length to be more meaningful. The CV's associated with mainstem variables were up to 25%. Although this figure is not unacceptable it would obviously improve the analyses if it could be reduced. It is not easy to suggest a sample size for future use, because many of the problems were created by different densities within the quadrat creating variability. Such variability would not necessarily be removed by increasing the sample quadrat area or using a larger number of plants. The number of plants within a sample varied between 10 and 30 and at the later samples only ten plants were sampled, because of the time taken to analyse a

plant when many variables are being measured. The most practical solution is therefore the use of transplants to reduce plant to plant variability. It is also suggested that in future more samples are taken within the periods of flowering and pod maturation.

Chapter 3

Field trials in 1987.

3.1 Introduction

Results from first year experiments had suggested that the plant-to-plant variability was reduced when a fixed plant density was imposed on the crop. In these preliminary trials, late, post bolting, applications of RSW0411 had promoted yield on high density crops (section 2.1.1.2.4). Thus, the main trial of the second year, experiment 6, was a high density transplanted trial in which post bolting applications of RSW0411 were investigated. The application times were chosen specifically to affect sidestem length and hence canopy structure. It had been observed in the previous year that sidestem extension in high density crops coincided with the commencement of flowering. The range of application times therefore started at this development stage.

In August 1986 a large field site of approximately 1 hectare, had been drilled. On this site it was intended to investigate the interaction of RSW0411 with applied spring nitrogen, but with a larger plot size than had been used in year 1, when the effect of autumn nitrogen was assessed. On this site, late applications of RSW0411 on the evening primrose crop were also to be investigated for their effects on yield and yield components. Large plot sizes were necessary to minimize variability when combining. With large plots variability in yield resulting from seed getting trapped in the 'guts' of the combine is reduced. Any error introduced from incomplete combining of the plots or the effects of neighbouring plots would also be reduced as a larger guard area can be left without affecting the accuracy of the yield calculation. Unfortunately establishment was very poor on this site as a result of residual herbicide damage and it had to be abandoned.

A smaller spring drilled site was established (experiment 7). A range of spray timings of RSW0411 were tested with this trial. From the results conclusions were drawn on the feasibility of spring drilling and the effect of RSW0411 on this physiologically different crop.

3.2 Experiment 6

The effect of timing of RSW0411 on the development and yield of a high density transplanted crop.

3.2.1 Materials and Methods

The trial was carried out on Burgate field, Wye College, on a heavy gault clay, pH 8.2. The site had been ploughed the previous autumn after the removal of the preceding cereal crop, it was harrowed in late March and rotovated on 10/4/87. Plants had been raised by a horticultural grower and were delivered on 6/5. Pelleted seed had been sown into paper pots (BS208 Plantpak) containing seeding compost (S.H.L. modular) eight weeks earlier. Seedlings were then kept in a glasshouse at 17 °C max, 15 °C min for four weeks, followed by two weeks at 10 °C and finally two weeks with no heating. A liquid feed (Nitram 25 g + potassium nitrate 100 g l^{-1}, total 23 g N l^{-1}, diluted 1:200) was applied weekly. The plants were transplanted by hand into the field to give a stand of 60 plants m^{-2}, row width 20 cm. Transplanting started on 11/5 and was finished by 15/5. An eight block trial was thus created with four plots in each block. Plot size was 2 m x 4 m. Nitrogen (Nitram, 34.5% N, I.C.I.) was broadcast at 40 kgN ha^{-1} on 9/6. The crop started to bolt on 26/6.

RSW0411 was sprayed on three dates (Table 3.1) @ 700 g ha^{-1} in 300 l ha^{-1} H_2O, @ 3.0 bars with orange F60 Lurmark nozzles using a Fox Motori 301 knapsack sprayer.

These three treatments plus the control gave a complete randomised block design, with eight replicates. Samples consisted of three adjacent 50cm rows from each plot, guard rows were always excluded. Plants were then taken for dissection (Table 3.2) in the laboratory where they were separated into normal, stunted and non-bolted plants. Non-bolted plants were those still in the rosette stage; at harvests S4 and S5 non-bolted plants also included some immature plants which had bolted, but had not produced pods. Only normal plants were analysed. No recordings were taken in earlier samples of those plots not yet treated with RSW0411.

To prevent the crop lodging, which had been previously experienced with a high density transplanted crop, blocks 5 to 8 were netted with pea and bean netting on 29/7. This proved invaluable when heavy rains on 21/8 (Appendix 5) caused non-netted blocks to lodge. These blocks were supported for the rest of the season by the use of fence posts and bailer twine. However, this proved ineffective in maintaining a crop with an open and upright canopy; therefore the data for S3 to S5 and final yield were taken from blocks 5 to 8.

Treatment	Date	Development stage
T1	14/7	First flowers open, 50 cm tall
T2	8/8	Sidestems extending, 100 cm tall
T3	3/9	Sidestems flowering, 115 cm tall

Table 3.1 - Application details of RSW0411 for experiment 6.

Sample	Date	Components measured
S1	6/8	plant height, number of leaves leaf weight, mainstem weight number of sidestems, sidestem weight number of mainstem pods number of mainstem flower buds number of stunted plants number of non-bolted plants reproductive weight
S2	19/8	as S1 plus: mainstem pod weight mainstem flower bud weight weight of stunted plants number of extended sidestems extended sidestem length
S3	1/9	as S2
S4	14/9	as S2 plus: length of reproductive spike
S5	12/10	as S4 plus: number of sidestem pods sidestem pod weight

Table 3.2 - Variables measured at each sample

The crop was desiccated on 21/10 with Reglone (200 g l^{-1} diquat, I.C.I.) @ 10 l ha^{-1} in 330 l ha^{-1} H_2O with Agral @1 litre in 1000 litres H_2O. A double pass was used to improve spray penetration and crop cover. Plots were combined on 5/11 using a Hege 125B plot combine.

3.2.2 Results

3.2.2.1 Component numbers

Treatment with RSW0411 reduced plant height (Fig. 3.1), but significant differences were only recorded at S3, when T2 was shorter ($p<0.05$) than the control and T1. Spike length was recorded at S4 and S5 (Table 3.3). The reproductive spikes of treated plants were shorter at both samples, but the differences were not statistically significant. Application of the chemical did not improve lodging resistance in any of the treatments.

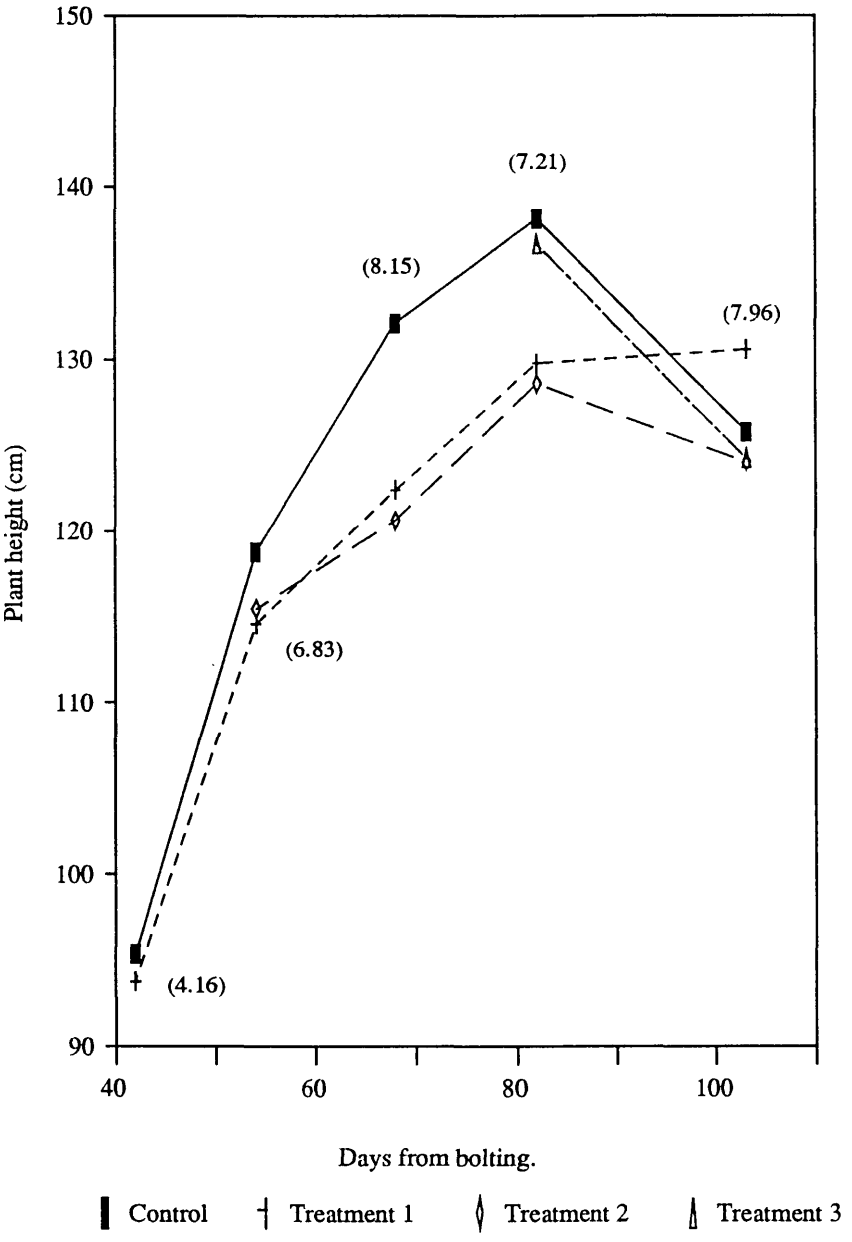
The number of mainstem leaves increased from S1 to S2 in all treatments. At S2, timing one had more leaves ($p<0.05$) than T2 and the control. The number of mainstem leaves on control and T2 plants increased at S4, but on T1 plants it continued to decline (Fig 3.2). The number of mainstem leaves per plant had declined on all treatments at S5.

The number of extended sidestems (e.s.s.) on control plants steadily increased over time (Fig 3.3). The difference between e.s.s. for T1 and control was greater than the LSD at S2, e.s.s. of T1 declined over subsequent samples and had the same value as the control at S5. T2 showed little difference from the control at S2, which was directly following the application of RSW0411. The e.s.s. of treatment 2 declined at S3, but then increased. T3 plants had fewer e.s.s. at S4 just after treatment. At S5, plants of treatment 3 had the same e.s.s. value as control and T1 plants. It should be noted that differences between treatments were never greater than one sidestem per plant.

The total sidestem length of control and T1 plants remained stable throughout sampling, with T1 always having a non-significantly longer length than the control (Fig. 3.4). T2 increased between S3 and S4, being greater than T3 and the control at S4 ($p<0.05$), but by the final sample this treatment had declined to the level of T1. Total sidestem length of T3 plants after being initially depressed by treatment at S4, was the same value as other treated plants by S5.

The average sidestem length did not vary between treatments at S2 and S3 (Fig. 3.5). At sample 4, T2 had a longer average sidestem length than other treatments and T1 was longer than T3 ($p<0.05$). At S5 the average sidestem length of T2 and the control had declined such that all treatments were of an equivalent length and control plants were shorter. This difference was not significant.

The number of mainstem flower buds declined steadily from S1 to S4 and flowering had finished by S5. This variable was unaffected by treatment at any of the samples, despite



Figures in brackets are mean mainstem weight (g) per plant at each harvest.

LSD 5% S1 = 5.55 S2 = 7.11 S3 = 9.33 S4 = 6.89 S5 = 9.33

Fig 3.1 - Effect of time of application of RSW0411 on plant height.

Sample	Spray timing				lsd	sig.	CV%
	C	T1	T2	T3			
S4	46.9	45.7	42.0	43.3	5.92	ns	8.3
S5	46.4	44.2	38.7	41.6	9.09	ns	13.3

Table 3.3 - Effect of time of application of RSW0411 on main reproductive spike length (cm).

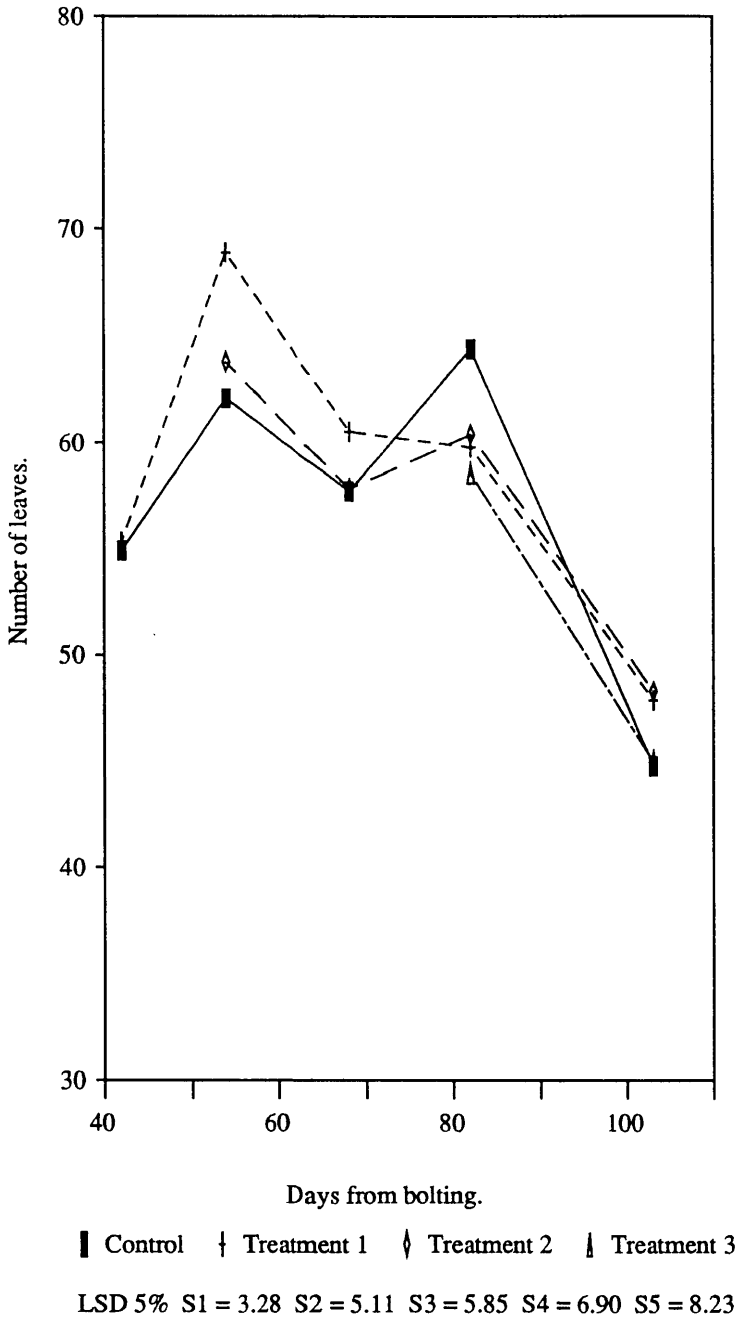


Fig 3.2 - Effect of application time of RSW0411 on the number of mainstem leaves per plant.

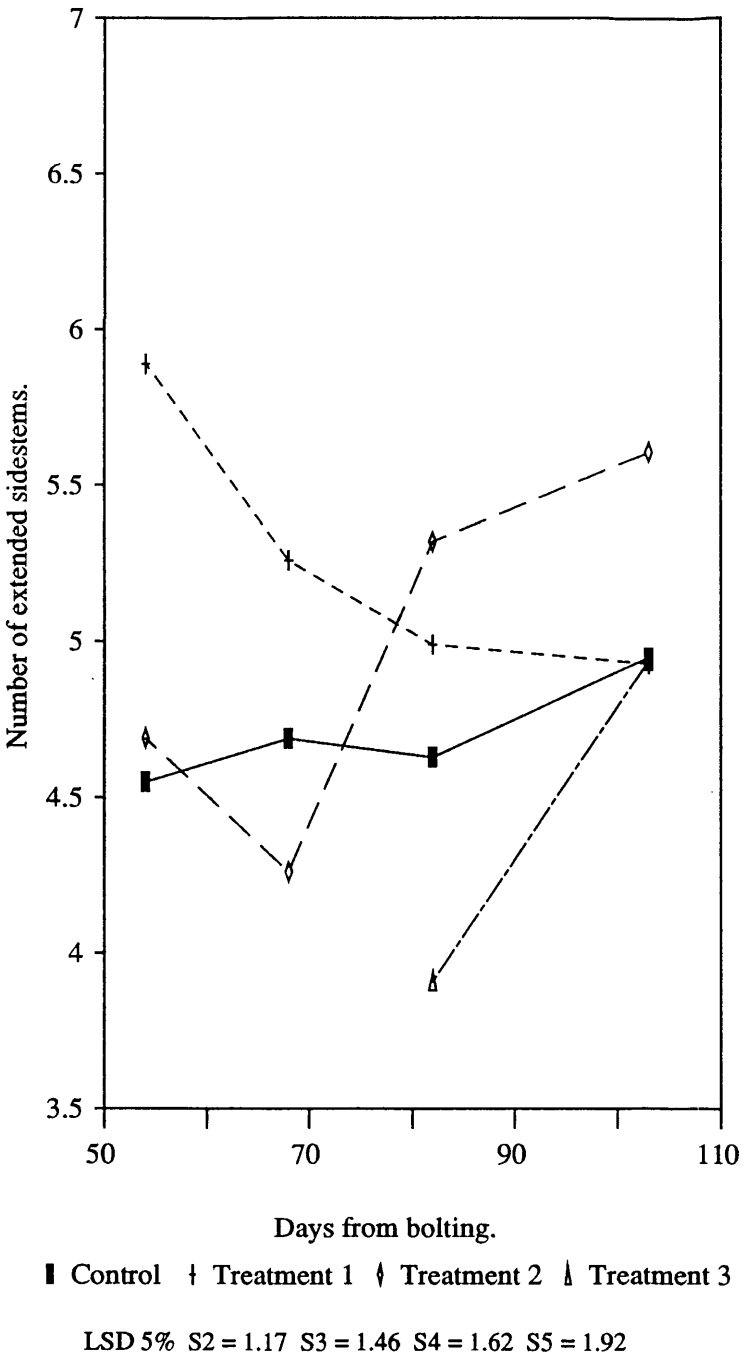


Fig 3.3 - Effect of application time of RSW0411 on the number of extended sidestems per plant.

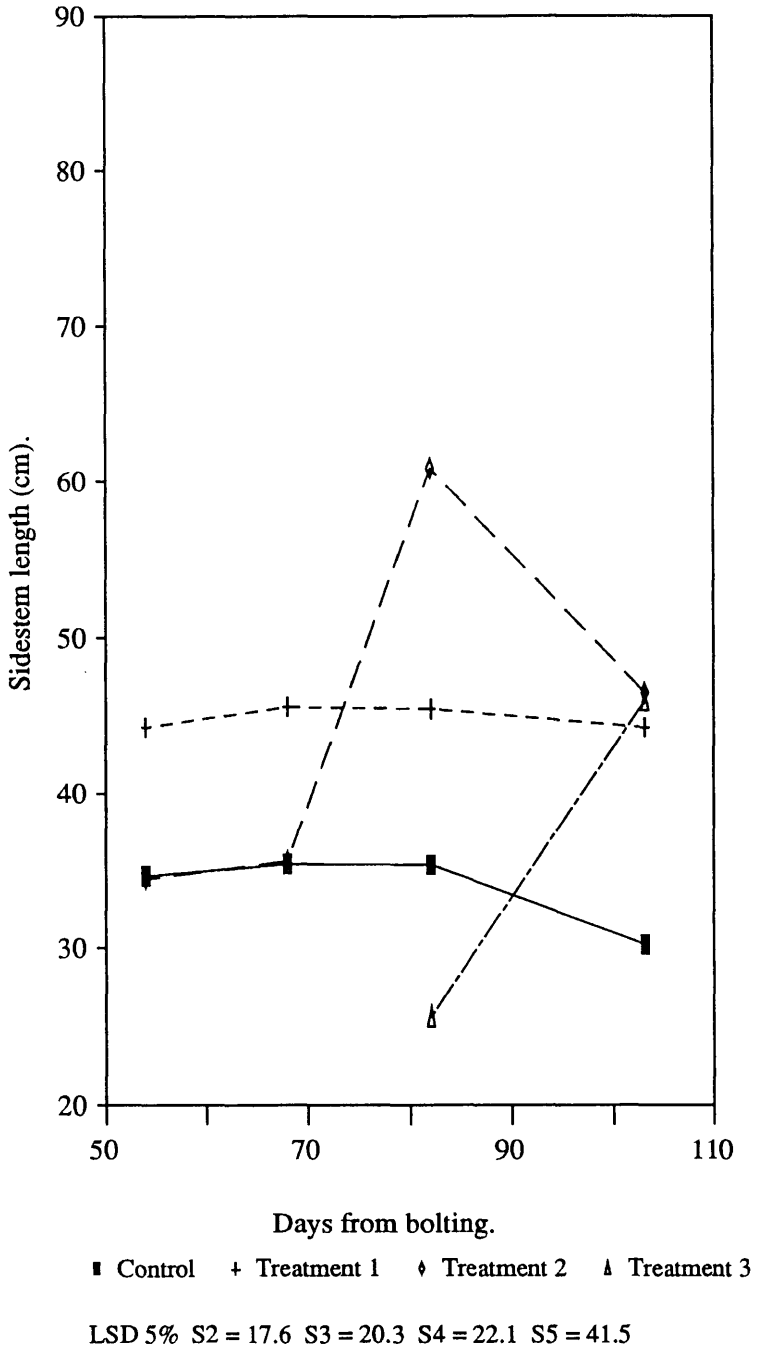


Fig 3.4 - Effect of application time of RSW0411 on total sidestem length per plant.

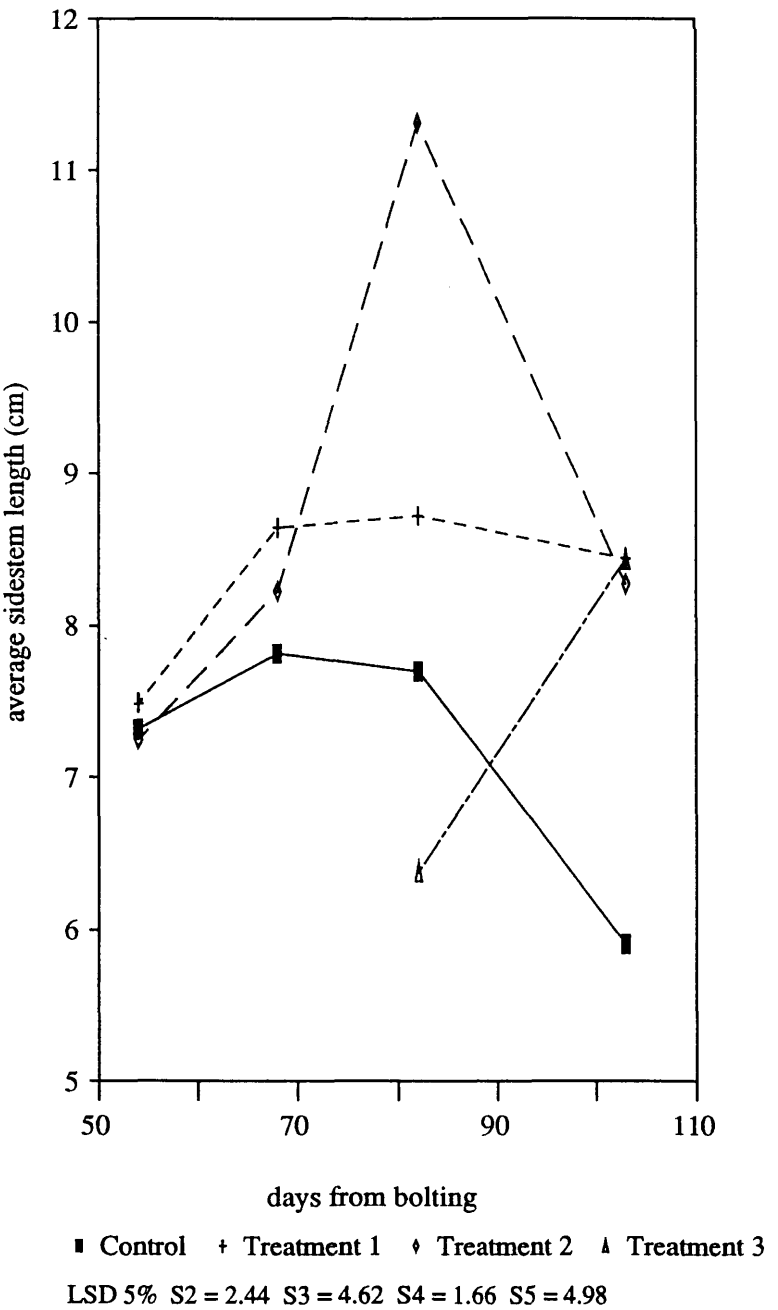


Fig. 3.5 - Effect of application time of RSW0411 on average sidestem length per plant.

differences being visible in the field. The number of aborted flower sites was increased by the chemical. An orthogonal contrast between treated and control plants was significant at S5 ($p<0.05$)(Fig. 3.6) for the number of aborted flower bud sites.

The number of mainstem pods increased from S1 to S3 in all treatments (Fig. 3.7). At S4 treated plants had fewer pods and an orthogonal contrast between treated and control plants was significant ($p<0.05$). This contrast was not significant at S5.

3.2.2.2 Component weights

Mainstem weight was not significantly affected by treatment. At S4, treatment 3 had a very low mainstem weight. Treatment 3 was lighter at this sample than the other treatments had been at S2 which was before T3 was sprayed (Fig 3.8).

Leaf weight declined steadily throughout the season (Fig. 3.9) even at S2 when the number of leaves per plant had increased. Control plants did show a small increase in this component at S4.

Sidestem weight followed a similar pattern to total sidestem length (Fig. 3.10). T2 was heavier than T3 at sample 4 ($p<0.05$).

Total mainstem pod weight was similar in all treatments at S2 and S3 (Fig. 3.11). At S4 and S5 treated plants had lower (ns) mainstem pod weights as expected from the lower number of pods recorded at these samples. Mainstem pod weight continued to increase at similar rate S3 to S5 ,as S1 to S3, although the number of mainstem pods increased much more slowly S3 to S5 compared with S1 to S3.

Sidestem pod weight was only recorded at S5, and there were no significant treatment differences, but sidestem pod weights on all treated plants were heavier than on the control. The high CV (104%) was probably responsible for the lack of significance. This was also true for numbers of sidestem pods (Table 3.4).

3.2.2.3 Yield

T1 and T3 depressed yield, although none of the differences were significant and only the difference between T2 and T3 and T1 is greater than the LSD (Table 3.5). The results for expected yield gave a highly significant regression with actual yield ($p<0.01$). The regression for actual yield and total pod weight was also significant ($p<0.05$), but the regression with yield ratio was not significant.

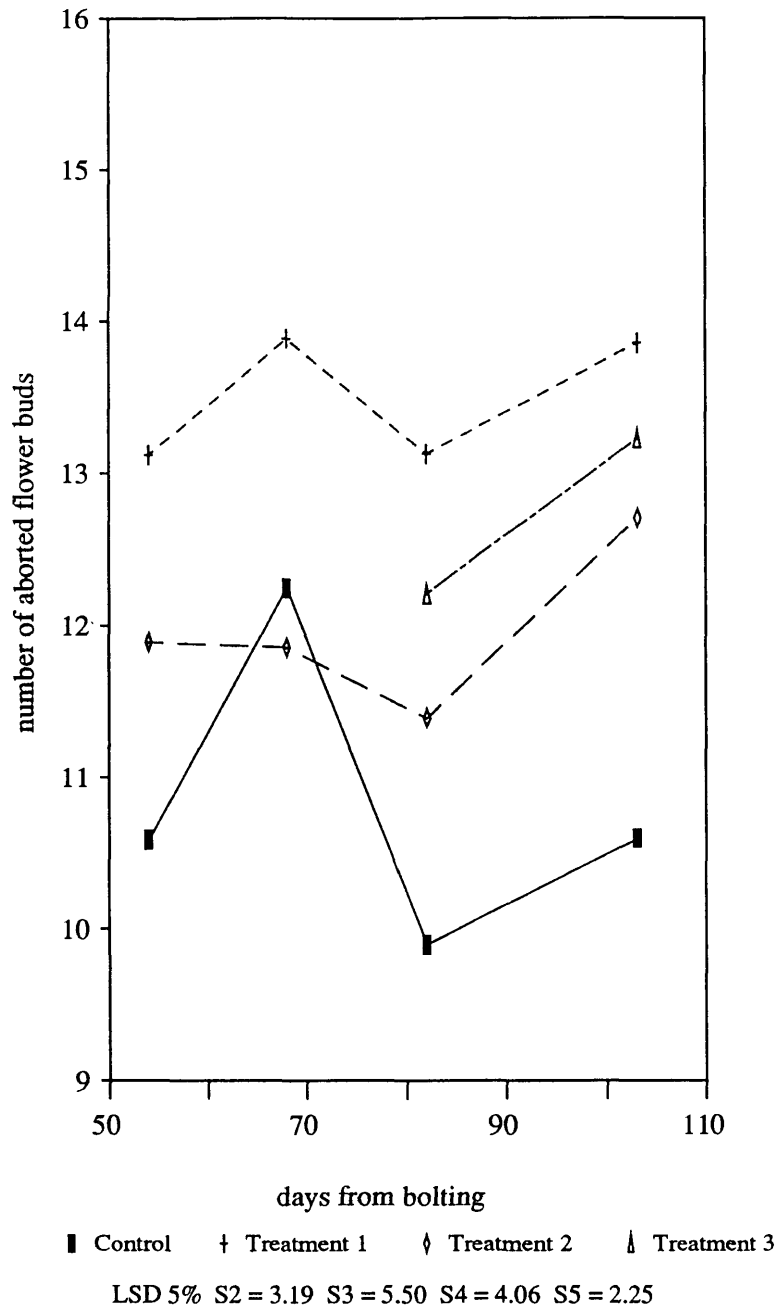


Fig. 3.6 - Effect of application time of RSW0411 on the number of aborted flower buds per plant.

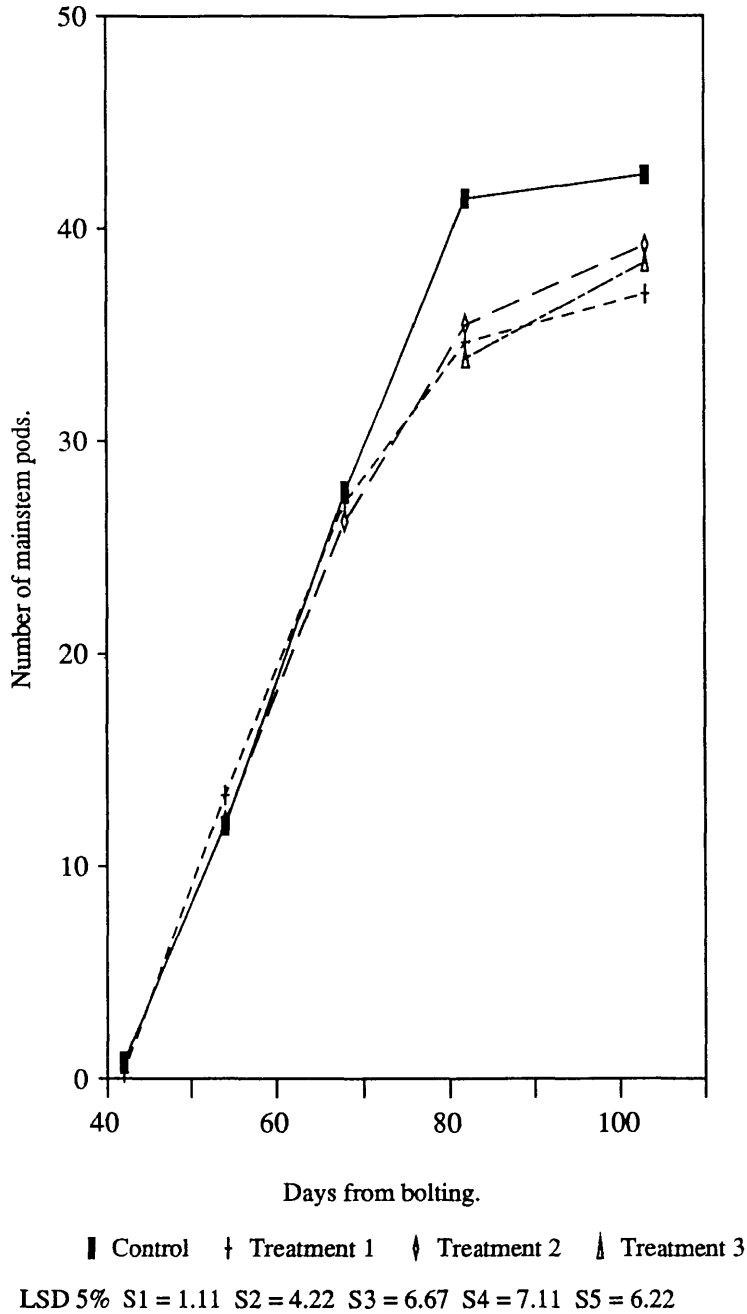


Fig. 3.7 - Effect of application time of RSW0411 on the number of mainstem pods per plant.

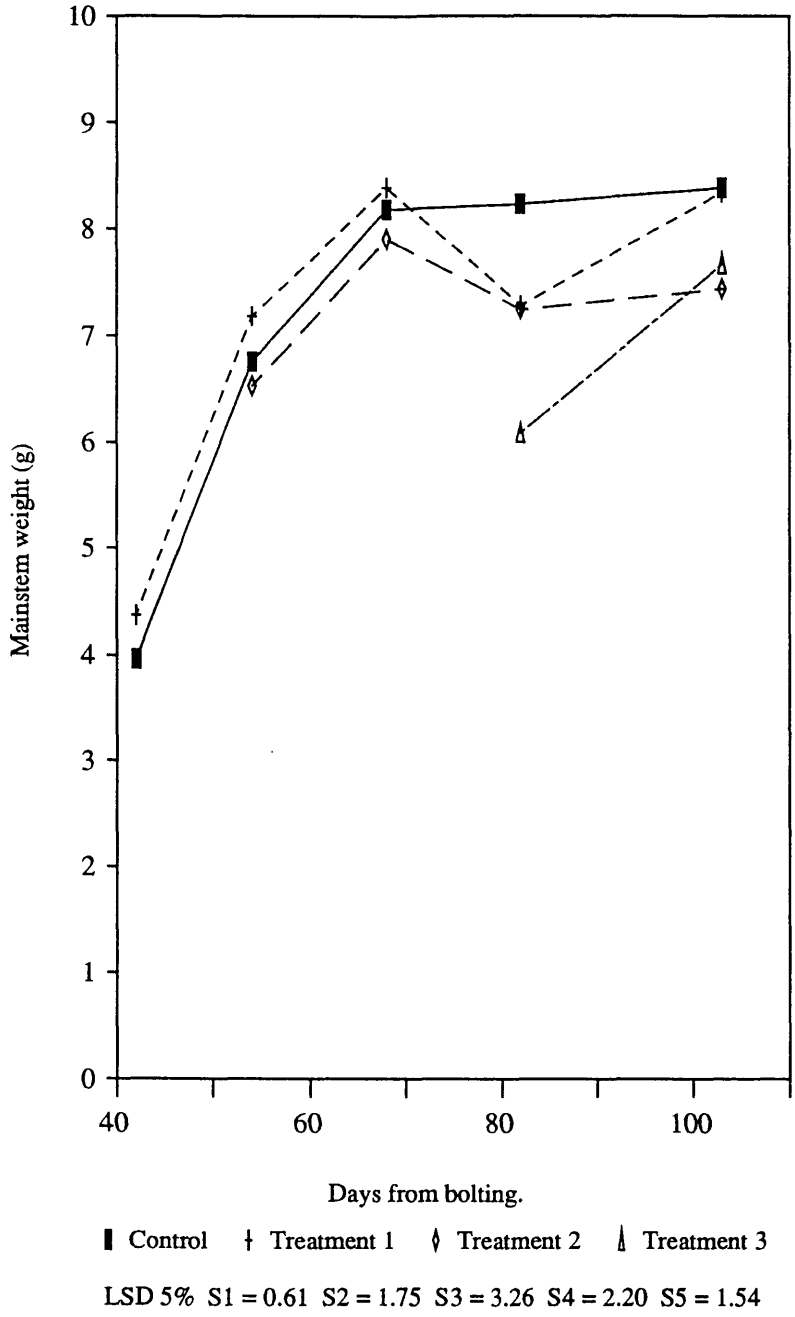


Fig 3.8 - Effect of application time of RSW0411 on mainstem weight per plant.

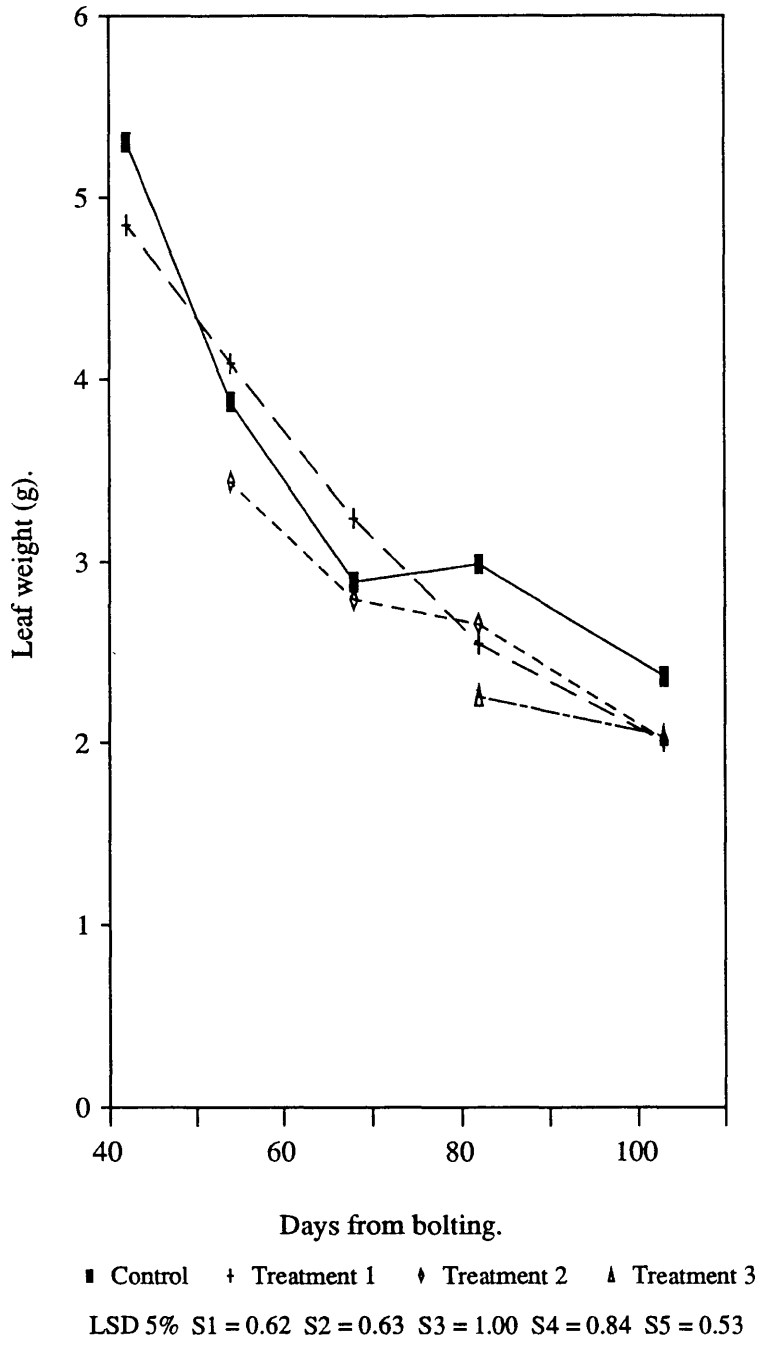


Fig 3.9 - Effect of application time of RSW0411 on mainstem leaf weight per plant.

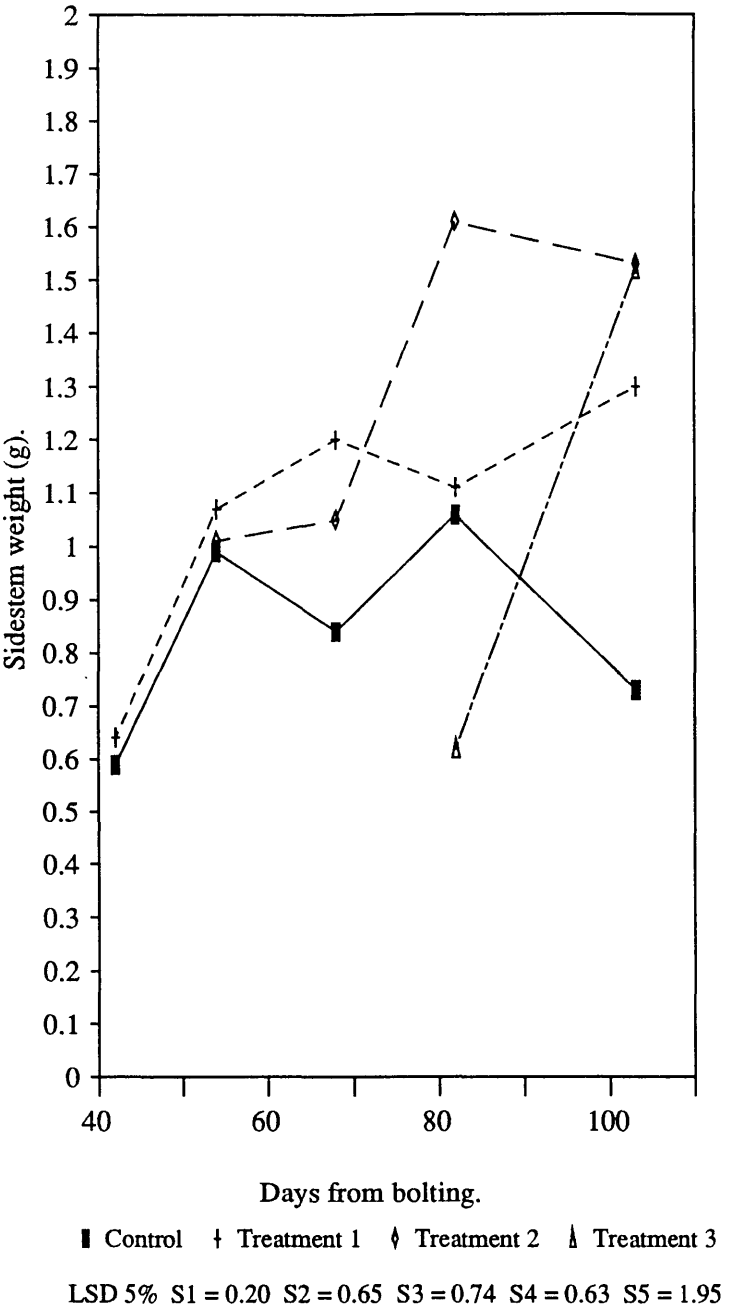


Fig 3.10 - Effect of application time of RSW0411 on sidestem weight per plant.

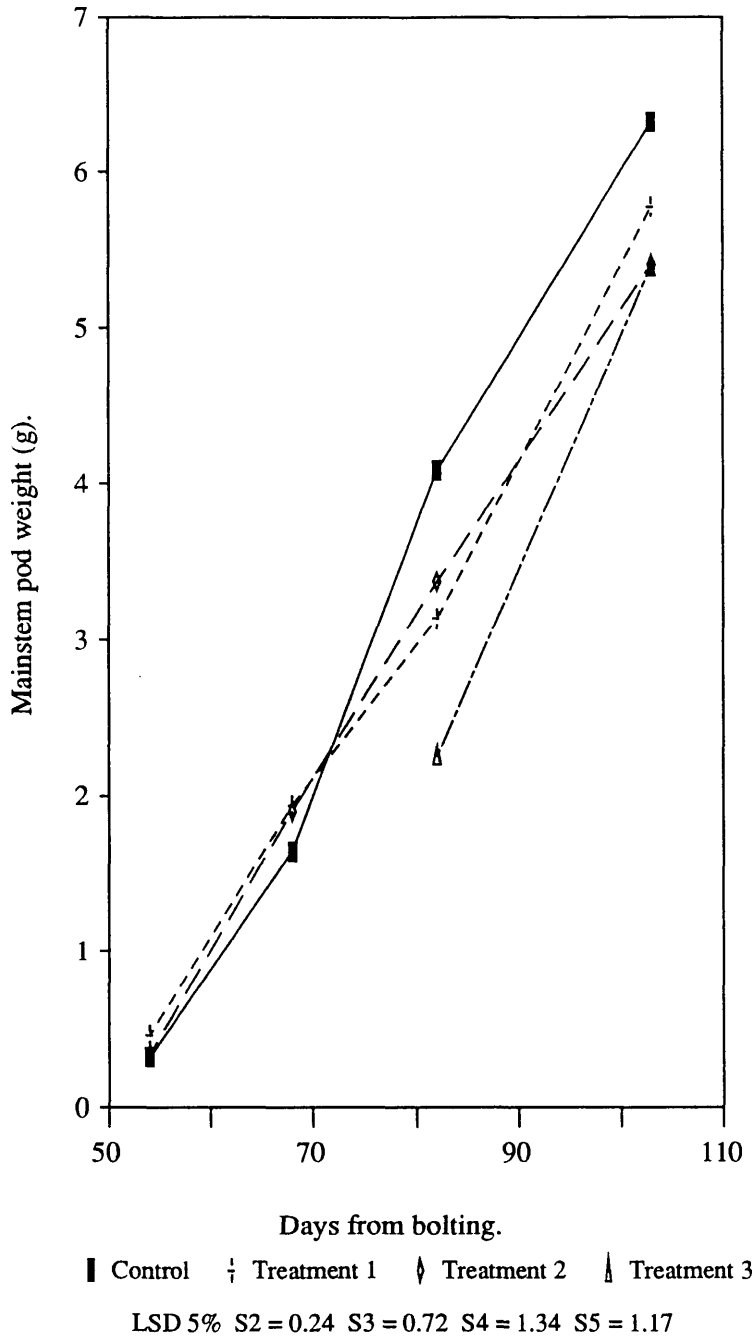


Fig 3.11 - Effect of application time of RSW0411 on mainstem pod weight per plant.

Component	Spray timing				lsd	sig.	CV%
	C	T1	T2	T3			
sidestem pod weight	0.11	0.42	0.59	0.52	0.71	ns	104.3
sidestem pods	1.5	5.2	8.5	7.7	10.8	ns	117.8

Table 3.4 - Effect of appliction time of RSW0411 on the number and weight of sidestem pods (numbers per plant, weight g per plant).

Component	Spray timing				lsd	sig.	CV%
	C	T1	T2	T3			
Yield	0.61	0.53	0.67	0.52	0.11	ns	11.5
Expected yield	1.25	1.23	1.31	1.15	0.37	ns	18.7
total pod weight	6.43	6.19	6.00	5.92	1.54	ns	15.8
Yield ratio	0.361	0.355	0.366	0.357	0.03	ns	5.3

$$Expected\ yield = kx \frac{pod\ weight\ per\ square\ metre}{2}$$

pod weight is divided by 2 to give seed weight
k = constant to convert units to t ha^{-1}

Yield ratio was calculated using data from S5.

Table 3.5 - Effect of time of application of RSW0411 on yield, yield ratio, expected yield and total pod weight (yields are t ha^{-1}, weights are g per plant).

3.2.3 Discussion

Few treatment differences were significant and when they were, they were not sustained from one sampling date to the next. This is probably a result of variables at samples 1 and 2 being measured from eight blocks, then from just four blocks for the last three samples. This resulted in the residual degrees of freedom being very low, S1 = 7, S2 = 14, S3 = 6, S4 = 9, S5 = 9. In a more stable crop such as wheat it is suggested that one should have at least 15 df (Scarisbrick , Clewer and Daniels, 1984), so this could account for significant differences not being found. However, despite this the use of transplants did reduce the variation of some sidestem variables (Table 3.6).

The higher CV% for the number of sidestem pods in experiment 6 compared to experiment 1, was a result of plants having fewer sidestem pods in this experiment and some replicates having zero sidestem pods, which resulted in high variability. To remove the variability of sidestem pods would be difficult, as it appears that some sidestems grow into gaps in the canopy where sufficient PAR is available to support them. These sidestems produced pods, while those sidestems growing in the areas of the canopy where light was limited did not. This is suggested to be the main cause of the variability. Although the density of the transplanted crop was lower than that of experiment 1, the more regular spacing reduced the area available for exploitation by the sidestems, because no large spaces were created as there were in the uneven plant stand of the direct drilled crop.

RSW0411 did, as in the previous year, reduce plant height. This reduction, although non-significant, was sustained. The site of reduction can be seen in the results for spike length. T2 and T3 reduced the spike length while T1 reduced the length of the stem below the flowering spike. These results for spike length, like those for height, declined between S4 and S5. This would support the observation that the reduction in plant height between these samples was a result of the apices dying back.

Leaf retention was observed after T1, as had been previously recorded, (section 2.1.1.2.1.), but was not detected in T2 and T3 plants. These later sprays could have produced their effect on side stem leaves. Such results would have gone undetected as sidestem leaves were not counted. The reduced mainstem leaf weight of T2 and T3, and T1 at later harvests, could also be a result of repartitioning of assimilate to the sidestems, assuming that the total leaf weight remained the same. Leaf weight declined in all treatments at S2 despite an increase in the number of mainstem leaves. This was a consequence of the senescence of the older larger basal leaves and the appearance of the smaller leaves that subtend the pods. The increase in leaf number and leaf weight from S3 to S4, resulted from low values being recorded at S3 because of leaf loss during the infamous October hurricane.

Variable	Experiment 1	Experiment 6
sidestem weight	35.0 - 84.7	27.7 - 68.7
number of sidestems	47.6 - 64.1	7.1 - 30.2
sidestem pod number	72.5 - 95.3	117.8

Table 3.6 - Comparison of coefficients of variation (%) between experiment 1 and experiment 6.

The large LSD recorded at S5 for the number of mainstem leaves was probably a consequence of an increased recording error because of the difficulty in deciding which leaves were dead and therefore not counted. Those leaves which had >50% of their leaf area senescent were considered to be dead. This difficulty in deciding on the appropriate dissection group may also account for the increased LSD's associated with sidestem variables at S5. Many of the apices of sidestems had died at this harvest, but the rest of the sidestems were still green. It was decided to record them only if more than half their length was still green.

There were no differences in flower production at any of the samples, however, differences were observed in the field (Plate 3.1a). These differences will only be elucidated if more regular monitoring can be undertaken and sidestem as well as mainstem flowers are included in the recordings. An increase in the number of aborted sites on treated plants was observed, but although this was significant at S5 it still only amounted to 2-3 more aborted sites per plant than the control. Nester and Zeevaart (1988) reported abnormal flower development in a gibberellin deficient mutant tomato. The interference with gibberellin biosynthesis of RSW0411 could therefore be directly responsible for this recorded increase in flower bud abortion. Dhiem and Browning (1988) noted reduced fruit set following the application of PP333 to apple trees.

Side shoots were most obviously affected by treatment. Control plants maintained their sidestem length and sidestem weight while increasing the number of extended sidestems. Treated plants had increased sidestem weights and a greater total sidestem length, but only T2 maintained an increase in the number of sidestems over the control until final harvest. The low figures for T3 at S4 may not be a result of the application of RSW0411 as very low mainstem weights were recorded for this treatment at this sample (section 3.2.2.2). All T3 data taken at sample 4 should therefore be treated with caution.

More detailed discussion of these results is difficult because of the high variation associated with sidestem measurements (see LSD's Figs 3.4, 3.5, 3.6), despite the fixed density imposed at transplanting. The results for average sidestem length are particularly important, because these would disagree with the results of Child *et al.* (1987), who recorded reduced sidestem lengths and total branch length in oilseed rape plants treated with triapenthenol (RSW0411). In experiment 6 there was no reduction in sidestem length as a result of chemical application and it is suggested that increased light penetration to the lower parts of the canopy did not occur. This had been proposed as the reason for the yield increases observed in experiment 1 (section 2.1.1.3).

(a)

(b)

Plate 3.1 - Differences in flowering as observed in the field following application of RSW0411. (a) Experiment 6 (b) Experiment 7.

Mainstem pod numbers and pod weight were reduced by treatment after S3. This could be a consequence of the increased assimilate partitioning to sidestems, as well as a reduction in reproductive sites as a result of flower bud abortion. This partitioning was not beneficial, although treated plants did have a higher sidestem pod weight this did not compensate for the reduced mainstem pod weight. Daniels, Scarisbrick, Chapman and Noor Rawi (1982) also observed a decrease in the number of pods on the terminal raceme but an increase in pods on the primary branches when the pgr Embark was applied to oilseed rape. These workers also recorded a reduction in yield following treatment.

Seed yield was depressed by T1 and T3. This was not expected from the sample data. Expected yield when calculated (Table 3.5) predicted the yield depression of T3, but not of T1. Alternatively total pod weight at S4 and S5 indicated a decline in yield with all regulator spray timings, the later the spray the larger the yield depression. None of the results in Table 3.4 was significant, but as seed yield was taken from a larger area 4.5 m^2 (c.f. 0.68 m^2 for hand samples) and had one of the lowest CV's of these measurements it is probably the most accurate value. Control and T3 results were constant for all three calculations, it is T1 and T2 that are anomalous , especially the low combine yield of T1. Raw data showed no distorting values for T1 combine yield and it is therefore difficult to find an explanation for the observed yield depression. The high combine yield of T2 was not expected from the total pod weight result. It is possible that T2 pods grew at a faster rate up to final harvest than those of the control and T1. The gradient of the line of pod weight against time was higher between S4 and S5 for treatment 2 than that of the control (Fig. 3.10); T2 also had more sidestem pods which were probably immature at S5 and grew rapidly upto final harvest and made a significant contribution to final seed yield.

From these results it is suggested that the application of RSW0411 improved the partition of assimilates to the sidestems. This was a result of the retardation of the growth of the mainstem as a result of the application of the chemical. Because there is little transport of triazoles from mature leaves (Quinlan and Richardson, 1986), and the mainstem spike would be expected to receive the majority of the spray in a crop of this density, the chemical retardation would be greatest in this plant part. This allows for increased light penetration down to the sidestems enhancing their growth. The maintenance of sidestems of treated plants to S5 was a result of the sink demand of their pods, control plants had fewer sidestem pods and their sidestem values declined (Figs 3.4 to 3.8). These results agree with those of Carlson and Brun (1985), working with soyabean (*Glycine max.*), who found increased

assimilate partitioning to a node when its reproductive load was increased. The higher sidestem pod values of RSW0411 treated plants were a result of the better light interception by treated sidestems, combined with an increased partitioning of assimilate to them.

In conclusion, the application of RSW0411 was most advantageous at the time of sidestem extension (T2) which gave the optimum balance of increasing numbers of sidestem pods while having the least effect on the number of mainstem pods. The later sprays had less aborted pods because of the differentiation of flower buds before spray application. In electron microscope studies it had revealed that the initiation of flower bud differentiation coincided with the commencement of bolting.

The application of RSW0411 was not as beneficial in this experiment as in experiment 1 where later sprays had increased yield. This could be a product of the cooler growing temperatures (Appendix 6), which would retard plant development. Luib *et al.* (1987) reported extended pod longevity following chemical application. The chemical also promoted sidestem pods which are less mature than those of the mainstem. A more rapid development would, therefore, benefit untreated plants. However, an extended growing period may not be desirable when one of the main detractions of evening primrose for farmers is its already long growing season.

3.3 Experiment 7

The effect of timing of RSW0411 on development and yield of a spring drilled crop.

3.3.1 Materials and methods

The trial was carried out on the same site as experiment 6 and received the same cultivations. On 5/5/87 plots, 6 x 1.83 m, were drilled using a Hege plot drill. The seed rate was 6 Kg ha^{-1}, sowing depth was 1 cm and each plot consisted of twelve rows with 15 cm between rows. The site was then consolidated with a Cambridge roller. Field emergence was first observed on 28/5/87, and bolting first noticed on 21/7.

Plots were sprayed with Fusilade (125 g l^{-1} fluazifop-p-butyl, I.C.I.), @ 3 l ha^{-1} in 300 l H_2O with Agral (I.C.I.) @ 1 litre in 1000 litres, to kill grass weeds and volunteer cereals. Couch grass (*Elymus repens*) was not controlled by this spray and continued to be a problem, as did broadleaved weeds. The site was hand weeded on 8/7/87. On 13/7/87 nitrogen (Nitram, 34.5% N, I.C.I.) was broadcast @ 40 kgN ha^{-1}.

RSW0411 was sprayed on three dates (Table 3.7), using a Fox Motori 301 knapsack sprayer @ 3.0 bars with orange F60 Lurmark nozzles, at 700 g ha^{-1} in 330 l H_2O.

Two samples were taken during the growing season; S1 (24/9) and S2 (3/11). All plants within a 0.25 m^2 quadrat were harvested and taken to the laboratory where they were separated into normal, stunted and non-bolted plants. Only normal plants were dissected in detail using a ten plant sub-sample. If less than ten normal plants remained then just these were analysed.

The crop was desiccated on 10/11/87 with Reglone (200 g l^{-1} diquat, I.C.I.) @ 10 l ha^{-1} in 330 l H_2O with Agral @ 1 litre in 1000 litres, using a bidirectional pass to improve crop cover and spray penetration. The crop was harvested on 27/11/87 using a Hege 125B plot combine.

Treatment	Date	Development
T1	8/8	Plants 20 cm tall
T2	3/9	Sidestems beginning to extend, plants 60 cm tall.
T3	29/9	Sidestems flowering, plants 100 cm tall.

Table 3.7 - Spray application details of RSW0411 in experiment 7.

3.3.2 Results

3.3.2.1 Component numbers

At S1 plants from T1 were shorter, but not significantly, than those sprayed at T2 or those of the control (Table 3.8). When results for plant height were analysed using covariance analysis with the number of non-bolted plants in the sample as a covariate, significant differences between treatments were found (S1a, Table 3.8). Plants from T1 were shorter ($p<0.05$) than the control. Plants of treatment T2 were also shorter than the control, though not significantly. At S2, T1 plants were significantly shorter than the other treatments ($p<0.01$) with the later applications of the chemical having little effect on plant height. When covariance analysis was used at S2 it did not improve the amount of variance accounted for. Spike length was not significantly affected by treatment.

Treatment with RSW0411 caused a non-significant increase in sidestem number per plant at S1. This increase was maintained at S2 for T1 and T2, but plants from T3, the last treatment date, were not different from the control. Spray applications at T1 and T2 gave numerical increases in total sidestem length. T3, conversely, showed a decrease in this variable compared to the control.

The differences recorded for mainstem flower bud number were not significant, but application of RSW0411 at T2 increased the number of flower buds compared to the control. Differences were clearly visible in the field (Plate 3.1b).

At S1 a numerical increase in the number of mainstem pods above the control was associated with T1, at S2 this difference had disappeared. T2 plants showed no differences from the control at sample 2. T3 plants had fewer mainstem pods at S2 than other treatments.

Plants of T1 had more sidestem pods ($p<0.05$) than the control at S1. T2 plants also had more sidestem pods than the control, but this difference was not significant. At sample 2, T1 and T2 had more sidestem pods, and T3 plants had fewer sidestem pods than the control. These differences were not significant.

At sample 1, T1 had more total reproductive parts than the control and the difference between these treatments was greater than the LSD. At S2 these differences were maintained, although still non-significant. At this sampling time T3 had numerically fewer total reproductive parts than the control. T2 did not differ from the control.

Component	Sample	Spray timing				lsd	sig.	CV%
		C	T1	T2	T3			
plant height	S1	98.6	92.4	98.0	-	6.22	ns	5.6
	S1a	99.3	93.1	96.6	-	3.92	*	3.4
	S2	107.1	95.2	107.1	108.0	5.54	**	4.7
spike length	S1	40.6	40.9	42.2	-	8.37	ns	17.4
	S2	44.5	44.6	47.5	42.3	7.71	ns	15.3
sidestems	S1	2.14	2.56	2.19	-	0.88	ns	32.5
	S2	3.06	4.34	4.05	2.76	2.17	ns	54.5
sidestem length	S2	31.3	52.7	35.2	26.7	27.8	ns	67.9
average sidestem length	S2	12.8	12.9	10.0	9.7	7.1	ns	55.4
mainstem flower buds	S1	4.92	4.25	5.68	-	3.12	ns	54.1
mainstem pods	S1	22.1	25.5	22.7	-	7.97	ns	29.3
	S2	28.5	29.8	29.8	25.5	6.20	ns	19.4
sidestem pods	S1	1.5	8.4	3.2	-	4.32	*	83.7
	S2	4.6	10.9	5.3	2.2	6.70	ns	103.7
total reproductive parts	S1	28.6	38.3	31.2	-	8.72	ns	22.9
	S2	33.1	40.7	35.2	27.7	10.00	ns	26.1

a - non-bolted plants used as a covariate.

Table 3.8 - Effect of time of aplication of RSW0411 on component numbers of a spring drilled crop (lengths are in cm per plant, numbers are per plant).

3.3.2.2 Component weights

At S1 chemical application had little effect on mainstem weight per plant (Table 3.9). At S2 treated plants had heavier mainstems.

The weight of pods on the mainstem and the sidestems were increased by PGR application at T1 and T2, but reduced by T3. None of these differences were significant.

Application of PGR increased sidestem weight per plant at S1 and the difference between T1 and the control was greater than the LSD. At S2 plants of treatments T1 and T2 showed a non-significant increase in sidestem weight. T3 had a lower sidestem weight than the control at this sample.

3.3.2.3 Yield

The yield ratios of T1 and T2 were a little higher than those of the control, whereas the yield ratio of T3 was lower (Table 3.10). The earlier PGR applications gave non-significant yield increases compared to the control; T1 (+8.8%) and T2 (+6.4%), while T3 reduced yield (-5.3%).

Component	Sample	Spray timing				lsd	sig.	CV%
		C	T1	T2	T3			
mainstem weight	S1	9.49	9.70	9.67	-	1.55	ns	13.8
	S2	9.95	11.87	10.17	10.86	2.34	ns	19.4
sidestem weight	S1	0.73	1.53	0.90	-	0.67	ns	54.2
	S2	1.11	1.84	1.14	0.58	1.29	ns	96.4
mainstem pod weight	S2	3.19	3.69	3.40	3.10	1.16	ns	30.8
sidestem pod weight	S2	0.56	0.95	0.80	0.17	1.06	ns	153.1
total pod weight	S2	3.75	4.64	4.21	3.27	1.23	ns	36.1
total weight	S1	10.23	11.23	10.57	-	2.03	ns	16.6
	S2	11.22	13.97	11.54	11.22	3.25	ns	24.0

Table 3.9 - Effect of application time of RSW0411 on the component weights of a spring drilled crop (weights are g plant^{-1}, pod weights are separate from stem weights).

Component	Spray timing				lsd	sig.	CV%
	C	T1	T2	T3			
Yield	0.277	0.311	0.295	0.263	0.052	ns	16.1
Yield ratio	0.339	0.349	0.369	0.280	0.097	ns	27.5

Table 3.10 - Effect of application time of RSW0411 on seed yield and yield ratio of a spring drilled crop (yield in t ha^{-1}).

3.3.3 Discussion

Not all timings of RSW0411 affected plant height. T1 reduced height, but later treatments were ineffective. As previously discussed the organ growing at the time of PGR application is that affected (section 1.2.1), so it is surprising that spike lengths were unaffected by treatment. These data could result from the non-uniform bolting, i.e. not all plants had flowering spikes at the time of application. At S1 an average of 34% of plants per quadrat had not bolted, while at S2 this figure was reduced to 15% of plants. This was probably the reason for the increased efficiency of the covariance analysis for plant height using non-bolters at S1 compared to S2, and why this analysis produced significant results at S1a.

The variability in bolting could have been a consequence of spring drilling, temperatures at this time may not fall low enough to satisfy the vernalisation requirement. In glasshouse experiments temperatures below 10 °C had promoted bolting (personal data). This treatment, however, had been applied for 24hrs a day. From the meteorological data (Appendix 7) it can be seen that the soil temperature from emergence was rarely below 10 °C. Grass temperatures did fall below this figure, but the data do not show how long these lower temperatures were maintained each day. Vince-Prue (1975) lists *O. biennis* as having a obligate vernalisation requirement and *O. lamarkiana* and *O. stricta* as having a facultative vernalisation requirement. Dodd (1988) referred to the variety 'Paul', used in these trials, as *O. spp.*, because it was not a distinct species. Therefore it is possible that the vernalisation response was not satisfied, or satisfied only later, in these trials. Kachi and Hirose (1983), had found 9cm diameter to be the critical plant size for bolting in dune populations of evening primrose, it is therefore also possible that the variability in bolting was a result of plants not being at this critical plant size simultaneously. Another reason for the lack of uniform bolting could be the genetic variability in vernalisation requirement.

From height and spike length data (Table 3.8) it can be seen that application of RSW0411 at T1 reduced the length of the stem below the flowering spike. The later sprays, T2 and T3, effected the length of sidestems. Thus it would appear that the growth of the mainspike had ceased when T2 and T3 were applied and this is supported by the small increases in both spike length and the number of mainstem pods that occurred between S1 and S2.

Individual treatments had the same effect on all sidestem variables. T1 increased the number of sidestems and had a longer total sidestem length than the control, the average sidestem lengths of these two treatments, however, were very similar. T1 also increased the sidestem weight and the number of sidestem pods compared to the control. T2 affected

sidestem variables in the same manner as T1 but the average sidestem length was shorter than that for the control. T3 had little effect on the number of sidestems, but reduced all other sidestem variables. These results are consistent with the theory of RSW0411 restricting the site extending at the time of application and would, therefore, support the hypothesis of Child *et al.* (1987) that changes in plant morphology following PGR application are a consequence of its time of application.

It is proposed that with T1 there was better synchrony of growth between the mainstem and sidestems, because of retardation of the mainstem. This improved synchrony also produced extra sidestems. T2 also increased sidestem production, but because of its later application it caused these sidestems to be shorter, and produced a more 'open' canopy allowing better light penetration. T3 had no effect on the production of side stems, but it did reduce their length and decreased flower production. The latter was an effect of the anti-gibberellin property of the chemical on flower bud development (section 3.2.3).

Yield increases above the control for T1 and T2 were not significant, though if repeated on a field scale could be of economic significance to growers of the crop. The variability in yield was higher than that encountered in the previous year's field trials where significant increases were found (year 1 CV=11.3%, year 2 CV=16.9%) and this may have been one reason for the lack of significance. These increases in yield of T1 and T2 were a result of increased pod weights which were observed at the later harvest. It is suggested that the increased pod weights result from increases in light penetration to the earlier formed, and thus more mature, pods lower down the canopy, increasing their photosynthetic rate. Tayo and Morgan (1979) reported older pods to be the major contributors to yield in oilseed rape, so an increase in the photosynthetic rate of these pods in evening primrose could have a major affect on yield. The yield increases do not occur with T3 because the late application delays flowering at a time in the season when it cannot recover like T1 and T2. This delay in flowering has also been observed by other workers (Scarisbrick *et al,* 1985, Child *et al,* 1987) following PGR application.

The yield of the spring drilled crop was much less than that of the summer drilled crop in the 85/86 season (year 2 grand mean=0.285 t ha^{-1}, year 1 grand mean=0.987 t ha^{-1}), but the former suffered very badly from bird damage, with virtually all pods affected. A further advantage of the summer drilled crop was its higher accumulated temperature. The summer sown crop had 1197.7 °C above 6 °C while the spring drilled crop had 903.7 °C above 6 °C, between bolting and harvest. The pod growth of the spring sown crop was also in the cooler autumn temperatures.

However, the spring drilled crop could provide the evening primrose grower with a useful alternative to summer sown crops because it is in the field for a much shorter time and its variable costs are lower than those for spring transplants. However, to produce good yields spring crops need good weed control, this crop could have been smothered had it not been hand weeded.

3.4 General Discussion

In both experiments application of RSW0411 at sidestem extension increased seed yield. Conversely application at sidestem flowering reduced yield compared to the control. Spray application before flowering depressed yield on the transplanted crop, but increased yield on the spring drilled crop. One of the possible reasons for the differential effect of T1 was a difference in the physiological age of the plants at this development stage. This was demonstrated by plants from the transplanted crop having a longer flowering period than the drilled crop and application of RSW0411 at T2 and T3 in the drilled crop also having no effect on spike length, because the growth of this component had ceased when the spray was applied.

An increase in flower bud abortion following chemical application was recorded in experiment 6. Scarisbrick *et al.* (1985) observed abscission of immature pods on the terminal raceme of oilseed rape after spraying paclobutrazol which also subsequently depressed yield. If the spring drilled crop was physiologically more mature at equivalent developmental stages and hence times of application than the transplanted crop, the chemical would then be expected to exert its affect on later produced pods. In experiment 7 the reduced effect of RSW0411 application at T1 might have been because only the very last mainstem pods, which contribute little to yield, were caused to abort by treatment. Whereas in experiment 6 it was the earlier formed mature pods which abort. That the chemical affects later produced pods is further supported by the reduced number of sidestem pods of T3 compared to other treatments in the spring drilled crop, while application at this time had no effect on the number of sidestem pods on the transplanted crop. It is suggested that the chemical did not have a negative effect on T2 plants in either experiment because this treatment only caused abscission of the late formed mainstem flower buds which was balanced by the increased partition of assimilates to the sidestem pods.

The other main differences between the two crops was the effect of RSW0411 on sidestem lengths. All treatments were longer than the control in experiment 6, yet were shorter for post flowering treatments in experiment 7. These differences could be a result of the different morphologies of the two crops. The regular density of the transplanted crop would have kept sidestems shaded by the main flowering spike. Thus the mainstem would have intercepted the majority of the applied chemical. The mainstem was then retarded, while the sidestems which did not receive potent quantities of the chemical grew away. The increased length of sidestems may then have resulted from their release from apical dominance as observed by Dhiem and Browning (1988). However, with the spring drilled crop the plant spacing was not regular and sidestems could exploit the open spaces created in

the canopy where higher levels of PAR were available. Ross and Harper (1972) working with cocksfoot (*Dactylis glomerata*) observed that plants grow into areas of least interference, where interference is expressed as reduced availability of resources. These exposed sidestems would intercept the PGR spray and consequently be retarded. The later the spray the less time that would be available for the sidestem to grow away from the restriction. Child (1984), using a range of growth retardants on oilseed rape, recorded decreasing lengths of the lower hierarchy branches with later spray applications, suggesting later formed branches have less ability to 'grow away'.

Dhiem and Browning (1988) proposed that compensatory growth following chemical application was a result of increased cell division and an increase in internodal ground tissue, because of cytokinin build up during the period of retardation, which enabled rapid growth once gibberellin levels rose. In older plants such a cytokinin build up would not occur, as lower cytokinin levels have often been recorded in senescing tissue (Morgan, 1981). Thus the plants of treatment 3 in experiment 7 which were at the end of their growth cycle would be less able to compensate.

Another reason for the differences could be the larger root network of the spring drilled crop, compared with transplants. The paper pots in which these plants grew initially did not breakdown in the field and restricted the root systems of the plants within them (Plate 3.2). As it has been frequently recorded that triazole compounds move within the xylem (Shearing and Batch, 1979, Richardson and Quinlan, 1986) any spray reaching the soil surface would be better absorbed by the spring drilled crop and have a more pronounced effect upon its growth and development.

In both these trials the yield ratio of the crop was greater than that for the summer drilled crop used in first year trials. It is suggested that this was a consequence of these plants been grown when the photoperiod was inductive for flowering and bolting and thus these processes took place more rapidly than in the previous season. The yield ratio may also have been improved because these crops had less time to accumulate storage products within the root system and therefore less resources were available at bolting for stem extension. These results could have consequence for evening primrose breeders. If cultivars could be bred with a reduced photoperiodic requirement less vegetative material would be produced, thus hopefully improving the harvest index of the crop and also reducing its growing season.

Plate 3.2 - **Differences between the root network of a transplant and direct sown plants (Direct sown plant on the left).**

Chapter 4

Glasshouse trial in 1988 (Experiment 8).

4.1 Introduction

In two years of field trials visual differences in the pattern of flower production of evening primrose had been observed between those plants treated with RSW0411 and controls. Such an effect with triazole plant growth regulators has been previously recorded (Child, 1984; Daniels *et al.*, 1982). A glasshouse trial was, therefore, undertaken to allow regular monitoring of pod production of the mainspike and sidestems. Pod production was measured instead of flower production as it was easier to define, and therefore measure, than a flower. Flower bud abortion is generally low except for late in the season when flowering is finishing. The easy access to plant material also enabled regular monitoring of plant height to observe any compensatory growth that occurred and the recording of any chemical effects on sidestem production.

4.2 Materials and methods

Evening primrose seed, cultivar Paul, was sown into seed trays as in experiment 2 (section 2.1.2.1). When plants were at the two true leaves stage they were transferred to 9 cm pots and moved to a glasshouse cubicle with no heating. Time was allowed for root growth to commence and then plants were transferred outside (7/9/87). The plants overwintered outside and thus received their vernalisation requirement. On 2/2/88 plants were returned to the glasshouse (set at: 17 °C day, 10 °C night). Plants were exposed to a sixteen hour day, in order to receive the long days required for bolting, by the use of supplementary lighting from fluorescent tubes (100 $\mu E\ m^{-2}\ s^{-1}$). Vince-Prue (1975) described *O.biennis* as an long day plant with a quantitative cold requirement. Bolting first started on 29/2/88 and the supplementary lighting was turned off on 11/4/88.

A Latin square design with four treatments and three replicates was used. There were 25 plants in each replicate, with all measurements taken from the central 9 plants to reduce edge effects. As far as possible plants of a uniform size were kept in each block. Plants were netted with pea and bean netting at 50 cm on 23/3 and at 50 cm increments as they grew. RSW0411 application was carried out as described in Table 4.1.

A fortnightly spray was carried out for mildew (*Oidium spp.*) using Nimrod (250 $g\ l^{-1}$ bupirimate, I.C.I.). The control conferred by this became increasingly ineffective as the plants grew and the canopy became more dense. Whitefly (*Trialeuroides vapariorum*) was controlled by a regular distribution of the biological control agent *Encarsia formosa*, this however did not give complete control and on 1/7 and 20/7 samova (1:100 rainwater) was applied to reduce the whitefly population so that the *Encarsia* control could be more effective.

The warm temperatures (a maximum of 33 °C was recorded on some days) and the fast growth of the crop once bolting had started resulted in the death of some plants and severe tip burn in others. This was thought to be a consequence of an insufficient water supply to satisfy the plants transpiration requirements. This problem was compounded by the 'sponge like' qualities of the concrete floor. These damaged plants were replaced.

Measurements carried out during the experiment are described in Table 4.2. The plants were harvested on 1/8/88.

Reference	Growth stage
T1	plants 10cm tall (25/3)
T2	first flower on mainstem (28/4)
T3	side stems extending (16/5)

Chemical application was calculated on 700g ha^{-1} by the pot area and applied to the soil surface in 50 cm^3 of water.

Table 4.1 - Spray application details of RSW0411 in experiment 8.

Parameter	Definition	Monitoring times
Stem height	Plant stem fom soil interface to the base of the flowering mainspike	1/8
Plant height	From soil interface to apex of mainstem	30/3, 9/4, 15/4, 2/5 7/6, 6/7, 1/8
Pod production	Stem ringed with wire above last reproductive structure with flower fully open. Number of pods between labels counted at final harvest	p1=9/5, p2=13/5, p3=16/5, p4=19/5, p5=25/5, p6=29/5, p7=2/6, p8=9/6, p9=14/6, p10=21/6, p11=1/8
Aborted sites	Those sites which had a scar where a flower was once attatched.	As for pod production
Sidestem production	Any side stem > 5cm ringed with wire	I1=9/5, I2=16/5, I3=25/5, I4=2/6

Table 4.2 - Details of components measured and their definition

4.3 Results

4.3.1 Reproductive parts

Pod production was first observed on 26/4 and increased linearly with time until 21/6 (p10) (fig 4.1, Table 4.3), after this date the slope of the line was reduced as pod production finished. Application of RSW0411 before flowering began (T1) and at the commencement of flowering (T2) increased pod production rate and significant differences were recorded at p4,p5 and p6 ($p<0.05$) when T1 and T2 plants had more mainstem pods than the controls and T3 plants. At p2 and p3 T1 had more mainstem pods than the control and T3 and this difference was greater than the LSD. The differences between T1,T2 and the control were greater than the LSD at p7, while at p11 the difference between T2 and T3 was greater than the LSD.

When the number of pods produced within each period was analysed the number of mainstem pods of T1 and T2 were greater than the control and T3 at p2 and p5 ($p<0.05$) (fig. 4.2, Table 4.4) and the difference between these two groups of treatments was greater than the LSD at p3. Initially, p1 and p2, T1 plants produced the most mainstem pods, but later p3 to p6 T2 produced the most mainstem pods.

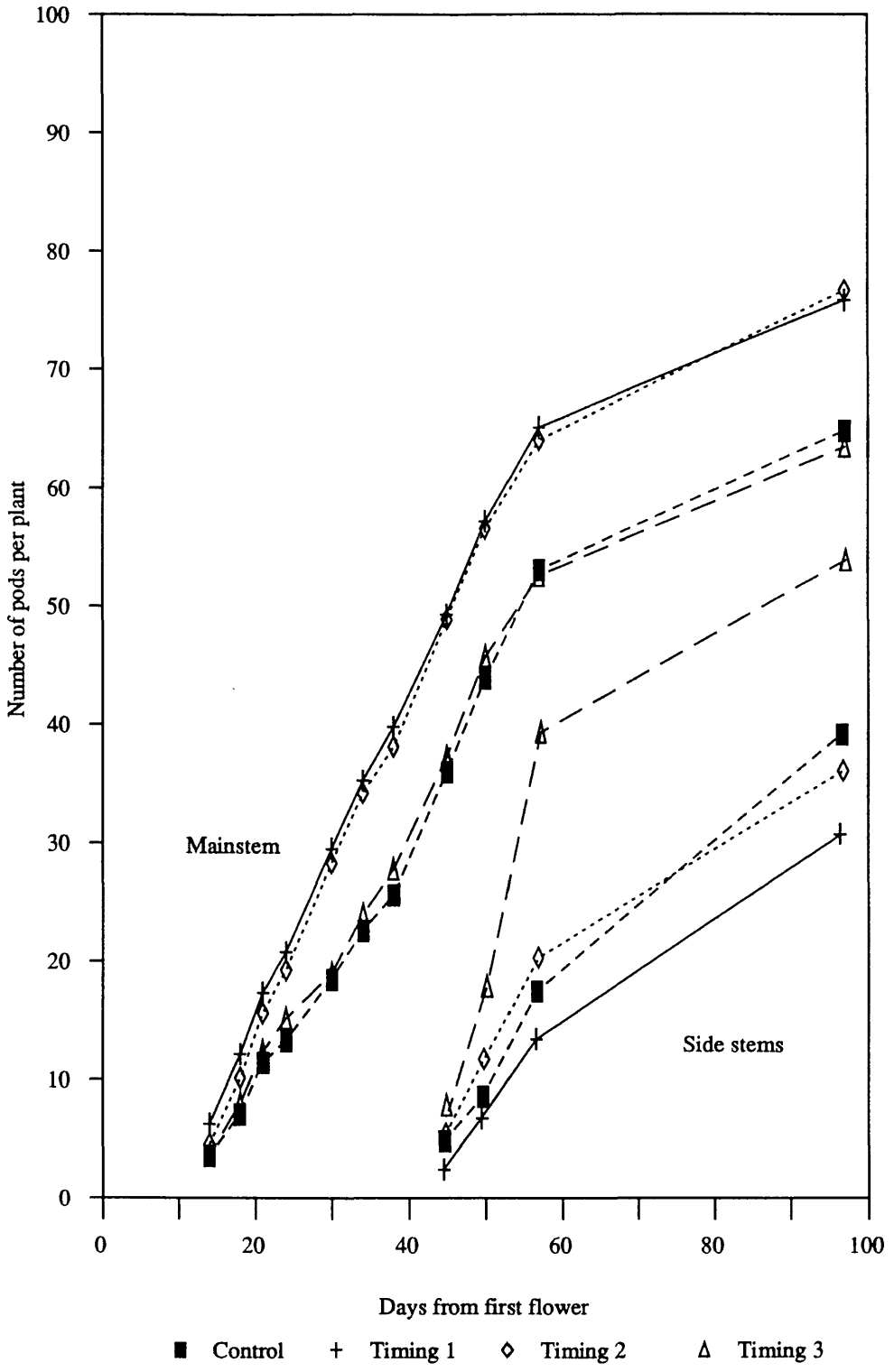
The production of sidestem pods was unaffected by treatments 1 and 2, but application at sidestem extension (T3) gave a non-significant increase over the control at p10, T3 also had the highest number of sidestem pods at p8 and p9 (fig. 4.3, Table 4.5). Control plants produced the most sidestem pods between p10 and final harvest. Large CV% values were associated with this variable (upto 115%). The number of sidestem pods was only recorded from p8 to p11 and their production in comparison to the mainstem number of pods can be seen in fig 4.1.

Pod weights recorded at final harvest showed non-significant increases in the weight of mainstem pods of treated plants (Table 4.6). Sidestem pod weight was reduced by the earlier chemical applications, T1 and T2, but was little affected by application at T3. Total pod weight was slightly increased (n.s.) by treatment as a result of the increases in mainstem pod weight. Sidestem pods contributed 17-30% to total pod weight, with the sidestem contribution to the total of indivivdual treatments being of the following ranking order T1<T2<T3<Control.

The number of aborted sites, those which had a scar from the abscission of a flower, showed a sharp increase in all treatments at p5, p6 and p11 (fig. 4.4, Table 4.7). However the period between p10 and p11 was much longer than previous periods which would

Pod position	Days from first flower	LSD	sig.	CV%
Mainstem	14 (p1)	2.95	ns	37.9
	18 (p2)	3.81	ns	23.5
	21 (p3)	4.85	ns	19.7
	24 (p4)	5.18	*	17.5
	30 (p5)	7.48	*	18.1
	34 (p6)	10.25	*	20.4
	38 (p7)	11.99	ns	21.1
	45 (p8)	15.24	ns	20.5
	50 (p9)	14.34	ns	16.3
	57 (p10)	14.51	ns	14.3
	97 (p11)	12.90	ns	10.6
Sidestem	45 (p8)	8.23	ns	117.9
	50 (p9)	13.80	ns	78.1
	57 (p10)	26.82	ns	71.6
	97 (p11)	29.90	ns	44.3

Table 4.3 - LSD's, significance and CV % for fig. 4.1.



The straight line between the final two sampling dates may not be completely correct. However, once a pod is produced, abscission is rare.

Fig. 4.1 - Effect of timing of RSW0411 on cumulative pod production

Pod position	Monitoring period	LSD	sig.	CV%
Mainstem	p1	2.95	ns	37.9
	p2	1.56	*	18.5
	p3	1.86	ns	22.2
	p4	3.07	ns	60.6
	p5	3.69	*	31.7
	p6	3.26	ns	36.6
	p7	2.32	ns	35.1
	p8	3.90	ns	22.4
	p9	1.51	ns	16.9
	p10	3.34	ns	24.5
	p11	6.41	ns	32.2

Table 4.4 - LSD's, significance and CV % for fig. 4.2.

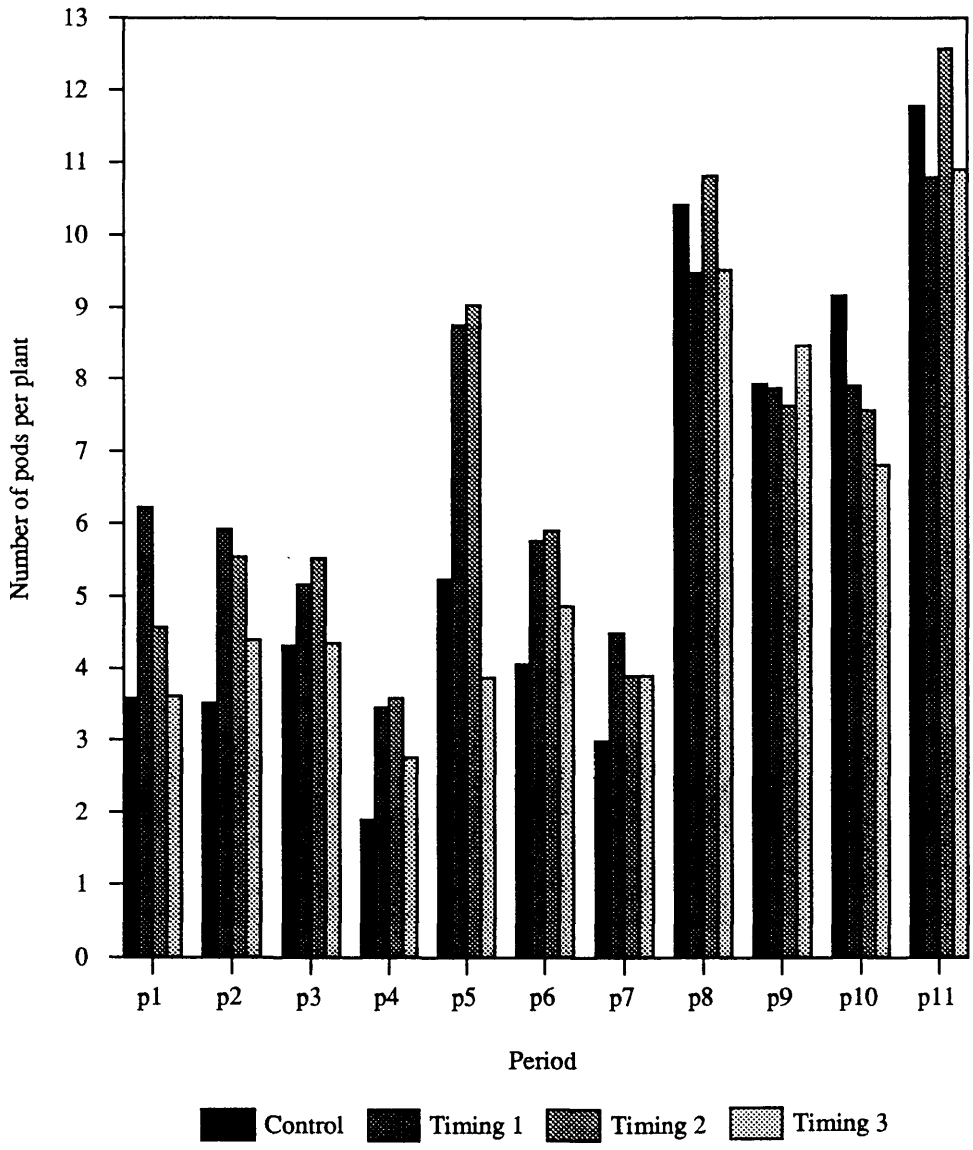


Fig 4.2 - Effect of RSW0411 on pod production on the mainstem.

Pod position	Monitoring period	LSD	sig.	CV%
Sidestem	p8	8.23	ns	117.9
	p9	13.80	ns	78.1
	p10	26.82	ns	71.6
	p11	29.90	ns	44.3

Table 4.5 - LSD's, significances and CV%'s for fig. 4.3.

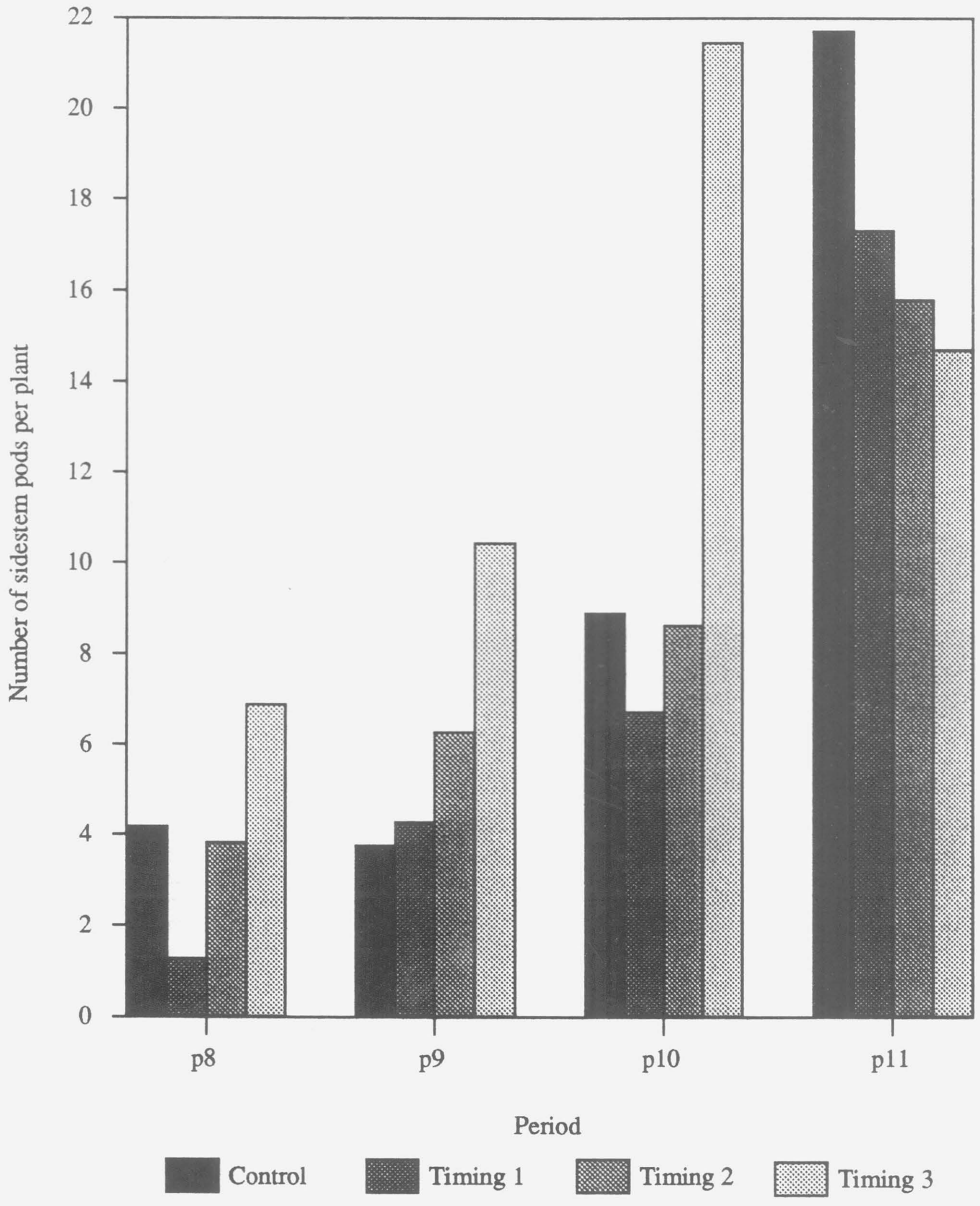


Fig. 4.3 - Effect of RSW0411 on sidestem pod production per plant.

Components	Treatment				lsd	sig.	CV%
	C	T1	T2	T3			
Mainstem weight	8.92	9.12	9.10	8.84	2.3	ns	17.2
Sidestem weight	8.02	6.53	7.46	7.66	5.46	ns	38.7
Mainstem pod weight	10.5	13.2	13.5	11.3	3.6	ns	17.0
Side stem pod weight	4.4	2.7	3.4	4.6	3.1	ns	48.5
Total pod weight	14.9	15.9	17.3	16.0	5.7	ns	20.7
Mainstem spike length	74.9	79.7	77.2	69.7	12.0	ns	9.2
Number of side stems	7.0	6.0	7.1	7.6	2.4	ns	19.6
Average side stem length	22.9	20.3	19.6	19.8	4.7	ns	13.0
Total side stem length	163.1	129.8	144.3	148.0	56.8	ns	22.4

Table 4.6 - Effect of timing of RSW0411 on a range of plant components. (Weights are g plant^{-1}, lengths cm plant^{-1}.)

Pod position	Monitoring period	LSD	sig.	CV%
Mainstem	p1	0.88	ns	161.3
	p2	0.68	ns	93.1
	p3	1.95	ns	132.5
	p4	0.51	ns	48.3
	p5	3.61	ns	59.2
	p6	3.23	ns	54.8
	p7	2.13	ns	71.7
	p8	1.50	ns	55.6
	p9	3.88	ns	141.4
	p10	1.48	ns	123.7
	p11	8.69	ns	72.6

Table 4.7 - LSD's, significances and CV%'s for fig 4.4.

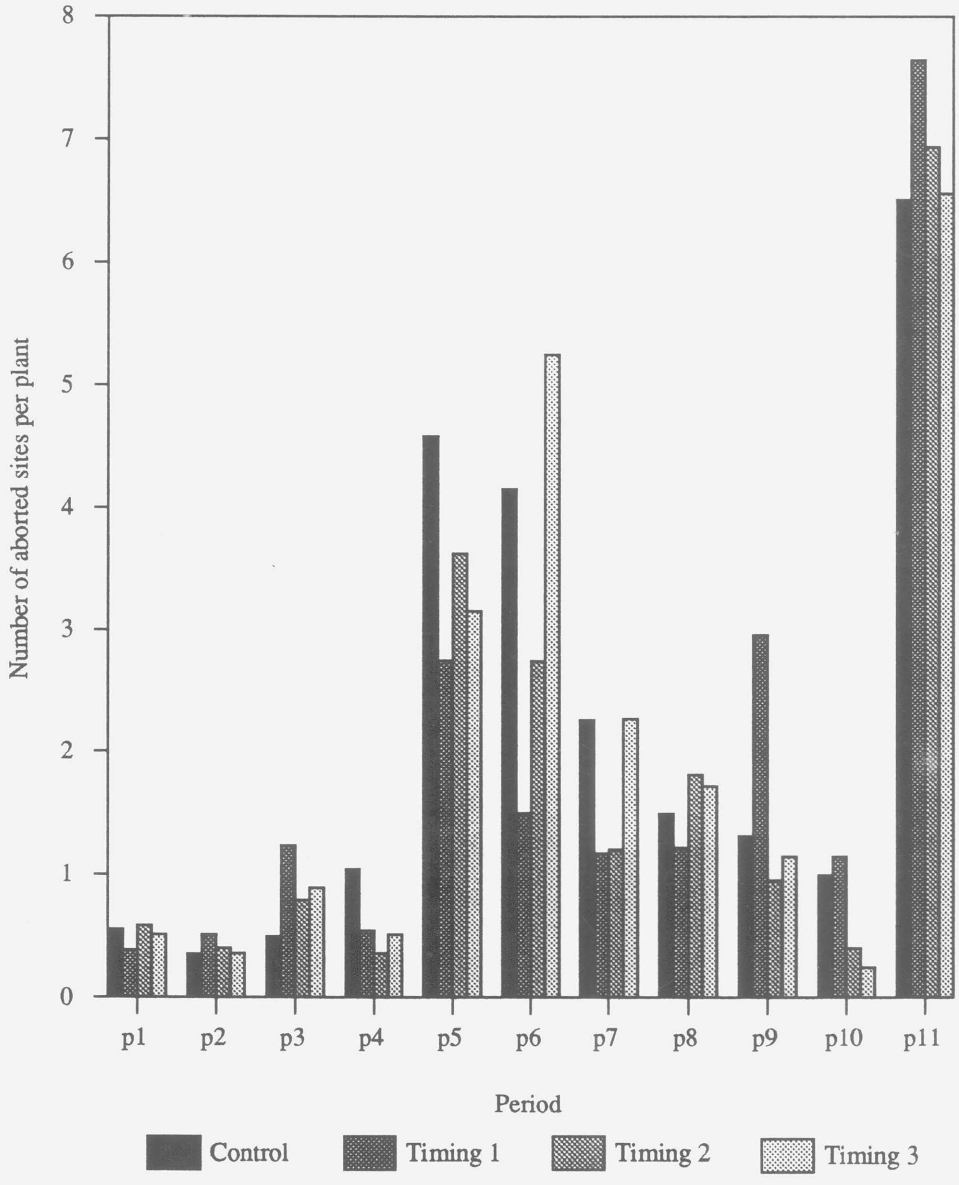


Fig. 4.4 - Effect of RSW0411 on the number of aborted sites on mainstem.

account for the increased number of aborted sites within this period. Significant treatment differences were not recorded, although at p4 the difference between C and T2 and T3 was greater than the LSD, as was that between T3 and T1 at p6 (fig. 4.4). When plotted cumulatively (fig. 4.5) no significant differences were recorded, but a higher level of pod abortion was recorded in C and T3 on the mainstem.

The number of aborted sites on the sidestems also increased steadily with time (fig. 4.6). No treatment differences were recorded. Sidestem pod abortion was proportionally much higher than that on the mainstem (fig 4.5). High C.V.'s were associated with this variable, upto 140%, which may have obscured any differences.

4.3.2 Sidestems

The rate of production of sidestems increased in all treatments upto I3 (fig. 4.7), but then declined to final harvest. The difference between the number of sidestems produced by the control and, T1 and T2, at I3 was greater than the LSD. When the cumulative totals were calculated no treatment differences were recorded (Table 4.6).

At final harvest the total sidestem lengths of the control plants appeared higher than those of the treated, the most marked reduction was in T1 (Table 4.6). The average sidestem length of treated plants was also lower (n.s.), but because of the reduced number of sidestems of T1, this parameter did not follow the same pattern as total sidestem length (Table 4.6).

When the length of sidestems were divided into five classes determined by length (fig 4.8) control plants had more sidestems in the largest class (>40cm) than those plants treated with RSW0411 ($p<0.01$).

4.3.3 Plant height

From 46 days after bolting to final harvest (154 days from bolting) the height of plants of Treatment 1 was always less than other treatments ($p<0.05$) (fig 4.9). From Table 4.2 it can be seen that the reduction in height of plants from treatment 1 was a result of the reduced length of the stem below the flowering spike (stem height) compared to other treatments. Stem height was also reduced in treatment 2, but not significantly. No significant differences were recorded in spike length, although it was reduced in treatment 3 (n.s.)(Table 4.6).

Pod position	Days from first flower	LSD	sig.	CV%
Mainstem	14 (p1)	0.88	ns	161.3
	18 (p2)	1.41	ns	89.3
	21 (p3)	2.65	ns	87.2
	24 (p4)	2.80	ns	68.1
	30 (p5)	5.84	ns	57.2
	34 (p6)	7.42	ns	46.1
	38 (p7)	8.23	ns	43.1
	45 (p8)	9.20	ns	42.2
	50 (p9)	11.48	ns	46.8
	57 (p10)	11.47	ns	44.6
	97 (p11)	11.71	ns	31.1
Sidestem	45 (p8)	4.21	ns	64.4
	50 (p9)	8.01	ns	42.3
	57 (p10)	11.81	ns	42.1
	97 (p11)	33.77	ns	35.0

Table 4.8 - LSD's, significances and CV%'s for fig. 4.5.

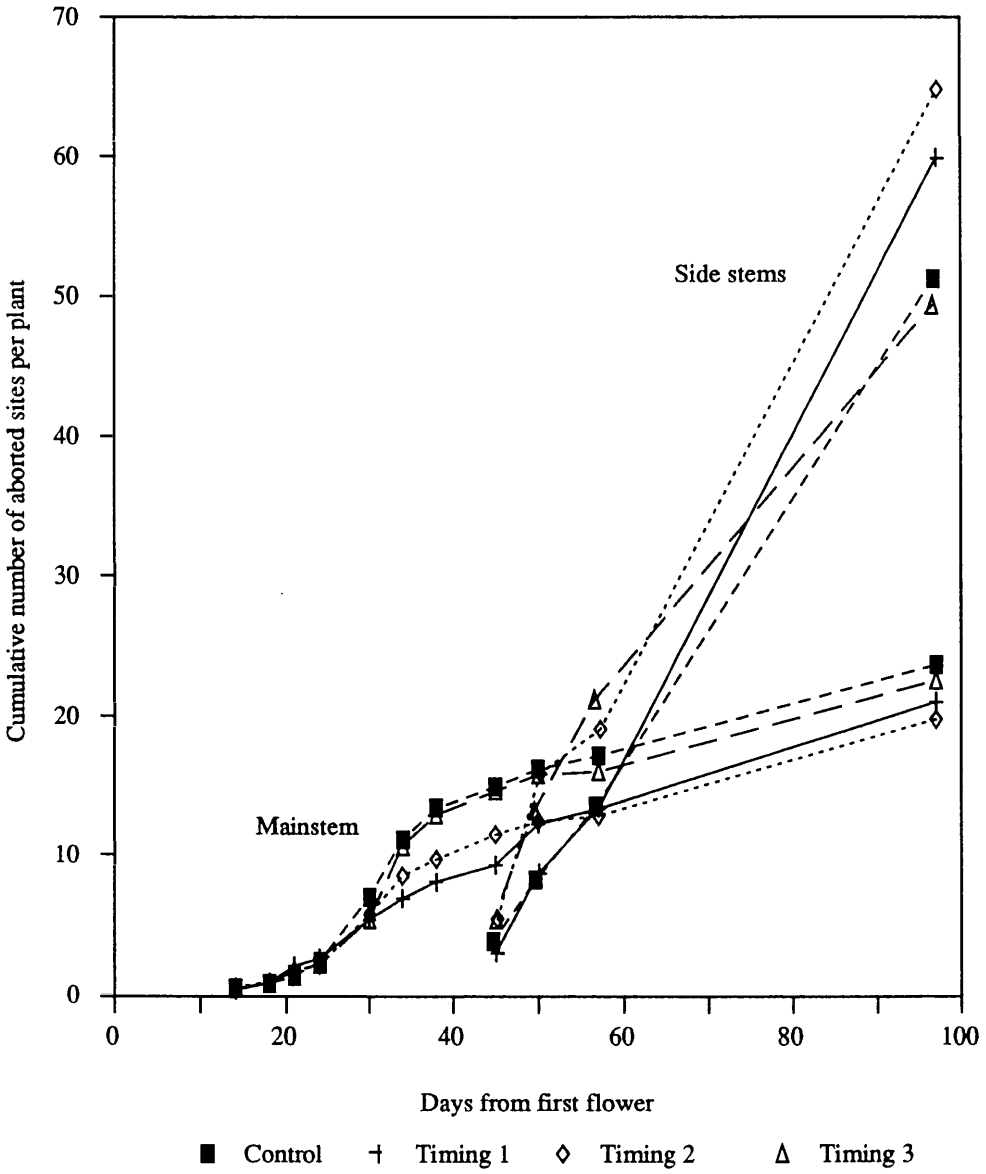


Fig. 4.5 - Effect of RSW0411 on the number of aborted sites.

Pod position	Monitoring period	LSD	sig.	CV%
Sidestem	p8	4.21	ns	64.4
	p9	6.32	ns	42.3
	p10	8.55	ns	42.1
	p11	31.02	ns	35.0

Table 4.9 - LSD's, significance and CV%'s for fig. 4.6.

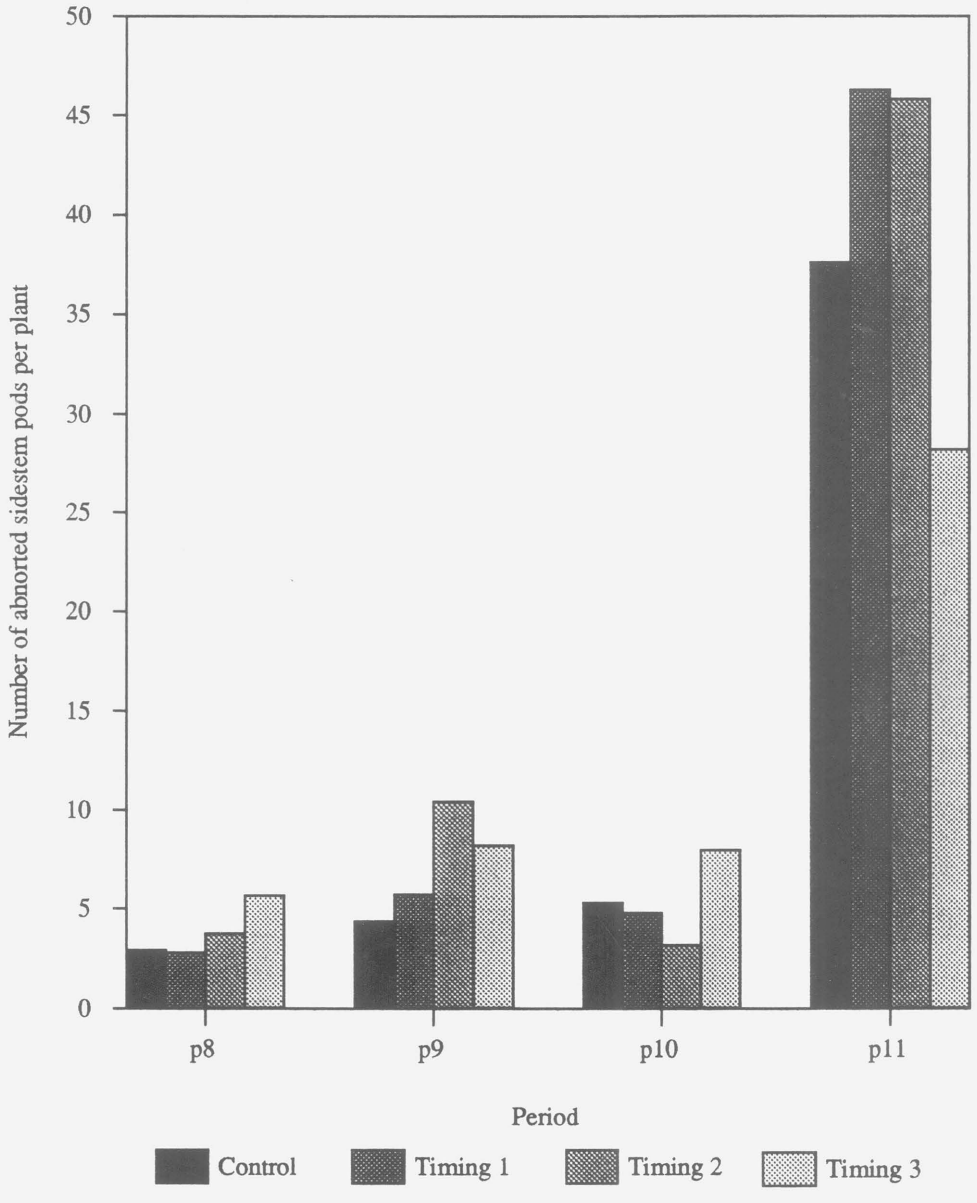


Fig. 4.6 - Effect of RSW0411 on the number of aborted pod sites on sidestems.

Initiation period	LSD	sig.	CV%
I1	0.92	ns	102.3
I2	1.78	ns	72.1
I3	1.17	ns	33.4
I4	0.69	ns	44.0

Table 4.10 - LSD's, significance and CV%'s for fig. 4.7.

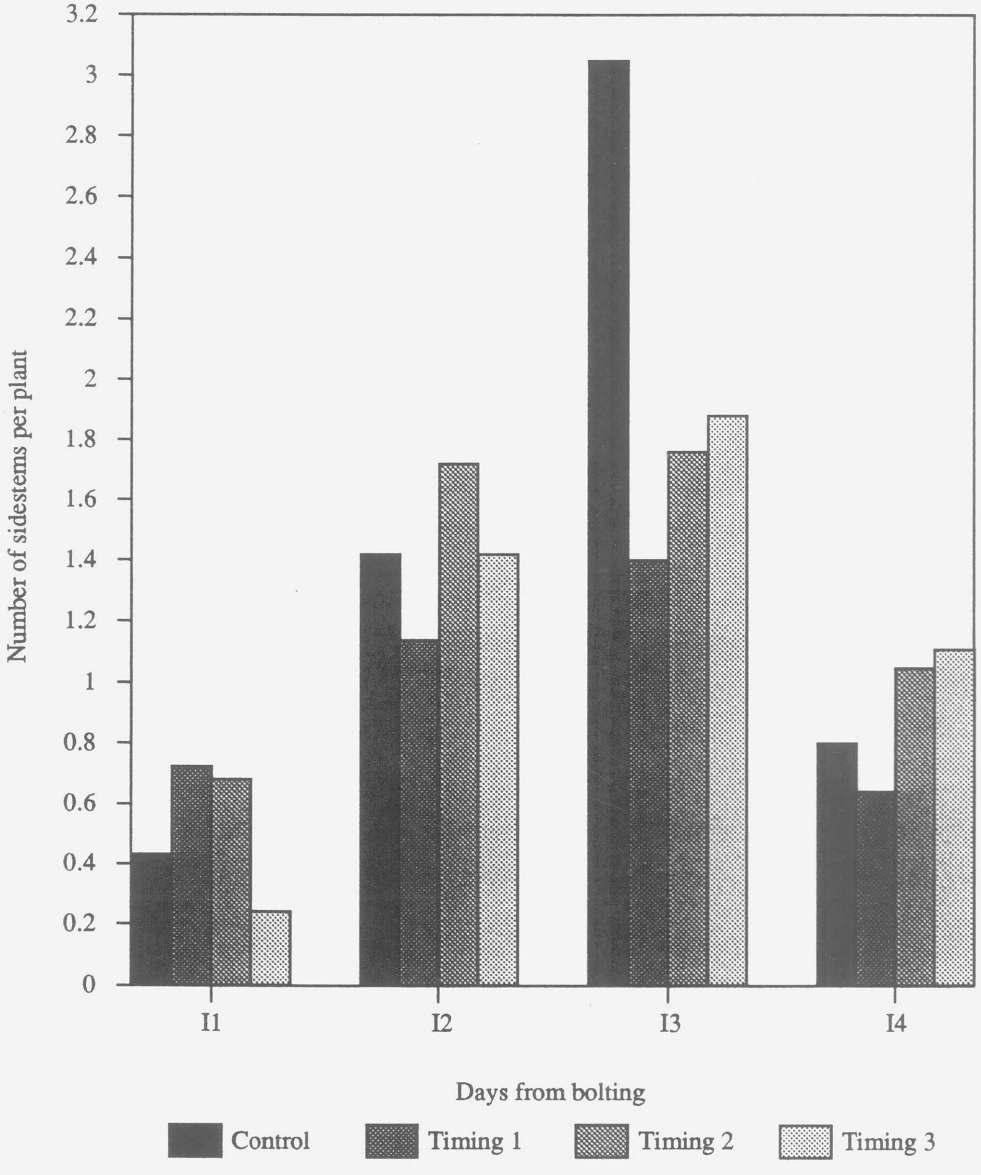


Fig. 4.7 - Effect of RSW0411 on the time of sidestem production.

Sidestem class	LSD	sig.	CV%
1-10	1.60	ns	41.4
11-20	0.78	ns	31.1
21-30	1.09	ns	46.1
31-40	1.14	ns	57.4
>41	0.29	**	18.5

Table 4.11 - LSD's, significance and CV%'s for fig. 4.8.

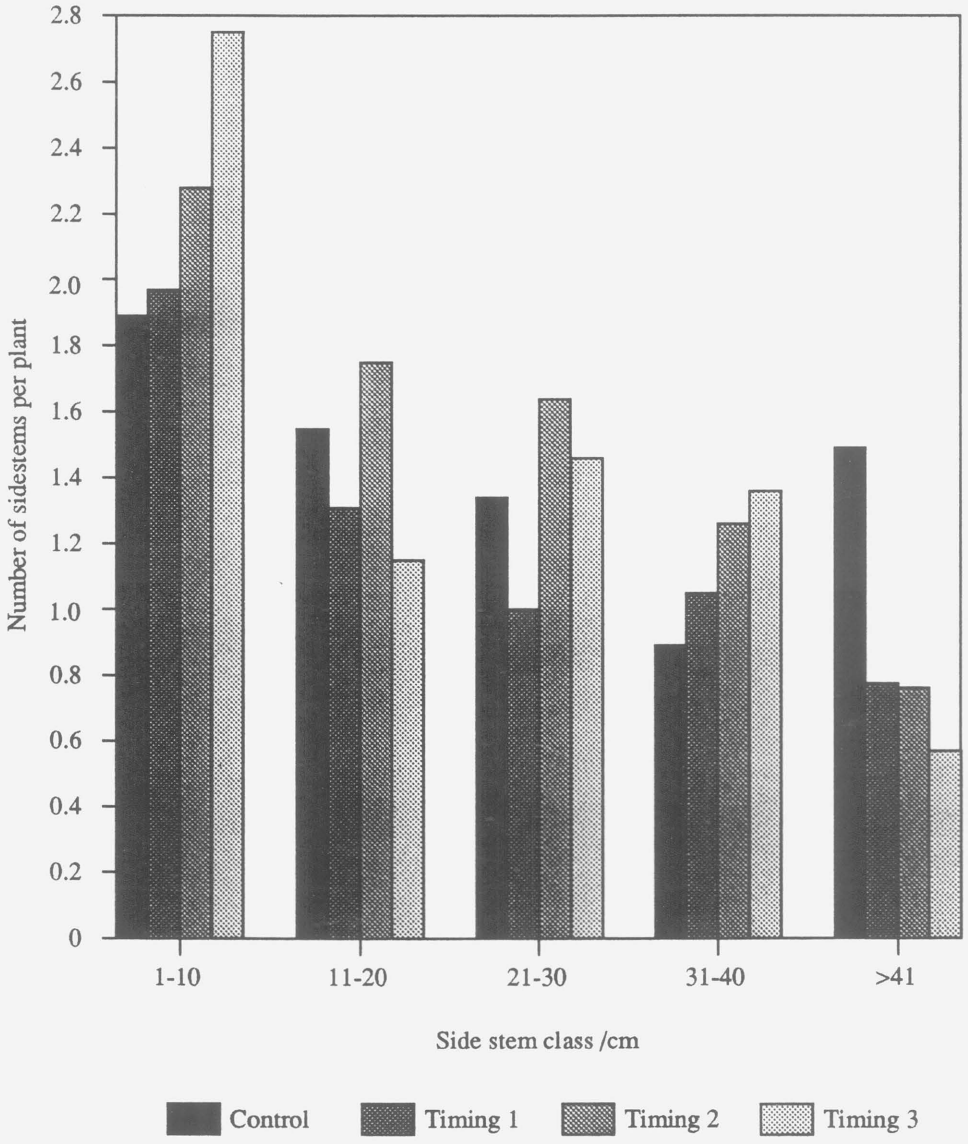


Fig. 4.8 - Effect of timing of RSW0411 on length of sidestems at final harvest (1/8/88).

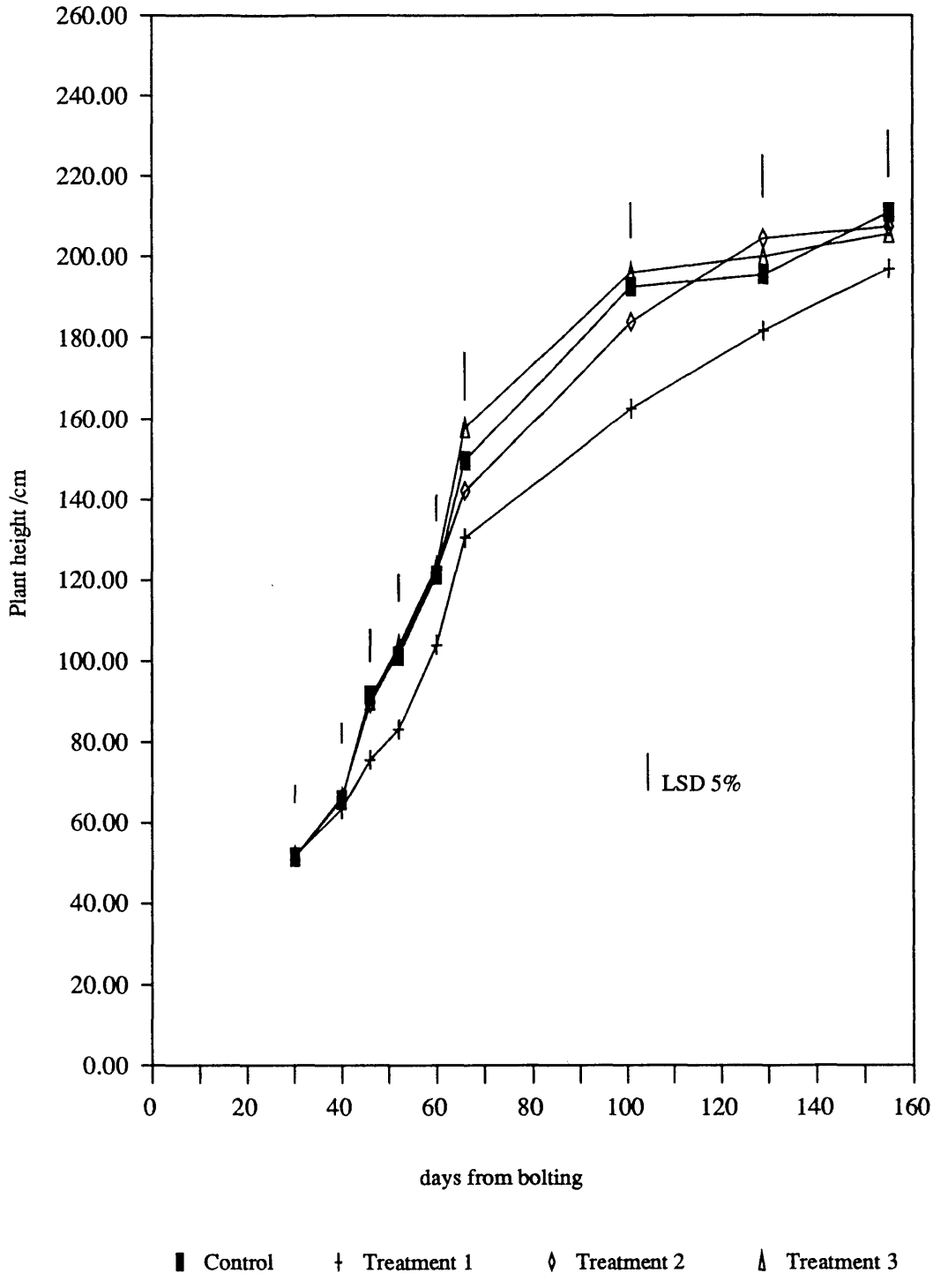


Fig. 4.9 - Effect of RSW0411 on plant height.

4.4 Discussion

The delay from the application of the growth retardant to its expression can be calculated from the flower production data, if promotion of flower production is considered to be a result of growth regulator application. T1 promoted flower production in the earliest monitoring periods, p1 and p2, T2 increased flower production in the later periods, p3-p6, and for T3 a promotion of flower production was seen on the sidestems. Thus the delay from application to effect was seen to be 45 days, 18 days and 24 days for T1, T2 and T3 respectively. Alternatively, if the retardation of plant height is used as an indicator T1 and T2 took 15 days and 6 days respectively to express their effect. T3 had no effect on plant height. The difference between time of application and effect between these two parameters are due to the different time for the processes to be affected. The process of flower differentiation is presumably much longer than the direct effect of reduced GA concentration on cell extension which reduces plant height.

Plants were growing faster at T2, if plants were following a sigmoidal growth curve as proposed by Hunt (1976), which may account for the shorter response time at this application date.

The reduction in plant height has been discussed previously. What was important in this experiment was the evidence of compensatory growth as the plant growth regulator lost its effect. This suggests that the plant's metabolism not only recovers from the retardation, but then accelerates to a level above that of the control. It has been suggested that this recovery arises because during the retardation a pool of gibberellin precursors accumulate which are then immediately available for use when the plant is alleviated of the restriction (Lever, 1986).

Early treatment with RSW0411 was seen to promote flowering on the mainstem, while treatment at sidestem extension promoted flowering on these sidestems. This contrasts with Scarisbrick *et al.* (1985) who observed that treatment with paclobutrazol increased abscission of immature pods in oilseed rape. However, the number of aborted sites were higher on the control and T3 plants, but the decline in pod abortion of T1 and T2 did not solely account for the increase in the number of pods of these treatments over the control and T3.

The results of other workers recording the effects of triazoles on flower production have been inconclusive. Hampton and Hebblethwaite (1985a) recorded an increase in the yield of a ryegrass seed crop as a result of an increase in the number of seeds per spikelet because of reduced seed abortion. Working with *azalea*, Oshio and Izumi (1986) recorded increased flowering in the second flush following application the previous season and

Iwahori and Tominga (1986) recorded an increase in flowering of the first flush of kumquat with the application of PP333. Conversely, when Menhennet (1984) applied PP333 to *Chrysanthemum moriflorum* and Child *et al.* (1987) applied RSW0411 to oilseed rape, both workers observed delayed flowering. Other workers have found no effect on flowering (McDaniel, 1983; Gianfagna and Wulster, 1986) while Baldev and Lang (1965) found application of a triazole growth retardant suppressed flowering.

These effects may be accounted for by the lowering of the GA concentration within the plant as a consequence of the application of RSW0411. In tomato it has been observed that a low GA concentration induces flower bud abortion, as does low light (Nester and Zeevaart 1988), while in high temperatures and low light application of chlormequat increased flower retention (Abdul, Conham and Harris, 1978). Kinet, Sachs and Bernier (1984) related a more complex picture; the early stages of inflorescence development are associated with a reduced GA concentration, but later in the initiation process GA's are promotive. Thus it may be that following the application of RSW0411 the temporary decline in GA content promotes the earlier flower initiation phase. Alternatively the increase in flower production could be a result of increased GA concentration. If a pool of GA precursors are produced as a result of the blocking of the synthesis pathway by RSW0411, once this blockage is overcome, as is suggested by the compensatory effects on plant height, this increase may then promote flowering. This is still in keeping with the work of Kinet *et al.* (1984) and is supported by Norris (1989) who found GA increased flowering in clover (*Trifolium repens).*

Zeevaart (1976) admitted that the GA metabolism of rosette plants is a complex situation, with gibberellins acting as promoters of flowering and bolting in some species and just bolting in others. The same work found GA's were to be inhibitory to flower initiation in *Fuchsia* and many woody perennials. In *Oenothera lamarckiana* GA promoted bolting and flowering, but with *Oenothera biennis* only bolting was promoted (Zeevaart, 1978).

It is concluded that the situation is complex and an increase in flower production as a consequence of reduced endogenous GA's may not be the sole cause of the observed flower promotion; although it is not always the total GA, but a particular GA that is important in the initiation of flowering.

An alternative theory that should be considered is the alteration of assimilate partitioning. Cook and Evans (1983) removed grains within a spike of wheat and observed that the yield of the remaining grains improved, which they attributed to improved assimilate supply. Tayo and Morgan (1979) reduced the assimilate supply, by leaf removal, in oilseed rape and recorded a reduced number of pods and seeds within the pods in this treatment.

Therefore with the reduction in the growth of the non-reproductive mainstem of treatments 1 and 2 it could be that the assimilate from this organ was transferred to flower bud production. Hampton and Hebblethwaite (1985b) found PP333 applied to a ryegrass seed crop increased assimilate demand within all sections of the ear. The increased pod abortion of the later monitoring times would support such an assimilate supply theory as outlined above. Thus later in the season maturing pods are better sinks for assimilate and attract available assimilate away from the newly formed flowers. Leaf senescence is also beginning to occur at these later dates increasing the competition for assimilates. These combined effects would increase the number of aborted sites in the later flowering periods.

The differing effects of the growth regulator timings on sidestem pod production observed here consist of two parallel effects. For T3 flower production on the sidestems is increased by those processes discussed for the mainstem in T1 and T2; it is a function of the timing of the regulator application. Secondly the greater sink of the mainstem pods in T1 and T2 may compete for assimilate with the sidestems thus reducing their numbers and their size.

4.5 Conclusion

Application of RSW0411 improved the pod yield of evening primrose non-significantly. Possibly on a larger scale this may prove economically important. It is suggested that this yield increase arises from a repartitioning of assimilate from the mainstem to the flower buds, improving the number initiated and reducing their abortion. Gibberellin metabolism may also be involved in this process, but the mechanism is complex and unclear.

The suggested time of application of the growth regulator is just after bolting though the spray window could extend approximately one month from this date. Later sprays improve the yield of sidestems, but the pods on these structures grow for a much shorter period and contribute less to final yield.

Chapter 5
Carbon 14 studies.

5.1 Introduction

Partitioning of photosynthetic product to individual plant organs can be studied by dry weight determinations throughout the season. However, the initial site of carbon fixation and the subsequent movement of photosynthate, plus any later remobilisation, may not always be revealed by this approach. It is, however, only when these underlying processes are known that rational judgements can be made on how to improve the performance of crop plants.

Radiolabelled carbon (^{14}C) has proved to be a useful tool in plant physiology studies. Hofstra and Nelson (1969) used labelled carbon to calculate the amount and rate of carbon export from leaves of different species. Flinn and Pate (1970) fed ^{14}C to the pod and its subtending leaf of field pea (*Pisum arvense*, L) to investigate their contribution to the seeds growing within the fed pod. Ismail and Sagar (1981) fed the third leaf of broad bean (*Vicia faba*, L) with $^{14}CO_2$ and monitored its fate over 7 days. They concluded that much of the labelled carbon remained in the fed leaf, unless there was a strong sink, such as fruits, nearby. Upward and downward movement of the ^{14}C was dependent on the position of such sinks relative to the fed leaf. They also reported that the stem acted as a temporary storage organ within the carbon economy of the plant.

The studies discussed thus far concern the feeding of various organs of single plants. Perhaps more realistic to the crop situation are field studies involving whole plant feeding such as those of Hume and Criswell (1973) with soyabean (*Glycine max*, L) and Parsons and Robson (1981) with ryegrass (*Lolium perenne*, L). Hume and Criswell (1973) observed ^{14}C accumulation in those plant organs growing most rapidly at the time of feeding, this resulted in the accumulation of ^{14}C in vegetative parts early in the life cycle and in the reproductive parts at ^{14}C feeds later in the season. Parsons and Robson (1981) reported that an increased proportion of the assimilate was partitioned to the roots between winter and spring, compared to that partitioned in the autumn to winter period, but this proportion decreased again with the onset of stem extension.

Labelled carbon has also been used to monitor differences in assimilate partitioning pattern as a result of PGR application. Hampton and Hebblethwaite (1985b) found paclobutrazol treated perennial ryegrass plants had a more uniform distribution of assimilate within the spike in comparison to untreated plants. Addo-quaye, Daniels and Scarisbrick (1985) fed carbon-14 to field grown oilseed rape (*B.napus*) plants at anthesis. They reported an increased partition of assimilate to side branches in those plants treated with paclobutrazol.

In the work reported in this study whole evening primrose plants, some of which were treated with RSW0411, were fed $^{14}CO_2$ at a range of development stages to elucidate the pattern of assimilate partitioning within the plants and the effect of the plant growth regulator upon this process.

5.2 Materials and methods

The establishment details and growing conditions of evening primrose for the two seasons of ^{14}C experiments are summarised in Table 5.1. On each feeding occasion a chamber, as described in Figure 5.1, was placed over the plants to be fed. A source of 100 microcuries Na_2CO_3 on Watman no.1 filter paper was then placed at 'a' where it was attached to the frame with 'blu-tack'. 1 kg of 'dryrite' (anhydrous copper sulphate, $CuSO_4.7H_2O$) was placed in foil boats on the floor of the chamber to reduce the humidity within it. This kept the stomata open, providing good CO_2 uptake, and prevented condensation on the sides of the chamber.

A 500 gauge polythene bag (250 x 50 x 50 cm) was then placed over the frame. At the bottom of the chamber excess polythene was laid flat and covered with soil to provide an effective seal. An excess (approximately 2 ml) of 5M H_2SO_4 was injected onto the source and the insertion hole sealed with tape. The electric fan 'b' was then started. The fan increased air movement within the chamber thus maintaining good gaseous exchange conditions by preventing the build up of leaf boundary layer resistance. Each labelling took place before 11 a.m., exposure was for 0.5 hr. Harvest details are in Table 5.1.

After harvest plants were immediately placed in a cold box and then taken to the laboratory for dissection. The dissection details are shown in Figure 5.2. Samples were dried at 60°C for 48hrs in a forced air oven.

Dried plant samples were weighed and then ground in a Dangoumau analytical ball mill. Approximately 0.5g of each sample was weighed accurately into a quartz boat and oxidised for 4 minutes in a Harvey Ox400 biological material oxidiser. The combustion occurred at 900°C in a stream of pure oxygen. The resultant gases were passed over a catalyst at 700°C (to remove impurities) and CO_2 plus $^{14}CO_2$ were absorbed in 14ml of scintillation cocktail (27% phenylethylamine, 27% industrial methylated spirit and 46% NE233 liquid scintillater) in a glass trap. ^{14}C activity of each sample was counted for 10 minutes in an SL33 Kantron Intertechnique liquid scintillation counter. Standards of 5000 counts per minute and blank determinations were also oxidised to determine the efficiency of the machine. It was assumed that the efficiency calculated for the standard was the same for all samples oxidised on that day.

Data are expressed as sink strength (percentage ^{14}C) and sink intensity (SI) after Heithott, Egli, Leggettand MacKown (1986).

Year	Plant establishment and inputs	Treatments used for C14 studies	Experimental design and harvest details	Date	Feed	Development stage at feeding
1987 Experiment 9	See section 3.2	Control and T2	3 plants chosen for uniformity were harvested at 0.5 hr, 24hr and 3 wks. There were four replicate blocks	11/8	Feed 1	Mainspike still flowering with lower pods maturing
				7/9	Feed 2	Flowering on mainspike finishing, but side stems in full flower
1988 Experiment 10	See section 4.2	Control and T2	3 plants harvested at 0.5 hr, 24 hr and final harvest. Plants were replicates.	15/5	Feed 1	Flowering started
				29/5	Feed 2	Majority of flowers on mainstem.
				14/6	Feed 3	Majority of flowers on side stems
				30/6	Feed 4	Flowering finished
				2/8	--	Final harvest

Table 5.1 - Experimental details of two seasons of feeding.

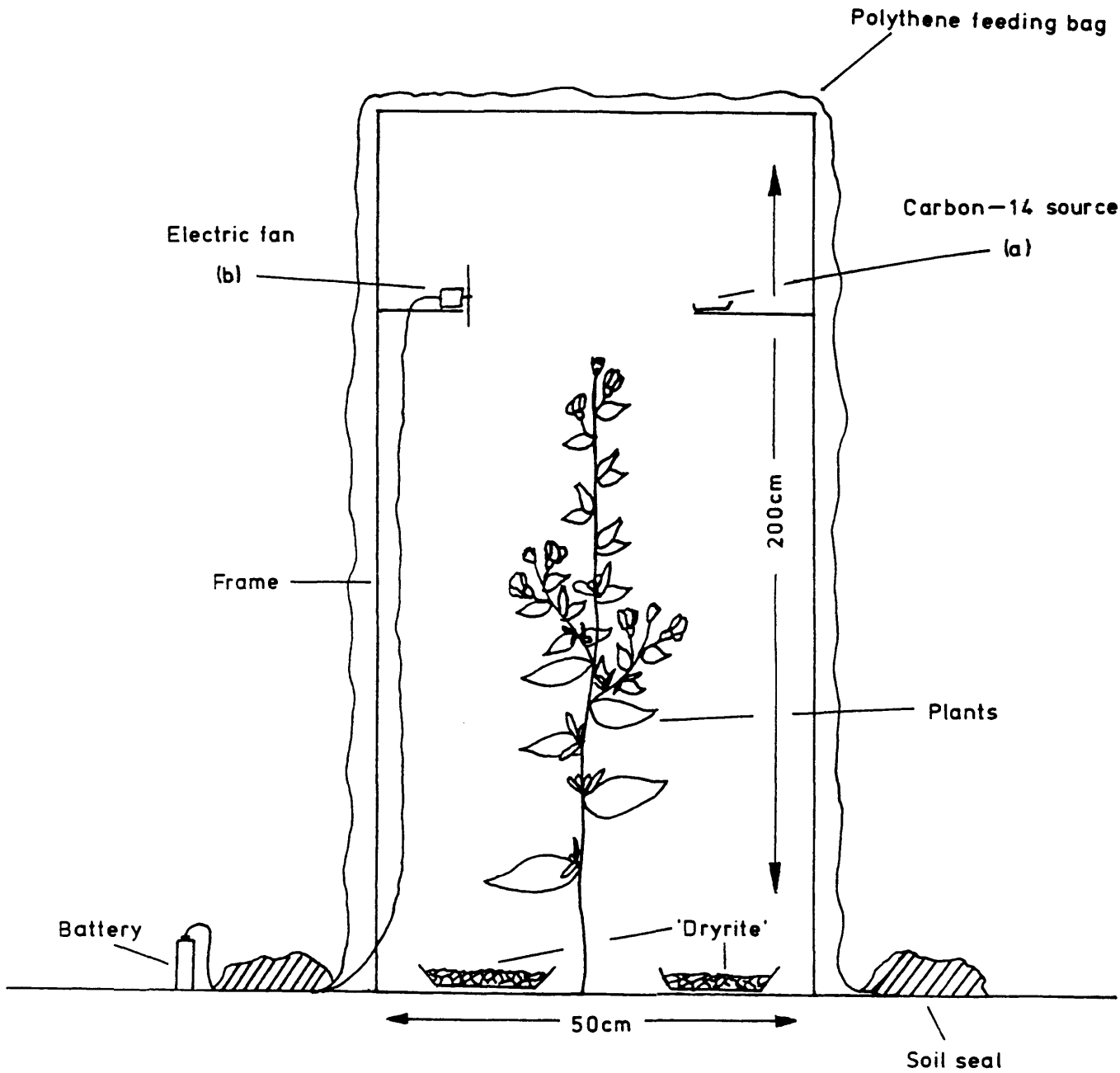
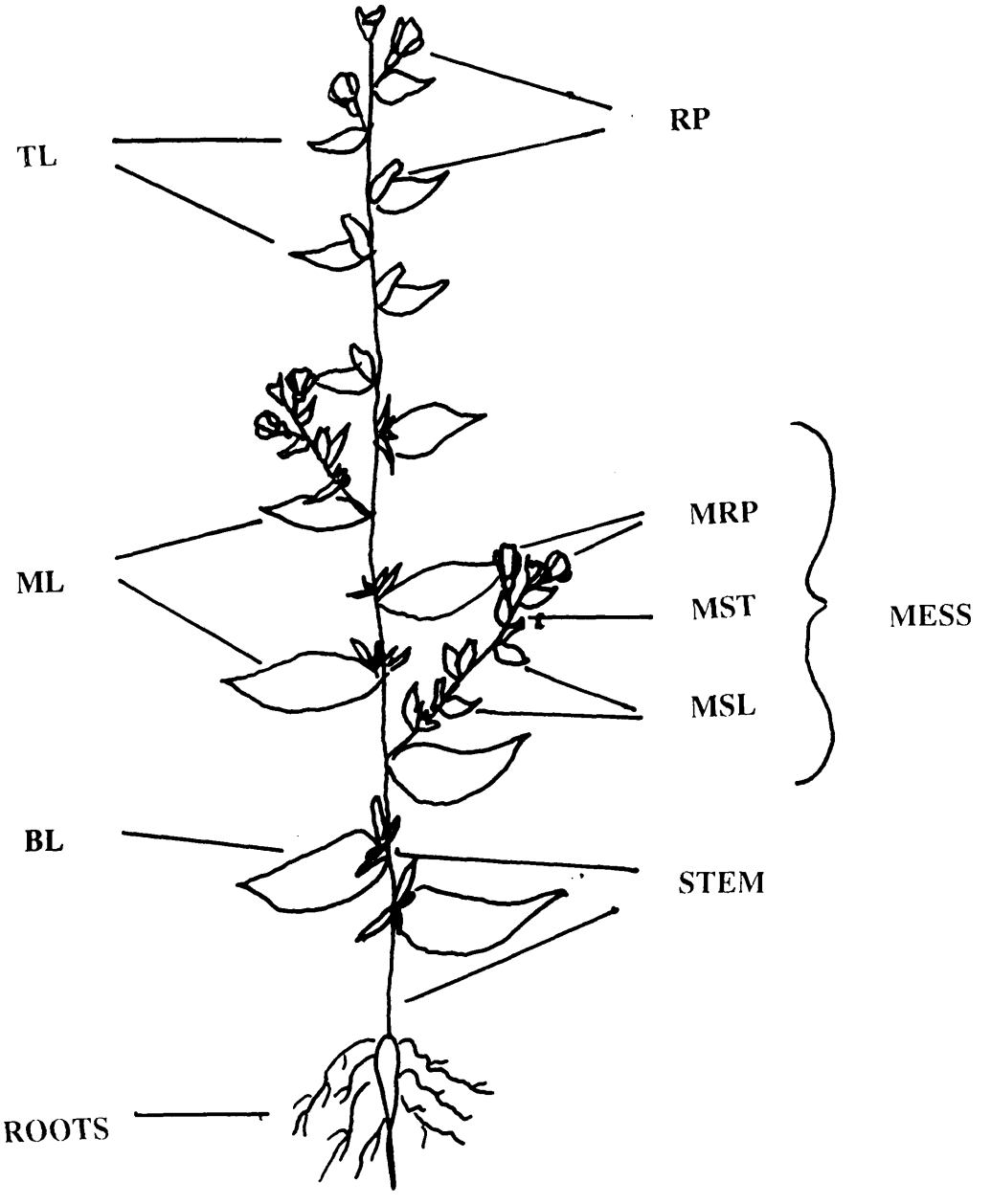


Fig. 5.1 - Cross-secton of carbon-14 feeding chamber.



RP reproductive parts

TL top leaves, those associated with reproductive parts.

ML middle leaves, those from the first extended sidestem to the base of the reproductive spike.

BL bottom leaves, leaves from the base of the plant to the first extended sidestem.

MRP reproductive parts of extended sidestems

MST stem of extended sidestems

MSL leaves of extended sidestems

MESS extended sidestems

Fig. 5.2 - Dissection details of plants after exposure to carbon-14

$$\text{Sink strength} = \frac{\text{d.p.m. recovered in plant part x 100}}{\text{total d.p.m. recovered in plant}}$$

$$\text{Sink intensity} = \frac{\text{sink strength}}{\text{weight of plant part}}$$

Sink strength is a measure of a particular components import of total radioactivity, i.e. $\%^{14}C$. Sink intensity is a measure of the concentration of that activity per unit mass. Within the text sink strength is referred to as percentage ^{14}C to avoid confusion between the two parameters. The unit for sink intensity is $\%^{14}C\ g^{-1}$ dry weight, and this is consistent throughout.

5.3 Results

5.3.1 1987 season

5.3.1.1 Feed 1 - mainspike still flowering with lower pods maturing.

All plant components showed differences in sink intensity between harvests. The sink intensity of reproductive parts increased between 0.5 and 24 hrs and declined to 3 wks ($p<0.01$), as did that of roots (Table 5.2). Top leaves and middle leaves declined in sink intensity across harvests ($p<0.01$). The sink intensity of the middle leaves of treated plants was higher than that of the controls at 0.5hrs. The bottom leaves sink intensity declined between 0.5 and 24hrs but did not decline further. The sink intensity of extended sidestems did not change between 0.5 and 24 hrs, but declined to 3 wks ($p<0.01$). The sink intensity of stem tissue increased between 0.5 and 24 hrs ($p<0.05$), but did not change thereafter. The sink intensity of roots also increased between 0.5 and 24 hrs ($p<0.01$).

0.5hrs after exposure at F1 the majority of the photosynthate (56%) was in the leaves, primarily in the middle leaves (Fig. 5.3). At the 24hr harvest the percentage ^{14}C of the leaves had declined, while that of the reproductive parts (flower buds and pods), stem and roots had increased. At three weeks the ^{14}C of the leaves had declined further (Fig. 5.3) with the main recipient of labelled assimilates being the stem.

5.3.1.2 Feed 2 - Flowering on the mainspike finishing, but the side stems are still in full flower.

The leaves were again the primary components of carbon fixation at feed2 having the highest sink intensities at 0.5 hr which then declined across harvests ($p<0.01$) (Table 5.4), only the sink intensity of the top leaves did not decline between 24 hrs and 3 wks. The leaves of extended sidestems had higher sink intensities than those of the control at this feed ($p<0.05$). The reproductive parts of the mainstem and extended sidestems and the roots increased in sink intensity between 0.5 and 24 hrs ($p<0.01$) and did not change subsequently. The sink intensity of reproductive parts of extended sidestems increased between 0.5 and 24 hrs, but despite this difference being greater than the $lsd_{0.05}$ harvest differences were not significant.

At F2 the main sites of carbon dioxide fixation, those with the highest percentage ^{14}C, were top leaves and middle leaves and to a lesser extent the bottom leaves and leaves of extended side stems (Fig. 5.4). The main sink for the assimilate at 24hrs after feeding at F2 were the reproductive parts (Fig. 5.4), with slight increases in the percentage ^{14}C of the stem

Component	Treatment	Harvest			Significance			CV%
		0.5hrs	24hrs	Final	t	h	t x h	
RP	C	0.93	4.38	1.03	ns	**	ns	21.3
	T	0.89	4.21	1.00	0.39	0.48	0.68	
TL	C	4.84	3.14	1.90	ns	**	ns	31.8
	T	6.52	3.75	1.91	1.04	1.27	1.80	
ML	C	3.48	2.01	0.97	*	**	**	27.8
	T	5.70	1.97	0.97	0.62	0.76	1.08	
BL	C	1.81	1.07	1.55	ns	*	ns	55.7
	T	2.48	1.12	0.53	0.71	0.87	1.22	
MESS	C	3.35	3.03	0.90	ns	**	ns	30.4
	T	4.27	3.06	1.45	0.72	0.89	1.25	
STEM	C	0.77	1.25	1.37	ns	*	ns	29.9
	T	0.80	1.38	0.93	0.29	0.35	0.50	
ROOTS	C	0.01	0.59	0.42	ns	**	ns	36.6
	T	0.02	0.73	0.46	0.12	0.15	0.21	

Numerical values in significance column are $lsd_{0.05}$.

Table 5.2 - Sink intensity of plant components at feed1, 1987.

Component	Significance			CV%
	t	h	t x h	
RP	ns 4.90	** 6.01	ns 8.50	46.9
TL	ns 2.89	** 3.55	ns 5.07	32.0
ML	ns 4.47	** 5.49	ns 7.76	29.9
BL	ns 4.18	** 5.12	ns 7.23	49.0
MESS	ns 5.12	ns 6.28	ns 8.87	65.8
STEM	ns 8.06	** 6.58	ns 11.40	18.4
R	ns 0.64	** 0.74	ns 1.11	34.4

Table 5.3 - lsd's, levels of significance and CV's for variables in fig 5.3.

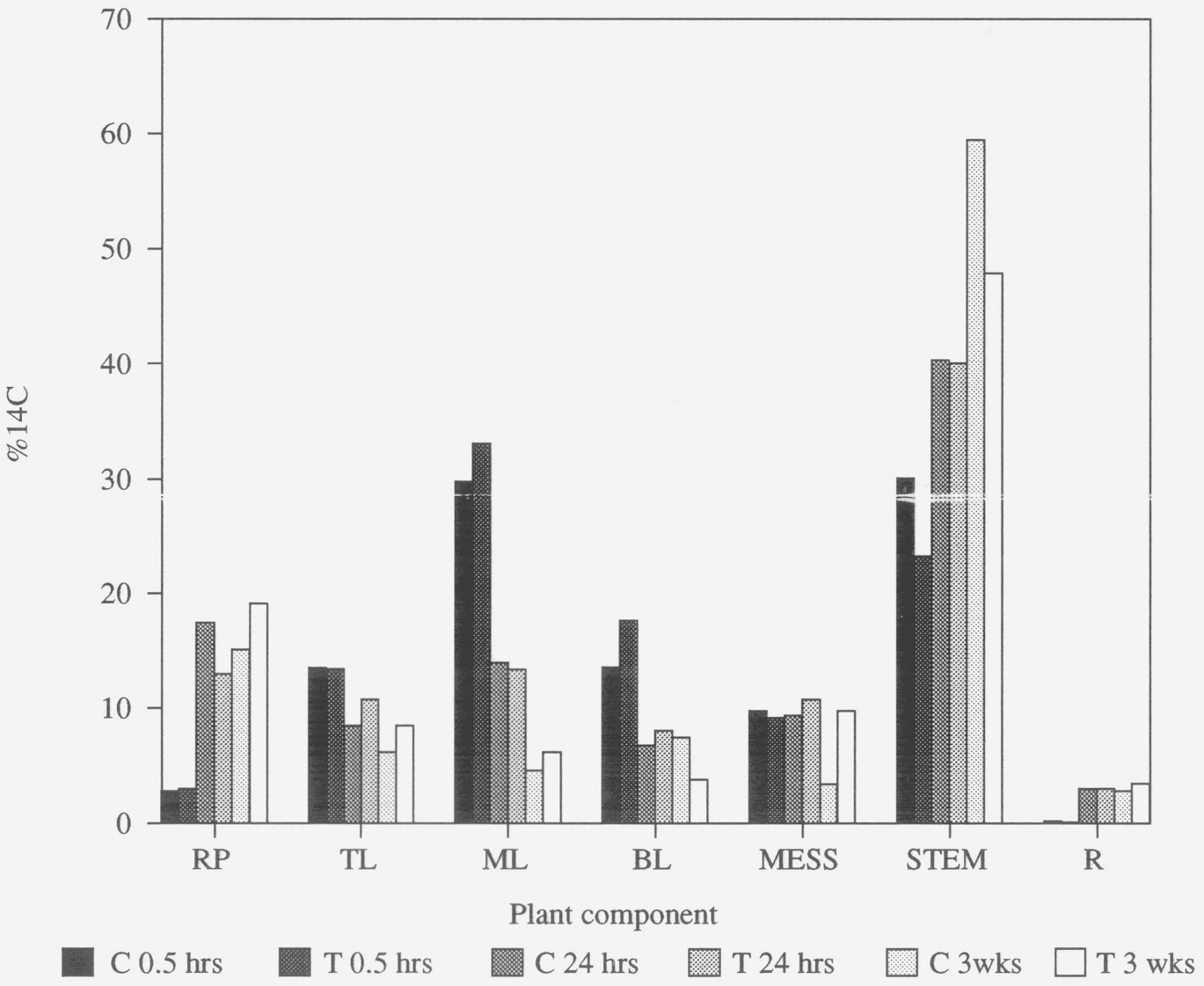


Fig. 5.3 - Percentage distribution of 14C at feed 1, 1987.

Component	Treatment	Harvest			Significance			CV%
		0.5hrs	24hrs	Final	t	h	t x h	
RP	C	0.54	4.29	4.31	ns	**	ns	17.8
	T	0.81	4.82	4.52	0.53	0.65	0.92	
TL	C	6.12	3.93	2.20	ns	**	ns	32.2
	T	7.91	2.89	2.04	1.24	1.52	2.15	
ML	C	4.04	3.14	1.16	ns	**	ns	26.1
	T	5.21	2.42	1.45	0.70	0.86	1.21	
BL	C	3.41	2.30	0.70	ns	**	ns	41.5
	T	4.83	1.99	1.13	0.92	1.12	1.59	
MRP	C	1.45	3.73	4.55	ns	ns	ns	72.3
	T	1.34	3.99	0.45	1.73	2.11	2.99	
MSL	C	3.36	2.50	0.89	*	**	ns	50.2
	T	7.54	4.16	1.39	1.53	1.88	2.66	
MST	C	2.30	1.87	2.30	ns	ns	ns	90.2
	T	2.20	1.10	2.90	1.06	1.29	1.83	
STEM	C	0.58	0.88	0.65	ns	ns	ns	32.8
	T	0.68	0.82	0.49	0.21	0.25	0.36	
ROOTS	C	0.03	0.35	0.51	ns	**	ns	63.2
	T	0.03	0.35	0.26	0.15	0.18	0.26	

Table 5.4 - Sink intensity of plant components at feed 2, 1987.

Component	Significance			CV%
	t	h	t x h	
RP	ns 9.04	** 11.08	ns 15.68	26.4
TL	ns 3.98	** 4.84	ns 6.85	38.7
ML	ns 1.66	** 2.03	ns 2.88	17.2
BL	ns 3.70	** 4.53	ns 6.41	74.0
MRP	ns 6.29	** 7.69	ns 10.88	145.7
MST	ns 3.25	ns 3.98	ns 5.63	94.2
MSL	ns 3.77	** 4.61	ns 6.53	66.4
STEM	ns 6.94	* 5.68	ns 9.84	29.4
R	ns 0.58	* 0.71	ns 1.00	65.1

Table 5.5 - lsd's, levels of significance and CV's for components in fig. 5.4.

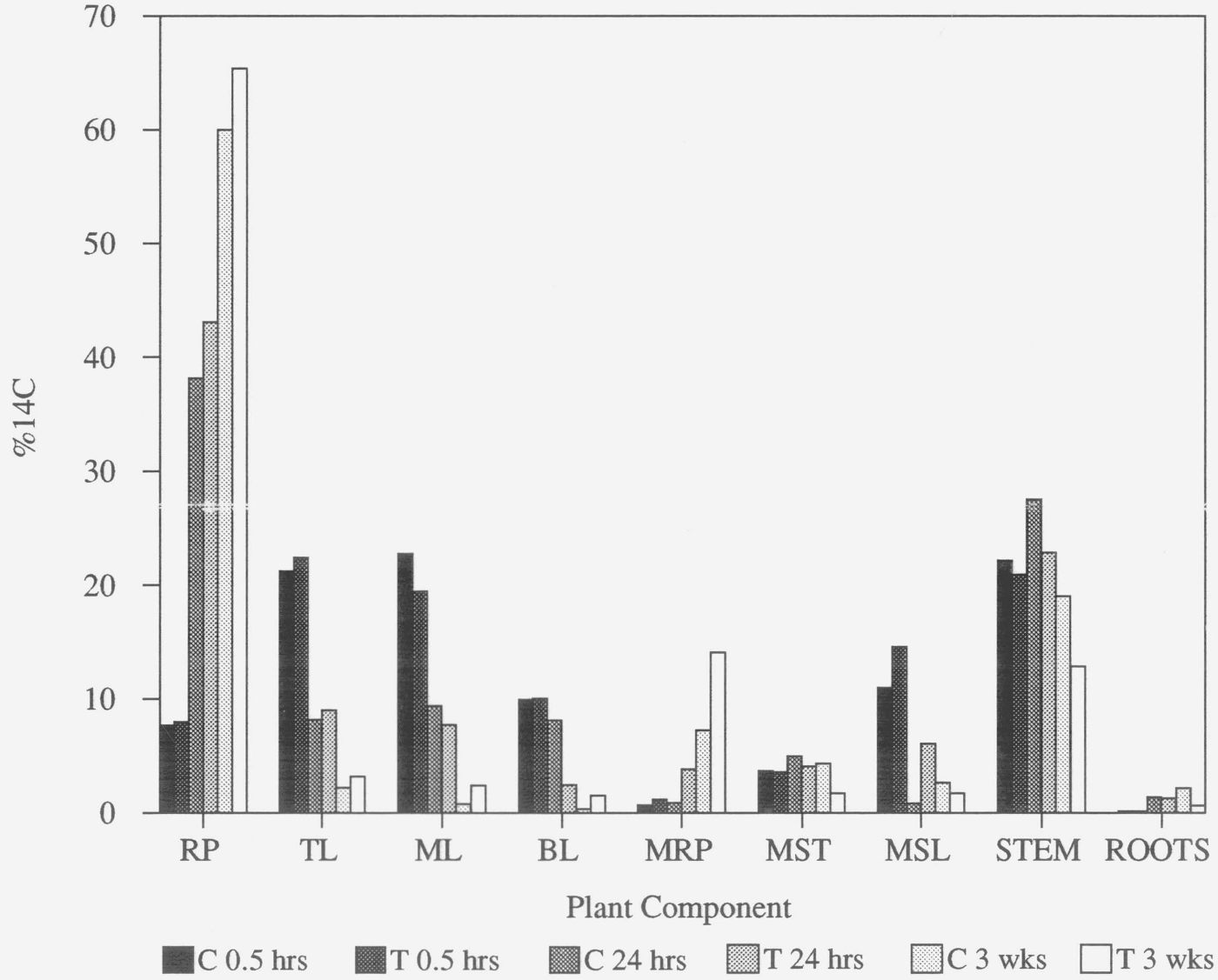


Fig. 5.4 - Percentage distribution of 14C at feed 2, 1987.

and roots. All leaf groups declined in percentage ^{14}C between 0.5 hrs and 24 hrs. At three weeks the reproductive parts, now just pods as flowering had finished, continued to be the main sink for labelled assimilate. Reproductive parts of extended side stems also imported labelled assimilate between 24 hrs and 3 wks.

5.3.2 1988 season

5.3.2.1 Feed 1 - Flowering just commenced.

At this feed treated plants had higher sink intensities in their reproductive parts than control plants ($p<0.05$) (Table 5.6). The sink intensity of reproductive parts did not change between 0.5 and 24 hrs, but declined to final harvest ($p<0.01$). Top leaves declined in sink intensity across all harvests ($p<0.01$), whereas the middle leaves, base leaves and extended sidestems declined (n.s.) to 24hrs and continued to decline to final harvest ($p<0.01$, $p<0.05$ and $p<0.01$ respectively). Stem tissue declined in sink intensity from 24 hrs to final harvest ($p<0.05$), the sink intensity of the stem of treated plants was greater than that of control plants at 0.5 hrs ($p<0.05$). No significant changes were observed in roots.

The majority of the radiolabel at feed 1 was concentrated in leaves, extended side stems and stem at 0.5 hrs (Fig. 5.5). At the 24 hr harvest there was little change in these values. At final harvest assimilate had been exported to pods and extended side stems which increased in percentage ^{14}C ($p<0.01$), while the radiolabel in leaf groups declined ($p<0.01$).

5.3.2.2 Feed 2 - Majority of the flowers produced on the mainstem, sidestems just beginning to flower.

At feed 2 the sink intensity of reproductive parts increased between 0.5 hr and 24 hr ($p<0.05$) (Table 5.8), but then declined to final harvest. The sink intensity of top, middle and bottom leaves did not change significantly between 0.5 and 24 hrs, but declined to final harvest ($p<0.05$, $p<0.05$, $p<0.01$ respectively). The extended sidestem sink intensities declined between 0.5 and 24 hrs ($p<0.01$), that of the treated plants was greater than the control ($p<0.05$). The sink intensity of of stems did not change across harvests, but at 0.5 hrs stems of treated plants had a higher sink intensity than controls.

The results for percentage ^{14}C, show that the majority of the fixation at F2 occurred in the leaf tissues as in F1, with the highest values recorded in the middle leaves (Fig 5.6). The percentage ^{14}C declined in top and middle leaves across harvests. Base leaves imported assimilate between 0.5 and 24 hrs. Significant differences were recorded between the 24 hr and final harvests in top leaves, middle leaves and bottom leaves ($p<0.01$). The difference

Component	Treatment	Harvest			Significance			CV%
		0.5 hrs	24 hrs	Final	t	h	t x h	
RP	C	2.38	2.79	1.43	*	**	ns	43.0
	T	5.85	5.07	0.94	1.36	1.66	2.38	
TL	C	8.79	5.48	2.22	ns	**	ns	30.6
	T	6.07	6.16	0.28	1.52	1.86	2.63	
ML	C	4.19	2.61	0.75	ns	**	ns	47.6
	T	2.73	3.41	0.39	1.14	1.41	1.99	
BL	C	3.75	2.29	0.80	ns	*	ns	66.6
	T	3.36	2.66	0.88	1.57	1.92	2.71	
MESS	C	4.44	2.52	0.92	ns	**	ns	52.1
	T	4.39	4.32	0.97	1.57	1.92	2.71	
STEM	C	1.26	1.55	1.47	ns	*	*	18.9
	T	1.92	1.85	0.99	0.29	0.36	0.51	
ROOTS	C	1.61	1.24	0.97	ns	ns	ns	103.7
	T	0.59	0.76	2.21	1.31	1.60	2.27	

Table 5.6 - Sink intensity of plant components at feed 1, 1988.

Component	Significance			CV%
	t	h	t x h	
RP	ns 1.88	** 2.31	ns 3.26	68.3
TL	ns 1.88	** 2.31	ns 3.26	26.1
ML	* 4.68	** 5.73	ns 8.12	54.6
BL	ns 6.47	** 7.93	ns 11.20	59.5
MESS	ns 6.25	** 7.65	ns 10.81	34.4
STEM	ns 5.42	ns 6.67	** 9.41	14.0
R	ns 9.35	ns 11.44	ns 16.19	91.7

Table 5.7 - lsd's, levels of significance and CV's for variables in fig 5.5.

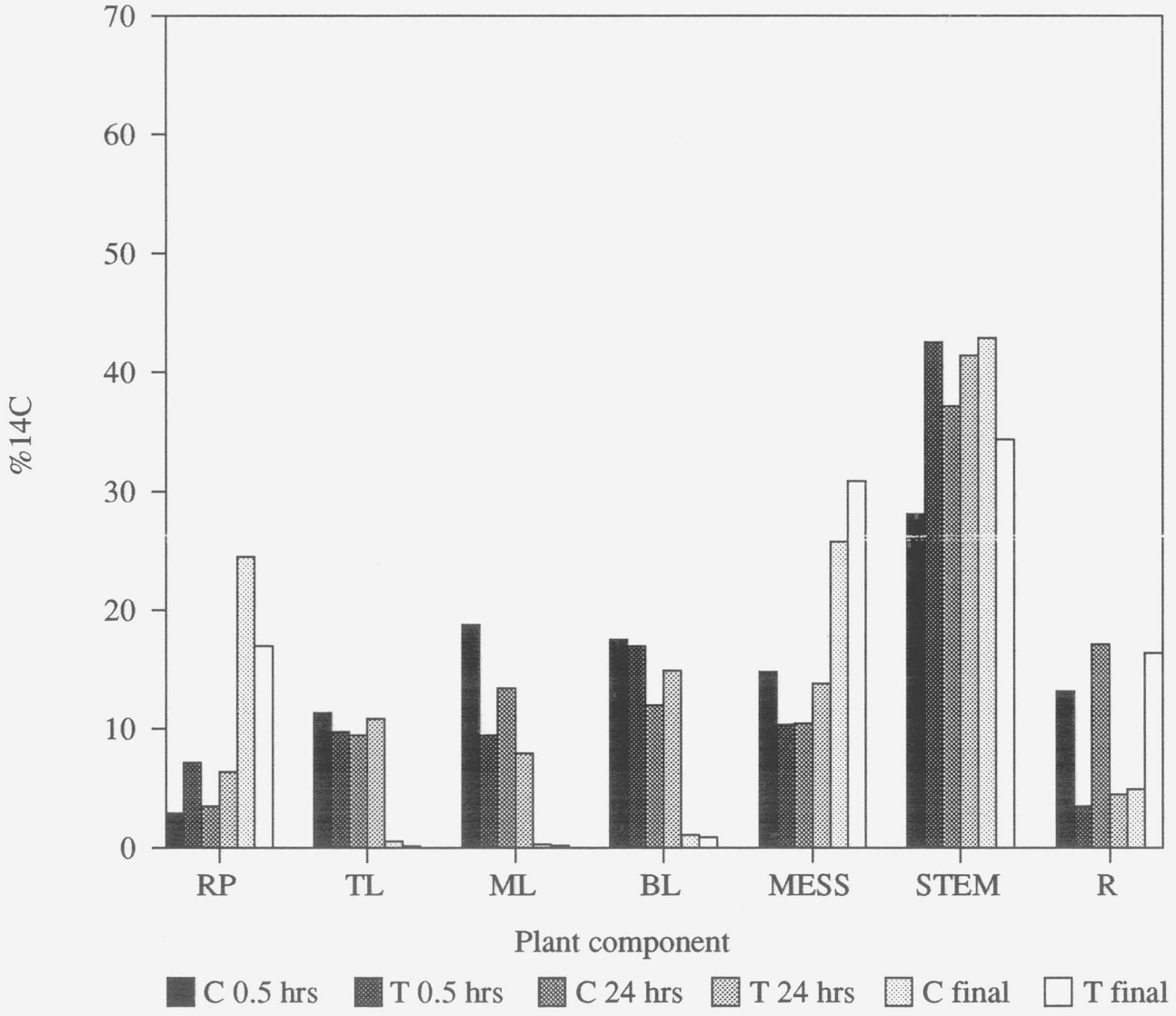


Fig. 5.5 - Percentage distribution of 14C at feed 1, 1988.

Component	Treatment	Harvest			Significance			CV%
		0.5hrs	24hrs	Final	t	h	t x h	
RP	C	2.28	3.12	1.82	ns	*	ns	73.1
	T	0.93	6.85	1.72	2.05	2.52	3.56	
TL	C	4.79	2.15	0.57	ns	*	ns	56.7
	T	3.73	5.76	2.11	1.82	2.23	3.16	
ML	C	3.72	2.43	0.67	ns	*	ns	80.6
	T	4.08	1.72	0.23	1.74	2.13	3.01	
BL	C	1.33	3.30	0.67	ns	**	ns	49.8
	T	2.95	2.61	0.67	0.96	1.18	1.67	
MESS	C	2.23	1.15	1.14	*	**	ns	40.9
	T	3.89	1.96	1.15	0.79	0.97	1.37	
STEM	C	0.53	1.21	1.09	ns	ns	*	24.4
	T	1.26	0.88	1.34	0.26	0.32	0.45	
ROOTS	C	0.68	1.06	0.86	ns	ns	ns	69.4
	T	0.61	0.47	1.11	0.56	0.68	0.97	

Table 5.8 - SInk intensity of plant components at feed 2, 1988.

Component	Significance			CV%
	t	h	t x h	
RP	ns 9.92	* 12.15	ns 17.20	52.7
TL	ns 4.82	** 5.48	* 8.26	66.0
ML	ns 8.96	** 10.87	ns 15.36	65.2
BL	ns 4.69	** 5.69	ns 8.04	60.9
MESS	ns 7.48	** 9.06	ns 12.8	48.0
STEM	ns 8.04	** 9.85	** 13.92	25.4
R	ns 7.11	ns 8.63	ns 12.2	87.3

Table 5.9 - lsd's, levels of significance and CV's for variables in fig 5.6.

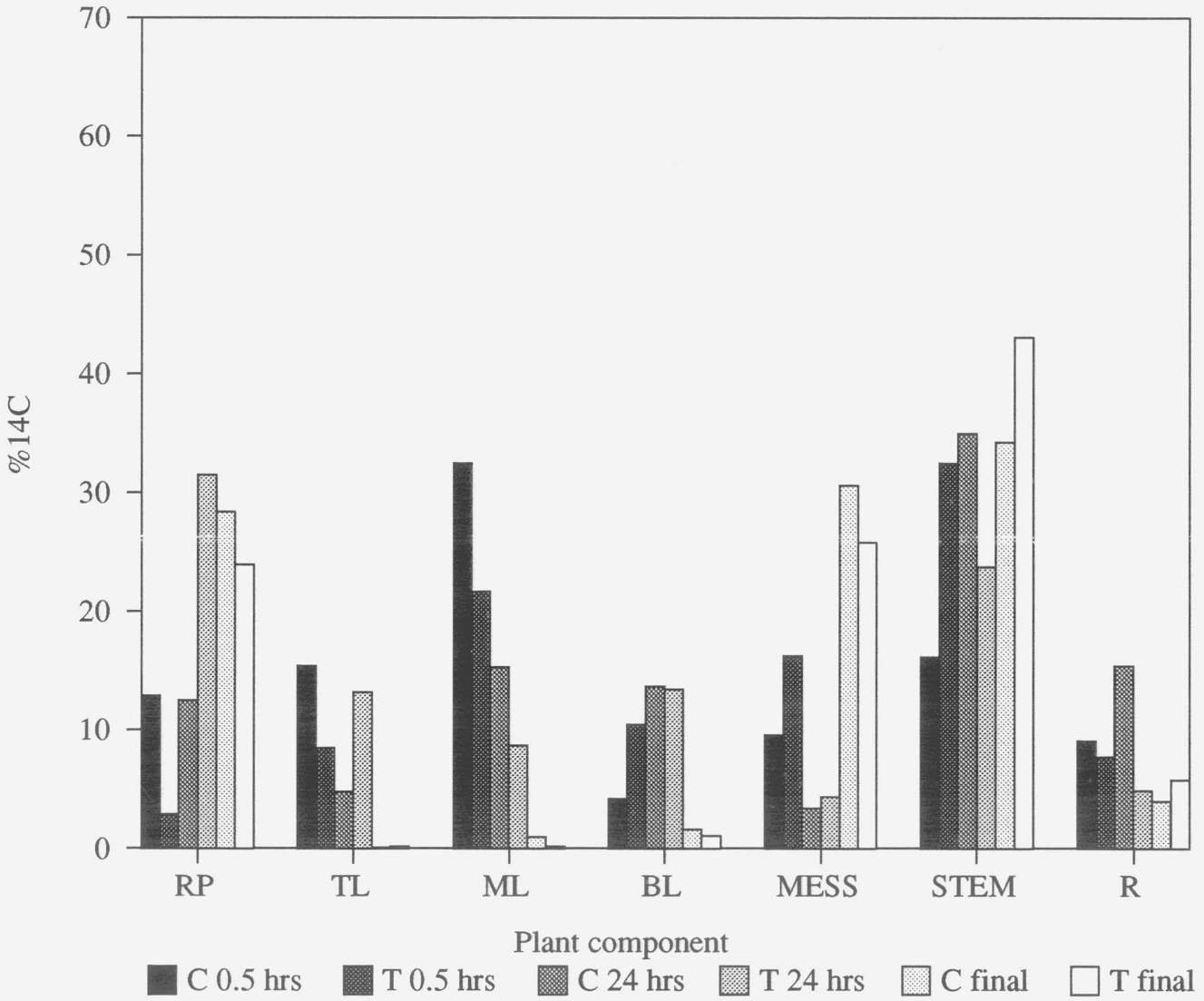


Fig. 5.6 - Percentage distribution of 14C at feed 2, 1988.

between 0.5 and 24 hrs was also significantly different for middle leaves ($p<0.01$). The pods displayed large increases in their percentage ^{14}C between 0.5 and 24 hr harvests, this was predominantly due to treated plants. The percentage ^{14}C extended side stems declined between 0.5 and 24 hr harvests , but then increased to final harvest in both treatments.

5.3.2.3 Feed 3 - Majority of flowers now on the sidestems

The sink intensity of reproductive parts increased between 0.5 and 24 hr, but did not change to final harvest ($p<0.01$) (Table 5.10). Top and bottom leaves declined across all harvests ($p<0.01$), whereas middle leaves only declined between 0.5 and 24 hrs ($p<0.01$) and leaves of extended sidestems declined between 24 hrs and final harvest ($p<0.01$). The reproductive parts of extended sidestems increased between 0.5 and 24 hrs then declined to final ($p<0.01$). The sink intensity of the stem of extended sidestems declined in sink intensity between 24 hrs and final harvest ($p<0.01$). There was no change in the sink intensity of mainstems. Overall roots declined in sink intensity across harvests ($p<0.01$), but the data was not uniform; control plants declining between 24 hrs and final harvest and the sink intensity of treated plants increasing in the same period ($p<0.01$).

At feed 3 the leaves were again the major sites of fixation containing over 50% of the labelled carbon at 0.5 hrs (Fig. 5.7). At final harvest the majority of the labelled carbon was retained in the reproductive parts (mainstem pods and extended side stem reproductive parts); 68.6% and 34.2% in control and treated plants respectively. The lower value of the treated plants was because of ^{14}C retained in the stems and leaves of extended side stems.

5.3.2.4 Feed 4 - Flowering finished.

The reproductive parts increased in sink intensity between 0.5 hrs and final harvest ($p<0.01$) (Table 5.12), but the difference between 0.5 and 24 hrs was not significant. The sink intensity of top leaves and the leaves of extended sidestems did not change significantly across harvests. Middle leaves' sink intensity declined across harvests ($p<0.01$) and the sink intensity of bottom leaves declined between 24hrs and final harvest ($p<0.05$). The reproductive parts of extended sidestems showed no change, but maintained a high sink intensity across harvests. The stem of extended sidestems increased in sink intensity between 0.5 and 24 hrs and then declined to final ($p<0.01$). The sink intensity of roots increased between 0.5hrs and final harvest ($p<0.01$).

The distribution of radiolabel at feed 4 is illustrated by the percentage ^{14}C results in Fig. 5.8. Pods, there were no longer any flower buds, increased in percentage ^{14}C across harvests with 0.5 hrs < 24 hrs < final ($p<0.01$). Top leaves declined from 0.5hrs to final, with the

Component	Treatment	Harvest			Significance			CV%
		0.5 hrs	24 hrs	Final	t	h	t x h	
RP	C	0.88	1.81	3.24	ns	**	ns	32.4
	T	0.81	2.17	1.99	0.60	0.74	1.05	
TL	C	3.80	1.82	1.26	ns	**	ns	30.6
	T	3.46	2.66	0.88	0.73	0.89	1.26	
ML	C	4.43	1.91	0.80	ns	**	ns	51.6
	T	6.51	3.00	1.36	1.59	1.95	2.76	
BL	C	3.37	2.26	0.87	ns	**	ns	34.1
	T	3.98	3.78	0.88	0.88	1.08	1.53	
MRP	C	2.35	3.88	1.52	ns	**	ns	28.0
	T	4.25	5.73	1.03	1.22	1.50	2.12	
MST	C	2.95	2.32	0.95	ns	**	**	23.7
	T	1.29	2.40	1.71	0.47	0.58	0.82	
MSL	C	4.36	3.55	0.95	ns	**	ns	34.5
	T	5.08	3.56	1.71	1.13	1.39	1.97	
STEM	C	0.75	0.91	0.78	ns	ns	ns	36.7
	T	0.90	0.71	1.39	0.34	0.42	0.59	
ROOTS	C	1.78	2.60	0.28	ns	**	**	28.1
	T	1.59	0.27	1.34	0.38	0.46	0.65	

Table 5.10 - Sink intensity of plant components at feed 3, 1988.

Component	Significance			CV%
	t	h	txh	
RP	ns 5.19	** 6.34	** 8.96	26.3
TL	** 1.08	** 1.32	ns 1.87	18.5
ML	* 4.16	** 5.10	ns 7.21	53.3
BL	ns 3.77	** 4.62	ns 6.53	34.0
MRP	ns 6.12	ns 7.34	ns 10.35	59.9
MST	ns 2.65	ns 2.01	** 4.34	34.0
MSL	ns 2.56	** 3.13	** 4.43	22.1
STEM	ns 8.15	ns 9.97	ns 14.12	35.0
R	* 1.46	* 1.79	** 2.53	24.1

Table 5.11 - lsd's, levels of significance and CV's for the variables in fig. 5.7.

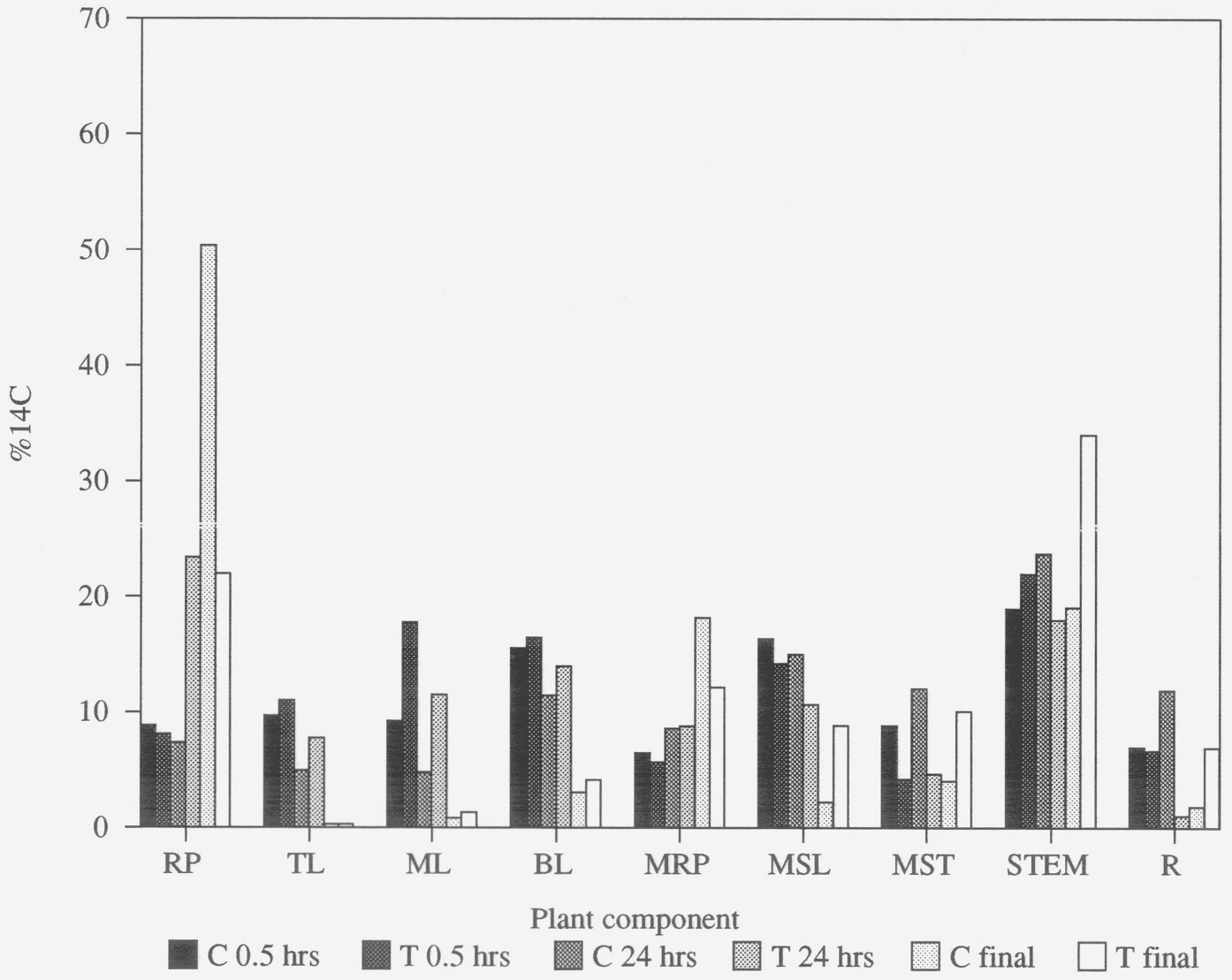


Fig. 5.7 - Percentage distribution of 14C at feed 3, 1988.

Component	Treatment	Harvest			Significance			CV%
		0.5hrs	24hrs	Final	t	h	t x h	
RP	C	0.38	2.26	2.98	ns	*	ns	65.8
	T	0.39	0.80	1.74	0.96	1.18	1.67	
TL	C	3.40	2.90	1.40	ns	ns	ns	40.9
	T	5.20	4.10	2.10	2.36	2.89	4.09	
ML	C	6.89	4.51	0.78	ns	**	ns	28.3
	T	6.83	4.51	1.08	1.19	1.46	2.06	
BL	C	5.97	5.16	1.73	ns	*	ns	58.3
	T	3.39	4.28	0.76	2.12	2.60	3.68	
MRP	C	4.73	3.18	5.55	ns	ns	ns	43.7
	T	4.45	4.25	4.20	1.97	2.41	3.41	
MST	C	1.09	7.18	2.06	ns	**	ns	72.2
	T	1.03	4.72	1.72	2.20	2.70	3.87	
MSL	C	3.02	2.79	2.98	ns	ns	ns	56.2
	T	2.07	3.77	1.96	1.59	1.96	2.77	
STEM	C	0.36	0.64	0.61	ns	ns	ns	36.2
	T	0.52	0.76	0.50	0.21	0.26	0.36	
ROOTS	C	0.05	0.08	0.49	ns	**	ns	65.0
	T	0.03	0.12	0.35	0.13	0.15	0.22	

Table 5.12 - Sink intensity of plant components at feed 4, 1988.

Component	Significance			CV%
	t	h	t x h	
RP	ns 6.00	** 7.27	ns 10.30	37.2
TL	ns 3.69	** 4.48	ns 6.33	43.6
ML	ns 8.43	** 10.22	ns 14.45	55.1
BL	ns 12.08	ns 14.64	ns 20.70	118.7
MRP	ns 10.96	* 13.42	ns 18.98	57.9
MST	ns 4.64	ns 5.62	ns 7.98	61.7
MSL	ns 7.97	ns 9.67	ns 13.68	77.7
STEM	ns 4.55	ns 5.58	ns 7.91	33.3
R	ns 0.36	** 0.44	ns 0.62	44.4

Table 5.13 - lsd's, levels of significance and CV's for variables in fig. 5.8.

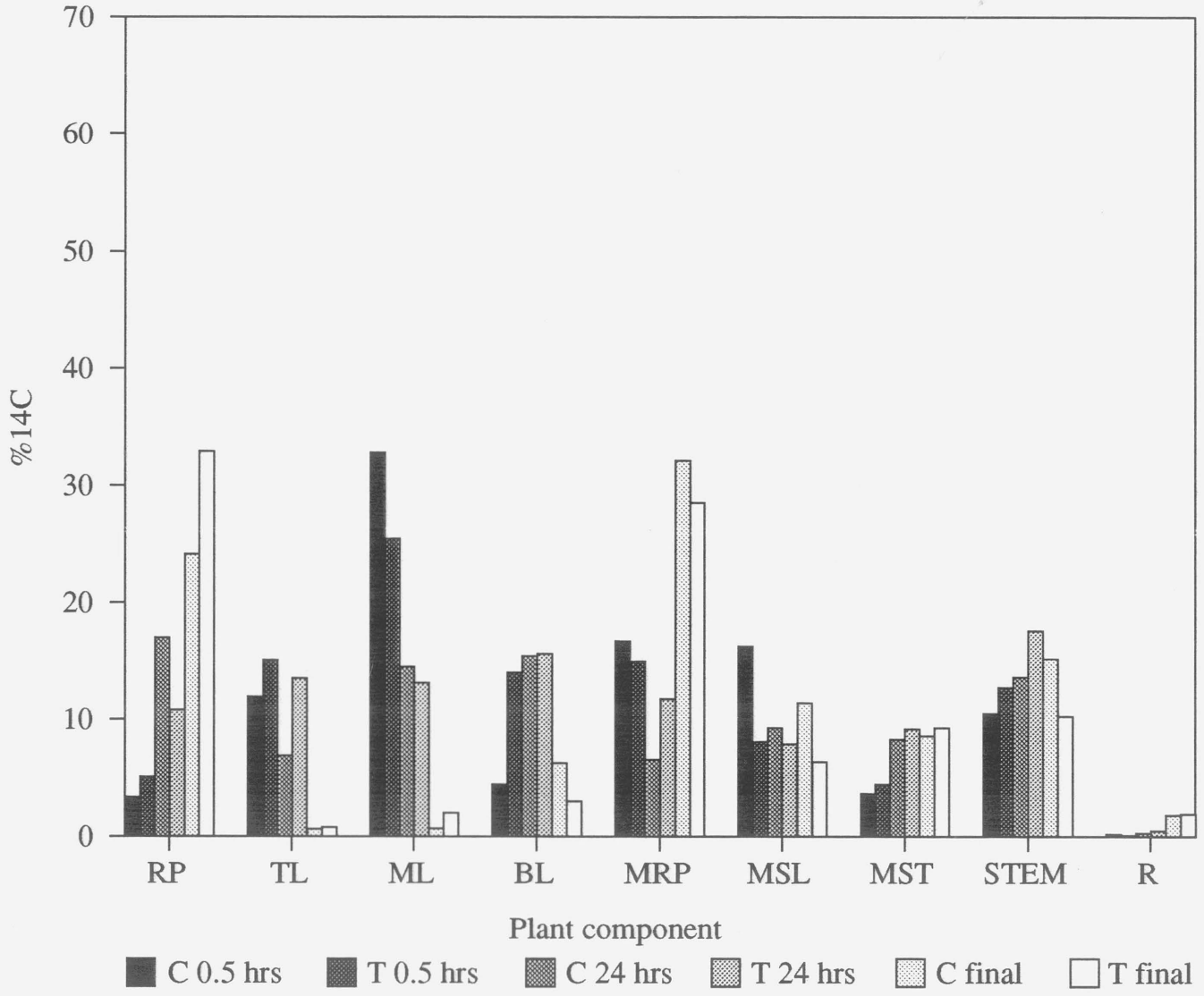


Fig. 5.8 - Percentage distribution of 14C at feed 4, 1988.

results for 0.5 hrs and 24 hrs being greater than that for final ($p<0.05$). Middle leaves also declined across harvests with 0.5 hrs > 24 hrs > final ($p<0.01$). The percentage ^{14}C in extended side stem reproductive parts declined between 0.5 and 24 hrs and then increased to final harvest, but only the difference between 24 hrs and final was significant ($p<0.05$). No significant differences were recorded for leaves of extended side stems.

5.4 Discussion

At F1 in 1987 assimilate was moved to reproductive parts, stem and roots, from all leaf groups. This movement to pods and roots occurred between 0.5 and 24 hrs. The sink intensity of pods also increased in this time, but declined between 24 hrs and final harvest. During this period the weight of pods increased dramatically (Appendix 8). This incoming assimilate would 'dilute' any of the initially fixed radiocarbon producing the observed decline in sink intensity. This process was also observed in the roots though the accumulation of dry matter between 24 hrs and final harvest was not as pronounced in this component. The sink intensity of the stem did not change between 24 hrs and final harvest, but percentage ^{14}C increased within the same period as a result of an increase in its weight. This movement did not occur in the pods as previously discussed. It is therefore suggested that the stem is a preferred sink at this feed. From experimental observations it is known that stem growth occurs before the pods begin to accumulate dry matter, which would account for these differences in sink intensity.

At F2 in 1987, the majority of the fixation occurred equally in the top leaves and middle leaves, with bottom leaves providing a smaller amount. A rapid decline in the percentage ^{14}C occurred in all leaves between 0.5 and 24 hrs, the subsequent decline to 3wks was not as great. This agrees with Ismail and Sagar (1981) who reported a rapid decline in the percentage ^{14}C in broad bean leaves between 0 and 3 hrs with a slow decline to 3 wks, and Farrar (1980) who also observed a biphasic export pattern from leaves of barley. Leaves of extended side stems declined in percentage ^{14}C across harvests, stem tissue remained static, while the percentage ^{14}C in reproductive parts increased as did their sink intensity. Mainstem pods were the main sinks at feed 2 with the percentage ^{14}C increasing across harvests, with leaves acting as the primary sources. Ismail and Sagar (1981) found the percentage ^{14}C in reproductive parts at 24 hrs increased from 15% to 90% between early/late flowering and pod ripening, which equate with the results for F1 (18 %) and F2 (68 %) observed here.

At feed 1 in 1988 leaves were the main sites of fixation (C=47.6%, T=36.3%). A high proportion of the ^{14}C at 0.5 hrs was also contained in the extended side stems and the stem. Sink intensity values were higher in leaves and extended side stems than stem. This suggested that these were the major sites of fixation and that the large percentage ^{14}C of bottom stem is a consequence of its larger weight (Appendix 9). In all components there was little change in the sink intensity and percentage ^{14}C values between 0.5 hrs and 24 hrs. It is proposed that at this development stage the sink tissues, such as pods, are small and therefore do not import photosynthate in large enough quantities to affect the results. This is supported by the results of previous workers; Carlson and Brun (1984) found increased

partition of assimilate to the reproductive node in soyabean, with increased reproductive load at that node, and Chamberlain and Wilson (1982) reported that the leaves of grain-sorghum retained over 60% of the labelled assimilate after 48 hrs when fed before panicle initiation.

At final harvest of feed 1 the percentage ^{14}C had moved predominantly to three sites; pods, extended side stems and stem. These components totalled 93.3% and 85.3% of the labelled carbon in control and treated plants respectively. The sink intensities of leaves declined significantly between 24 hrs and final harvest, suggesting that these were the sources of the labelled carbon. Unfortunately, there was no way of calculating the amount of ^{14}C lost to respiration and how much is translocated. Even if all the assimilate was translocated 10% would be respired as a result of the translocation (Penning de Vries, 1972). The decline in sink intensity of the stem and extended sidestems was a result of growth dilution (Appendix 9)

At feed 2 middle leaves fixed a greater percentage of the labelled carbon than at feed 1, this was especially true in control plants, but in both treatments the values were 10 % higher than those recorded at feed 1. The upper half of the canopy was thus seen to be the most important area for carbon fixation at feed 2. This had also been recorded in the previous year and was observed by Hatfield and Carlson (1978) who reported that in a mature soyabean crop 80% of the photosynthesis took place in the upper 20% of the canopy, which contained 33% of the LAI and intercepted 90% of the PAR.

All leaf groups acted as sources as illustrated by their declining percentage ^{14}C and sink intensity between 0.5 hrs and final harvest. In treated plants export between 0.5 hrs and 24 hrs was to the pods, and this was supplied by the extended side stems and middle leaves. In control plants increases in the percentage ^{14}C and sink intensity during the same period were seen in the stem and roots. A high sink intensity was also recorded in the reproductive parts of treated plants at 24 hrs. An equivalent sink intensity would have been expected for control plants, however, in two of the three control plants a low dpm/g was recorded in the pods (data not shown). The sink intensity in the top leaves of these two control plants were also low at 24hrs whereas in treated plants they remained high. Perhaps these plants were in some way stressed, such as drought caused by uneven watering, which lead to a lower fixation by the top leaves and hence reduced ^{14}C activity in the pods.

At F2 mainstem extended side stems' sink intensity declined from 0.5 to 24 hrs but did not change to final harvest, however the percentage ^{14}C increased between 24hrs and final harvest. It is thus suggested that initially the leaves on the extended side stems supply the mainstem of the plant. Clifford, Marshall and Sagar (1973) recorded that side stems (tillers)

of Italian ryegrass (*Lolium multiflorum*) translocated 50% of their assimilate to the mainstem and the roots in vegetative plants. Later, 24 hrs to final harvest, there was an increase in weight and a differentiation of reproductive structures which increases the percentage ^{14}C contained in the extended side stems. During this later period radiolabel must be imported fom other plant components, probably leaves, to maintain the sink intensity between 24 hrs and final harvest.

At F3 most notable was the repeat of the low percentage ^{14}C in pods of control plants at 24 hrs which occurred at F2. However, at F3 both treatments showed increases in sink intensity between 0.5 and 24 hrs. From the weight data for this harvest (Appendix 10) it was seen that the differences in percentage ^{14}C were primarily caused by differences in the weight of pods between treatments. At final harvest pods in control plants had increased in sink intensity, while those of treated plants showed no significant change. At previous feeds in this year a decline in sink intensity of pods had been recorded between 24 hrs and final harvest. The weight of mainstem pods increased significantly between 24 hrs and final harvest of F3 in control plants, as it did increase in the pods of extended side stems between these harvests. Yet there was an increase in the SI of control mainstem pods and a decline in SI of mainstem extended side stem reproductive parts. There was also a rapid increase in the percentage ^{14}C in the mainstem pods of control plants between 24 hrs and final harvest.

The reproductive parts of extended side stems increased in sink intensity from 0.5 to 24 hrs and then declined to final harvest, as the mainstem pods had at previous feeds. It was probable that the pods on the extended side stems were now in the rapid import of assimilate stage and that assimilate produced after the feed of labelled CO_2 supplied the extended side stem reproductive parts to final harvest. This later formed assimilate 'dilutes' the radiolabel reducing the sink intensity of the pods. The weight of the extended side stem pods increased rapidly between 24 hrs and final harvest which would support this hypothesis (Appendix 10). Flinn and Pate (1970) working on pea observed a peak in dry weight at 12 days after anthesis which then declined, yet the percentage ^{14}C peaked at twelve days and was maintained at this peak until 16 days after anthesis. Thus if the pattern of import is similar in evening primrose pods, the increase in SI of mainstem pods is a result of increased import of ^{14}C without concomitant increase, or an actual decline, in dry weight. The reproductive parts of extended side stems had yet to reach their peak dry weight so an increase in SI did not occur. The difference between the percentage ^{14}C in control and treated mainstem pods may be because of similar maturity differences as discussed above, but this time caused by the

effect of RSW0411. The effect maybe one of retarded pod production as reported by Child *et al.* (1987) or one of extended pod longevity as discussed by Luib *et al.* (1987). Also the weight of the pods of control plants was greater at the final harvest.

When exposed to ^{14}C at feed 4 (flowering completely finished) mainstem pods increased in sink intensity (although the increase between 24 hrs and final was not significant) and percentage 14C across all harvests indicating that these structures were the primary sinks. The sink intensity in mainstem pods of control plants at 24 hrs was greater than that of the treated plants (ns) and again this may have been due to possible differences in rate of import because of differences in pod maturity.

Extended side stem reproductive parts did not increase in sink intensity between harvests. There was, however, a dramatic increase in weight and percentage ^{14}C, suggesting import of radiolabel from other components for growth of the reproductive structures.

At this feed the sink intensity of middle leaves increased compared to the top and base leaves, it is a possibility that the middle leaves are contributing to the side stems. In their review Watson and Casper (1984) report that leaves usually supply assimilate to the fruits in their axils. In this study the extended sidestems are in the axils of the middle leaves by definition (Fig. 5.2). Also the mainstem pods were now maturing phase and not such strong sinks as at previous feeds. The top leaves would therefore be less active if the source were sink lead, ie top leaves activity controlled by the import of assimilate to mainstem pods, and hence their sink intensity would decline. One enigmatic result was the lack of significant change in the sink intensity or percentage ^{14}C of extended sidestem leaves across harvests. If, as suggested by Harvey (1973), leaves suply their nearest sink one would have expected export from this component to extended sidestem reproductive parts, this does not seem to have occurred.

5.5 Conclusion

At F1 1987, the pods, stem and roots were the growing structures and acted as sinks while the leaves and the extended sidestems acted as sources though the later only between 0.5 and 24 hrs. This finding agrees with that of Hume and Criswell (1973) who observed that ^{14}C accumulates in those structures growing most rapidly at the time of feeding.

At F2 1987, the productivity of the plant was higher in the canopy than previously. Pods on the mainstem were now the main sinks, they had greater than 60 % of the labelled carbon at the 3 wk harvest. The base of the canopy was now purely a supporting structure. The developing reproductive structures on the side stems were now sinks.

At F1 1988, there was little initial movement of assimilate because source sink relationships have not emerged. The stem is known to have stomata (Dodd, 1988) and therefore has the capability to support part of its own carbon needs. However, carbon fixed at this feed was recovered in the pods at final harvest and therefore contributes to yield. Such carbon was remobilised from other structures, probably from the structural carbohydrate fraction. Rapid growth of the extended side stems occurred after this feed.

By F2 1988 sources and sinks had emerged and the leaves were supplying the pods. The majority of the plant productivity was moving up the canopy as occurred in F2 1987. The extended side stems initially contributed to the mainstem of the plant, but later they differentiated and their pods imported carbon. This import was most probably from their own leaves. Lush and Evans (1980) noted the movement between competing sinks from a source was proportional to $1/d^2$ where 'd' was the distance from the source; which supports sources supplying the nearest sinks.

The pods on the mainstem were again the main sinks at F3, 1988 and were in the rapid pod fill stage. The pods on extended side stems were less mature and just beginning to fill. The main supply of assimilate was again coming from the upper half of the canopy and there appeared to be no evidence of remobilisation of stem reserves as found by previous workers (Chapman, Daniels and Scarisbrick, 1984; Ong and Marshall, 1975).

By F4 the pods of extended side stems were now in the rapid pod fill stage and continued importing upto final harvest. It is suggested that this assimilate might come from the remobilisation of structural carbohydrate from the leaves which had begun to senesce during this period. The mainstem pods were in the maturing phase and imported little carbohydrate.

To further clarify the source - sink relationships within the plant single leaf feeds within the canopy need to be done such as those by Shiroya (1968) and Ismail and Sagar (1981), and the respiration of the plant monitored. If more plants could be used and their partition of dry weight monitored closely this would increase clarity and provide better supporting evidence for the movement of assimilate between components than was possible here. However, these preliminary studies have indicated the important structures for photosynthesis and the overall general pattern of carbohydrate allocation.

Chapter 6
General discussion.

6.1 The mode of action of RSW0411

In the first year of field trials the evening primrose crop gave positive yield responses (upto 13%) to post bolting timings of RSW0411, with the optimum timing being when the crop was 10cm tall (Table 2.5). The yield increase was considered to be a result of increased P.A.R. penetration through the canopy, which consequently increased the photoproductivity of the more mature, higher yielding, pods lower down the canopy. This theory was developed from the work of Child *et al.* (1987) working with RSW0411 on oilseed rape, and the evidence from experiment 2, a widely spaced transplanted crop where light was not considered to be limiting, where RSW0411 did not increase yield when sprayed at the same range of timings as experiment 1 where the largest yield increases were recorded.

Also in the initial year a range of concentrations of RSW0411 were investigated, but the results proved inconclusive in terms of yield. The recommended rate of 700 g ha^{-1} (Bluett pers. comm.) was therefore maintained, as it was the lowest rate at which canopy structure had been altered. This was thought to be the reason for the seed yield increases in experiment 1 and hence such an alteration was vital.

No nitrogen response was observed, nor were any nitrogen x PGR interactions recorded contradicting the work of Herbert (1983). This may have been because the nitrogen, which was applied in the autumn, was leached from the zone of active root growth before it could be used by the crop. RSW0411 influenced crop height, but no other effects were observed in this trial. Only post bolting application timings had increased yield in experiment 1 and experiment 5 and the small effects observed here were probably because of the premature application of the chemical; in this trial application was carried out pre-bolting. Such an untimely chemical application may also have been responsible for the lack of effect of the varying concentrations of RSW0411 in experiment 3.

A trial with PP333 also gave yield increases with post bolting spray timings (Table 2.23). These increases were not significant, but this may have been a consequence of the small plot size used in this trial (Experiment 1 = 25 m^2, Experiment 5 = 10 m^2). Sufficient evidence was gathered to propose that PP333 and RSW0411 have a similar mode of action; both chemicals retarded plant growth, deepened leaf colour following application and increased the retention of leaves, and this agrees with previous work (Clemence, 1982).

In the following season (1987) a fixed high density transplanted trial was established (Experiment 6). By using an imposed density it was hoped to achieve a crop stand with a

regular and even plant spacing that would reduce the high coefficients of variation associated with sidestems in the previous year. To some degree this strategy succeeded, but the CV's associated with sidestem variables were still high (Table 3.6).

In this experiment RSW0411 did not increase yields, although all application dates were post bolting. In fact application at first flower (T1) and sidestem flowering (T3) depressed yield. In a spring direct drilled crop established in the same year (Experiment 7), RSW0411 produced small increases (upto 8.8%, Table 3.10) in yield when applied at an equivalent range of timings to those in experiment 6.

The reason suggested for the different responses in this year was the restricted root network of the transplanted crop compared to that of the direct drilled crop (Plate 3.2). It is well known that the triazoles move predominantly in the xylem (Shearing and Batch, 1979; Quinlan and Richardson, 1986; Lever, 1986) and therefore root uptake of the compounds is of major importance. Also there is little movement of traizoles from leaves to other plant parts (Wang *et al.* 1986). Another factor that may have been of importance was the water status of the soil. Hampton and Hebblethwaite (1984) found the uptake of paclobutrazol was profoundly influenced by post application rainfall. From the rainfall data (Appendix 5) it can be seen that all spray applications to the transplanted crop were preceded by a period of drought. This, combined with the reduced root network of the transplanted crop, would have reduced chemical uptake and may be the reason for the lack of significant effect.

In the 1986 and 1987 field trials it was noted that RSW0411 produced differences in flowering pattern (Plate 3.1). To further investigate this a glasshouse trial was undertaken to monitor the effect of RSW0411 on the flower production of evening primrose (Experiment 8). It was found that RSW0411 had an effect on flower production. Chemical application resulted in an initial increase in the number of flowers produced post application (Figs. 4.1, 4.2), although the total number produced was not significantly affected (Table 4.6). With the early applications there was a significant increase in pod weight because the earlier flower production resulted in a higher proportion of mature pods at harvest, which were considered to contribute more to yield.

The penetration of P.A.R. lower into the canopy could still have been a factor in the increased yields of this experiment; treated plants had more of their sidestems in the smaller sidestem classes without having an increased total number of sidestems (Fig 4.8 and Table 4.6). Thus more light could have penetrated lower down the canopy.

Three principal hypotheses of the mode of action of RSW0411 on evening primrose are proposed:

(i) There is an alteration of canopy structure allowing improved light penetration through the canopy, thus improving the photoproductivity and the seed yield of pods in the lower portion of the plant.

(ii) There is a repartitioning of assimilate from the mainstem to pods on the mainstem and sidestems, thus improving their yield.

(iii) There is an alteration of the plant's GA metabolism that beneficially affects the flowering pattern, resulting in the production of more mature pods at final harvest.

These theories will now be discussed in more detail.

The theory of altered plant structure resulted from the work of Child *et al.* (1987), who suggested that application of RSW0411 shortened side branches which then allowed improved light penetration to the more mature, and higher yielding, pods lower down the canopy. In the experiments reported within this thesis when sidestem lengths were measured inconclusive results were obtained. When RSW0411 was applied to a high density transplanted crop the total sidestem length was greater in treated plants compared to the control (Fig. 3.4) while the average sidestem length was not altered (Fig 3.5) indicating treated plants had more sidestems, but these were of an equal length to control plants. This would not necessarily create a more open canopy.

In experiment 7 total sidestem length was increased by PGR application at the first flower stage, but unaffected by later timings (Table 3.8). Average sidestem length was decreased by those spray timings applied during sidestem extension (Table 3.8). These results agree more closely with the findings of Child *et al.*, (1987). No increase in yield was associated with treatment in experiment 6 (Table 3.5), but in experiment 7 an increase in yield was associated with treatment (Table 3.10). In the glasshouse (experiment 8) both the average sidestem length and the total sidestem length were reduced by spray application and treatment increased total pod weight (Table 4.6). The increased efficacy of RSW0411 in experiment 8, could be a result of the soil application of the chemical, in a larger volume of water than was associated with the spray treatments in the previous experiments. It is known that water is needed for the activation of PP333 (Hampton and Hebblethwaite, 1984).The differences in uptake of RSW0411 in experiment 6 as a result of the restricted root network compared to the spring drilled crop, may have accounted for the differing response of sidestems of these two crops to chemical treatment.

However, these yield increases were not directly correlated to the shortening of sidestems. In experiment 7, T1 had the highest yield and the longest sidestem length, while in experiment 8, T1 had the shortest sidestem length, but had a lower pod weight than T2 (Table 4.6). The circumstantial evidence for increased light penetration to the base of the canopy is therefore not considered to be conclusive.

The repartition of assimilate from the mainstem to mainstem pods and sidestem pods could account for the recorded yield increases, particularly considering the ^{14}C findings that the mainstem does not act as a temporary storage organ. In experiments 1, 5, 6, 7 and 8 yield increases from RSW0411 application were associated with increases in the yield ratio (Tables 2.5, 2.23, 3.5, 3.10, 4.6). This relationship was also observed by Wiltshire, Hebblethwaite, Esslemont and McGilloway (1989), who applied RSW0411 (1 - 4 kg ha^{-1}) to a seed crop of *Lolium perenne*. In temperate cereals it has been improvements in harvest index that have led to significant increases in seed yield. Perry and D'Antuono (1989) recorded an increase in harvest index from 0.229 to 0.372 when comparing spring wheat cultivars introduced between 1860 and 1982. The yield ratio is approximately twice the harvest index because of seed weight being 50% of pod weight. Therefore the harvest index of evening primrose ranged from 0.12 to 0.17 in these trials.

In experiments 1 and 5 mainstem dry weight was reduced by PGR treatment (Tables 2.5, 2.23), however, the reduction in mainstem dry weight was highest for plants of the early application times, while it was the later application times that produced yield increases. In experiments 7 and 8 treated plants had higher mainstem weights than the control (Tables 3.9 and 4.6). Also in experiment 8 there was some evidence of a reduced side stem weight being associated with increases in mainstem pod weight, suggesting repartition of assimilate from sidestems, but this was not the case in other experiments, in fact in general treatment increased the weight and number of sidestem variables. The evidence for a repartition of assimilates is also therefore considered to be inconclusive.

The proposed hypothesis of the mode of action of RSW0411 was the effect of the PGR on flowering pattern which was seen in all years. The suggested mechanism for this effect was the alteration of GA metabolism which allowed for a temporary increase in the rate of flower initiation, although the precise mechanism needs some clarification (see section 4.4). The increase in flower production was clearly illustrated by the monitoring in experiment 8. Following application of RSW0411 an increase in flower production was observed 2 to 3 weeks later. This time delay between application was most clearly seen on the mainstem for T2 and the on the sidestems for T3. These increases in flower production lead to direct increases in pod weight. Increases in flower production have been recorded with other

triazole PGR's (Oshio and Izumi,1986; Lamont, 1986). In experiment 10 increases in the sink intensity reproductive parts of treated plants at feed 1 (Tables 5.6), which could well reflect an increased assimilate supply as a result of increased flower production. This result would cease to be significant later on as there was no significant difference in flower and pod numbers between control and treated plants later in the monitoring period. Because of the direct cause and effect relationship between pod weight and the early increase in flower production, and that the alteration of flowering pattern was observed in all years it is suggested that this is the most likely process producing the yield increases in treated plants.

One other hypothesis suggested by earlier workers (Lurssen and Reiser, 1985) was an increase in rate of photosynthesis in plant leaves and an increase in overall plant metabolism of treated plants. However, recent work by Butler, Pears, Child and Brain (1989), who applied RSW0411 to oilseed rape, found a reduction in photosynthesis of fully expanded leaves that lasted for two weeks post application of the triazole. In expanding leaves these workers also suggested that there was a reduction in the photosynthesis per milligram of chlorophyll which would run contrary to any suggested increase in plant metabolism.

6.1.1 Further research to clarify the mode of action of RSW0411.

Experiments should be conducted with a range of spray timings on a field crop of evening primrose. Solarimeters should be placed at a range of positions relative to the mainstem flowering spike of plants in each treatment. The P.A.R. at these various positions should then be monitored throughout the season. Thus a detailed account of any changes in the P.A.R. profile through the canopy as a result of chemical application would be provided.

Secondly, a series of experiments over several seasons, with one method of establishment, probably a summer sown crop, need to be monitored to eliminate some of the differences apparent between crops of different establishment techniques. Because of these different techniques it was difficult to know exactly what physiological age the crops were at which makes it difficult to suggest an exact application time. For example a six week old rosette of a spring drilled crop is physiologically more mature than a rosette of the same age from a summer drilled crop, because it grows in the extending daylengths of spring which induce bolting. However, the chemical did have an beneficial yield effect on crops under three of the growing regimes, and such adaptability will be useful following any future commercial release.

An electron microscope study of the plant apex and floral initiation following application of the chemical, would clarify any observed promotion of flower production. This would also provide useful information for timing of the chemical application as has been investigated by Craufurd and Cartwright (1989), who have used apical development to indicate the optimum time for PGR application to increase tiller number in spring wheat (*Triticum aestivum*).

6.2 Implications of results for the evening primrose crop

One of the frustrating things throughout the study was the high coefficients of variation associated with many of the measured parameters. The conclusion has to be drawn, like that of Scarisbrick *et al.*, (1984), who were considering the oilseed rape crop that the evening primrose is a "variable beast", but it is suggested that in the case of evening primrose the word "extremely" should be added to the quote for the sake of accuracy. If some of this variability could be removed it would improve the researchers lot and probably stop the crop giving such trepidation to farmers. Although the actual cause of variation cannot be pin-pointed, in the field trials here the major problems arose from variable germination. This may be a consequence of the small size of the seed, or a result of the relatively high temperatures required for germination. If it is the later then it may be easier for it to be improved.

Another suggested area that the plant breeders could investigate is the daylength required to initiate the bolting response. The earliest flowering date observed was May 6th and this allowed the crop to be harvested in late September in other cases the crop was harvested much later. During these later months rainfall is more likely, which would interfere with swathing and increase the likelihood of soil damage by harvesting machinery.

A shortening of the mainstem would leave less stubble and also make the crop less prone to lodging. The stem does not appear to have any significant assimilate storage function (section 5.3) so no yield potential would be lost. Such a reduction in the mainstem size could well be produced by developing a plant that was sensitive to a shorter daylength, and therefore flowering would commence at a lower position on the mainstem.

In these trials the seed used has been referred to as *Oenothera spp.*, species differences have been reported regarding the production of GLA in the seeds. Yaniv, Ranen, Levy and Palevitch (1989) working with *O. lamarckiana* reported that the GLA content of seeds increased with age, whereas Lotti, Izzo and Marchini (1980) working with *O.biennis* reported results to the contrary. However, both groups of workers found GLA content of seeds declined with increasing temperature at pod set. These results need clarification. For growers to achieve optimum yields of GLA, it may be that late grown transplanted crops produce a higher yield of GLA because of the cooler temperatures during pod growth.

From the labelled carbon studies it is suggested that leaves should be kept disease free throughout the season, as at all feeds they were found to be the primary sources of assimilates. The results also indicated that pods used assimilate that was produced before their growth began (Figs. 5.3, 5.5), thus any spray programme should commence prior to

bolting. A uniculm crop is also proposed as the crop ideotype, except for the transplanted crop where labour costs would prevent it from being viable. A uniculm crop would mature earlier and there would be no later formed side stem pods to consider at harvest. Sidestem pods also contribute less to yield than the mainstem pods. However, sidestems do contribute to the carbon economy of the mainstem before they become reproductive. Further studies feeding single plant organs are suggested to further clarify source/sink relationships within the plant.

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Appendix 1.

ANOVA table for number of leaves at h1 .

SOURCE	DF	SOS	MS	VR	
blocks	3	34.53	11.51		
timing	4	44.13	11.03	8.661	**
error	12	15.29	1.27		
total	19	93.94			

Grand mean	SED	CV%
17.1	0.564	15.5

Treatment means	C	T1	T2	T3	T4
	17.6	18.9	16.1	16.5	16.1

ANOVA table for number of leaves at h1 with covariance analysis.

SOURCE	DF	SOS	MS	VR		COV. EFF. %
blocks	3	34.53	11.51			
timing	4	36.02	9.01	6.757	**	
covariate	1	0.63	0.63			
error	11	14.66	1.33			95.6
total	19	85.84				

Grand mean	SED	CV%
17.1	0.588	10.5

Treatment means	C	T1	T2	T3	T4
	17.6	18.8	16.2	16.6	16.2

$$cov.eff. = 100\frac{(Error\,MS\,of\,Y)}{\left(Error\,adjusted\,MS\,of\,Y \times \frac{1+Treament\,MS\,of\,Y}{Error\,SS\,of\,X}\right)}$$

X = density Y = no. of leaves

ANOVA table for leaf weight at h1.

SOURCE	DF	SOS	MS	VR	
blocks	3	0.324	0.108		
timing	4	1.334	0.334	4.652	*
error	12	0.860	0.072		
total	19	2.518			

Grand mean	SED	CV%
1.57	0.134	12.0

Treatment means	C	T1	T2	T3	T4
	1.74	1.83	1.44	1.52	1.34

ANOVA table for leaf weight at h1 with covariance analysis.

SOURCE	DF	SOS	MS	VR		COV.EFF. %
blocks	3	0.324	0.108			
timing	4	0.750	0.188	4.624	*	
covariate	1	0.414	0.414			
error	11	0.446	0.041			176
total	19	1.934				

Grand mean	SED	CV%
1.57	0.103	9.1

Treatment means	C	T1	T2	T3	T4
	1.71	1.77	1.45	1.53	1.40

Appendix 2.

ANOVA table

Source	df	SOS	MS	VR
Regression	1	55.19	52.18	36.37
Residual	33	47.35	1.43	
Total	34	99.54		

R-squared = 0.5473 R = -0.73

Equation is simple linear $y = a + bx$

y = number of sidestems

x = density

a = 0.749

b = -0.157

Regression analysis of plant density v. the number of sidestems

at sample 3.

Appendix 3

Treatment	Block		
	1	2	3
0 kg N D1 +	40	33	28
-	28	32	33
D2 +	39	36	33
-	28	36	20
D3 +	33	52	26
-	61	43	34
80 kg N D1 +	55	29	25
-	35	37	29
D2 +	36	57	30
-	27	*	29
D3 +	24	42	32
-	29	25	25

* - missing data

Plant density in sample area (0.25 m $^{-2}$) at sample 3 in experiment 4.

Appendix 4.

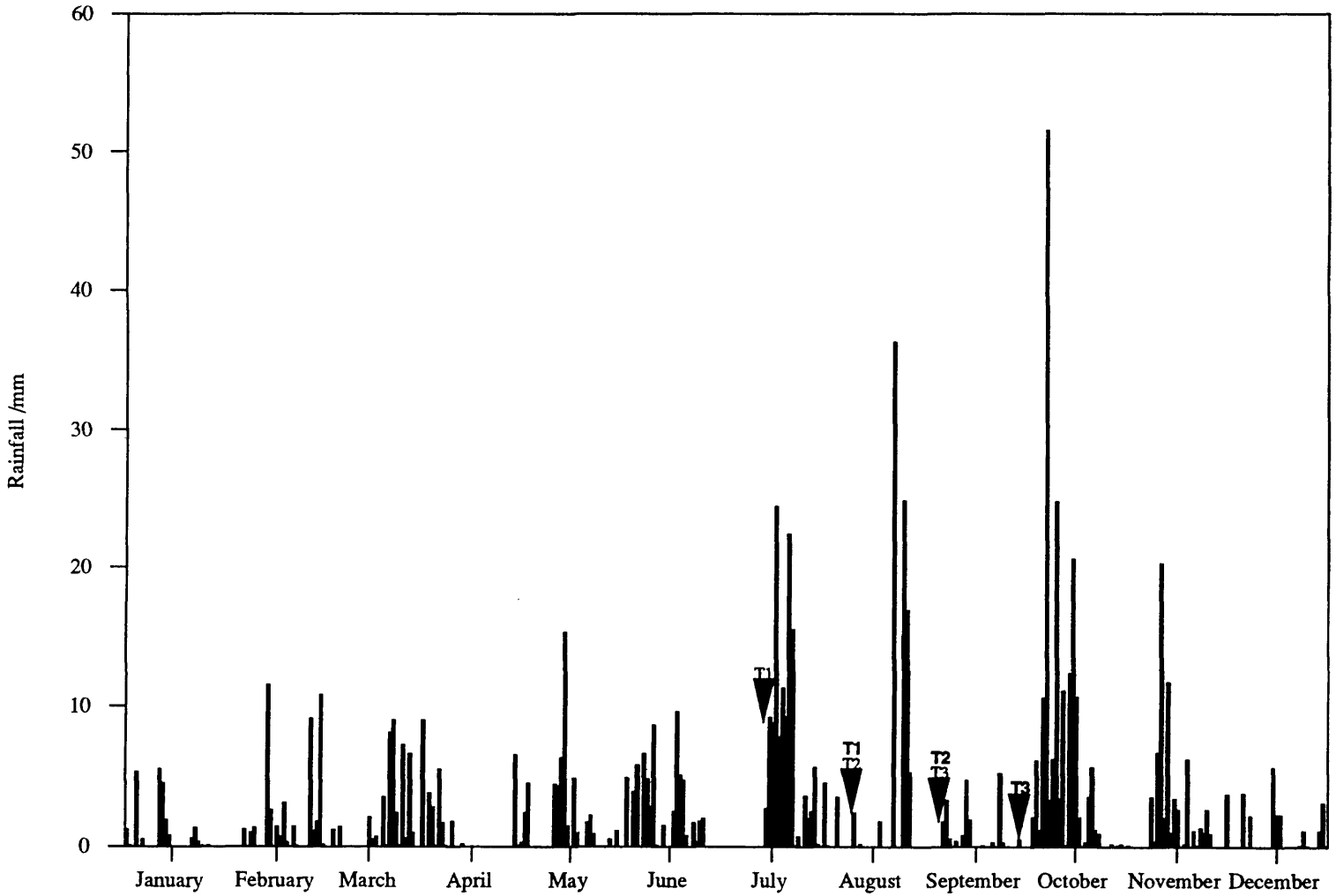
ANOVA table of seed moisture content at harvest

SOURCE	df	SOS	MS	VR
blocks	3	0.0080	0.0027	
timing	5	0.0077	0.0015	2.32
error	15	0.0099	0.0007	
total	23	0.0256		

Grand mean	SED	CV%
0.24	0.018	10.8

Treatment means	C	T1	T2	T3	T4	T5
	0.26	0.25	0.21	0.25	0.22	0.24

Appendix 5.

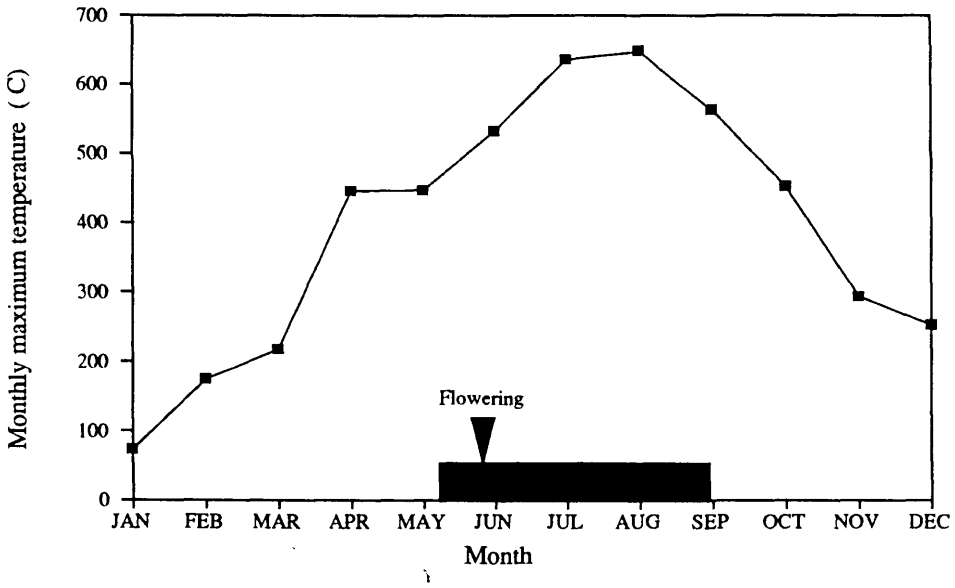


Experiment 6 appliction times in roman, Experiment 7 in bold.

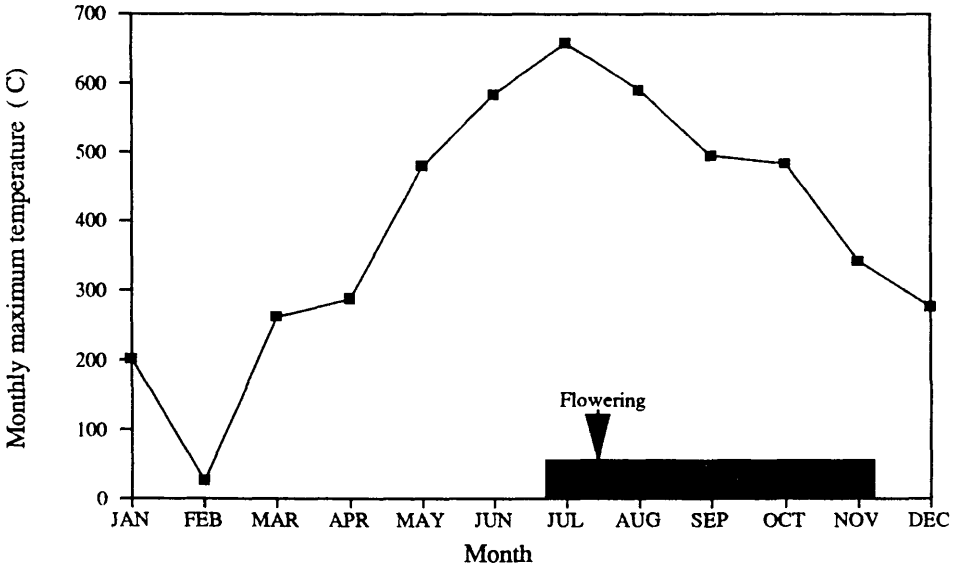
Rainfall 1987

Appendix 6.

Maximum temperatures in 1986



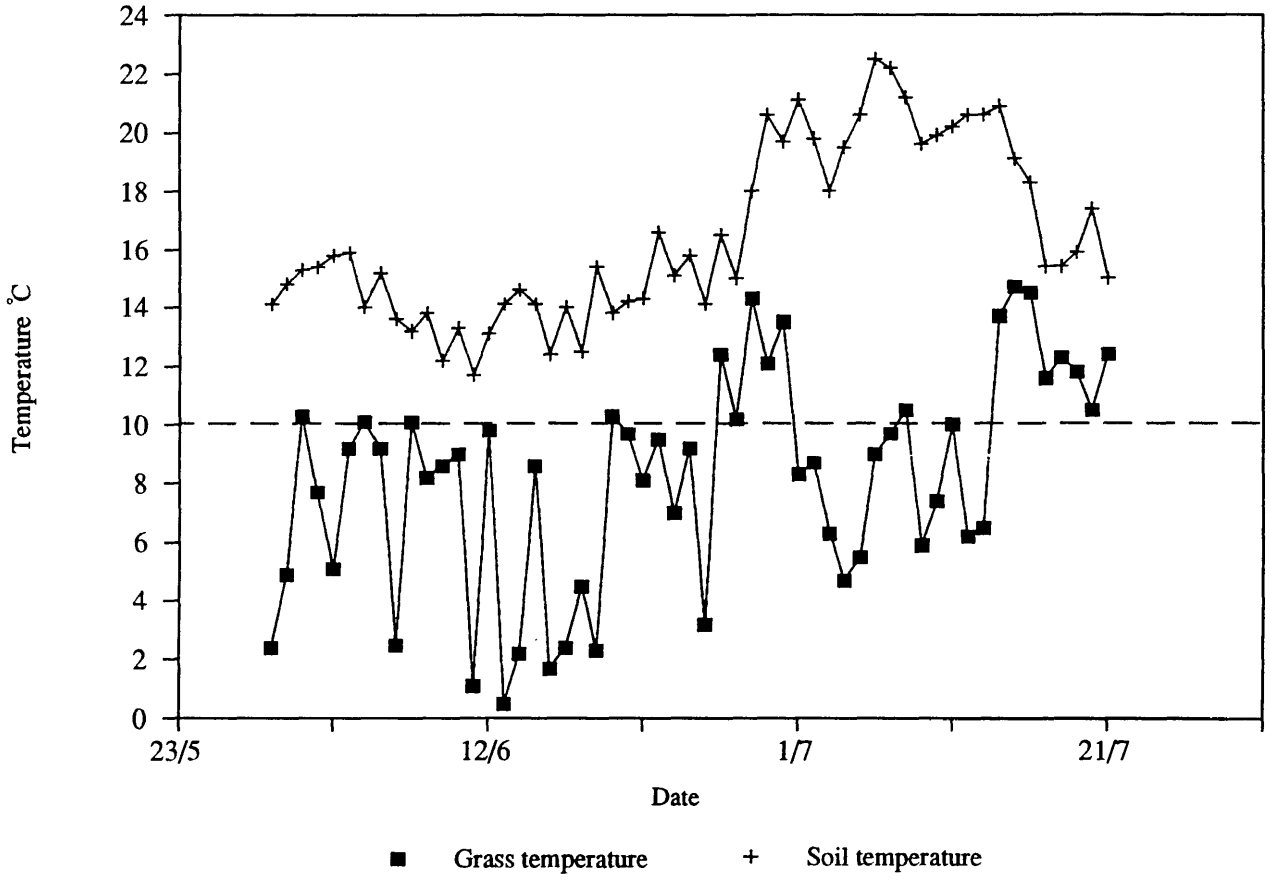
Maximum temperatures in 1987



Crop growth period bolting to final harvest

Monthly maximum growing temperatures and crop growth period in two field seasons.

Appendix 7.



Grass and soil (@ 10 cm depth) temperatures
from emergence to bolting in experiment 7.

Component	Treatment	Harvest			Significance			CV%
		0.5hrs	24hrs	Final	t	h	t x h	
RP	C	3.47	3.96	14.76	ns	**	ns	33.5
	T	2.38	3.30	18.05	2.28	2.79	3.96	
TL	C	3.22	2.75	3.35	ns	**	*	21.0
	T	2.13	3.07	4.48	0.59	0.73	1.03	
ML	C	7.38	6.89	5.08	ns	ns	ns	30.7
	T	5.43	7.18	6.87	1.77	2.17	3.07	
BL	C	7.29	6.47	5.46	ns	ns	ns	27.2
	T	6.41	7.44	6.84	1.61	1.97	2.79	
MESS	C	3.49	3.23	4.29	ns	ns	ns	63.2
	T	2.51	3.55	6.89	2.24	2.75	3.89	
STEM	C	34.8	32.4	45.5	ns	**	ns	18.2
	T	26.9	31.2	53.4	6.06	7.41	10.48	
ROOTS	C	6.01	5.03	6.83	ns	**	ns	21.1
	T	4.08	4.51	7.77	1.07	1.31	1.86	

Appendix 8 - Weight of plant components (g per plant) across harvests for plants exposed to ^{14}C at feed 1, 1987.

Component	Treatment	Harvest			Significance			CV%
		0.5hrs	24hrs	Final	t	h	t x h	
RP	C	1.46	1.25	16.48	ns	**	ns	38.0
	T	1.09	1.27	17.88	2.57	3.14	4.45	
TL	C	1.40	1.73	0.25	ns	**	ns	25.0
	T	1.62	1.76	0.25	0.30	0.37	0.52	
ML	C	5.13	5.13	0.12	*	**	ns	50.9
	T	3.19	1.34	0.21	1.41	1.72	2.43	
BL	C	5.23	5.23	0.89	ns	**	ns	25.1
	T	5.31	5.61	1.02	1.00	1.22	1.73	
MESS	C	4.20	4.20	28.5	ns	**	ns	37.2
	T	2.40	3.20	33.1	4.82	5.88	8.32	
STEM	C	23.9	24.0	30.1	ns	**	ns	16.3
	T	22.4	22.4	34.8	4.40	5.38	7.63	
ROOTS	C	13.74	13.74	5.14	**	ns	*	35.8
	T	5.34	5.88	6.70	3.10	3.80	5.36	

Appendix 9 - Weight of plant components (g per plant) **across harvests for plants exposed to ^{14}C at feed 1, 1988.**

Component	Treatment	Harvest			Significance			CV%
		0.5hrs	24hrs	Final	t	h	t x h	
RP	C	10.17	4.57	16.04	ns	**	**	19.7
	T	10.13	10.93	11.14	2.13	2.60	2.68	
TL	C	2.57	2.77	0.25	ns	**	ns	16.9
	T	3.27	2.93	0.24	0.35	0.43	0.60	
ML	C	2.10	2.52	1.04	ns	**	ns	43.0
	T	3.00	3.56	0.92	0.97	1.18	1.67	
BL	C	4.63	5.06	4.10	ns	ns	ns	42.1
	T	4.27	3.81	1.57	1.69	2.07	2.93	
MRP	C	2.83	2.49	11.29	ns	**	ns	57.2
	T	1.61	1.81	12.04	3.14	3.84	5.44	
MST	C	3.00	5.73	4.30	ns	ns	*	43.9
	T	3.33	1.96	6.47	1.86	2.28	3.23	
MSL	C	4.04	4.97	2.42	ns	ns	*	42.1
	T	3.00	2.97	5.49	1.65	2.02	2.86	
STEM	C	25.9	26.7	25.8	ns	ns	ns	18.3
	T	24.4	25.5	25.0	4.82	5.88	8.32	
ROOTS	C	4.13	4.63	6.38	ns	**	ns	16.0
	T	4.28	4.17	5.20	0.79	0.97	1.36	

Appendix 10 - Weight of plant components (g per plant) across harvests for plants exposed to ^{14}C at feed 3, 1988.