Experiments with Vegetative Tiller Manipulation in the Perennial Ryegrass (*Lolium perenne* L.) Seed Crop by the Application of Growth Regulators[1]

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ABSTRACT

Vegetative tillers formed after ear emergence in the perennial ryegrass (*Lolium perenne* L.) seed crop compete with the developing ears for assimilates and also create problems for direct combine harvesting. Experiments in 1981 and 1982 investigated the effects of the growth regulators paclobutrazol (PP333) and gibberellic acid (GA_3) on vegetative tiller production and seed yield in perennial ryegrass cv. S. 24.

GA_3 alone did not consistently reduce vegetative tiller numbers and had no effect on seed yield. PP333 applied at spikelet initiation stimulated vegetative tiller production prior to ear emergence in both years. After anthesis, vegetative tiller numbers were suppressed in PP333 treated plots in 1981, but not in 1982, when tiller numbers increased in all plots in response to rain after ear emergence. PP333 significantly increased seed yield in both years. Application of GA_3 to plots also treated with PP333 reduced vegetative tiller production prior to ear emergence, but differences were not significant after anthesis. Seed yields were not significantly different from those of PP333 alone.

Additional index words: **gibberellic acid, paclobutrazol, PP333, growth regulators, vegetative tillers, seed yield.**

INTRODUCTION

As the perennial ryegrass seed crop enters the reproductive phase, tiller production increases rapidly, usually reaching a maximum value at around ear emergence (Hebblethwaite et al., 1980). Coincident with stem elongation, there is a high tiller mortality which is then followed by a further increase in total tiller numbers brought about by the production of vegetative tillers. By peak anthesis, the number of these tillers may be rapidly increasing (Hebblethwaite et al., 1982), although their production is dependent upon rainfall, nitrogen (Hebblethwaite and Ivins, 1977) and lodging of the crop, which allows greater light penetration into the base of the canopy (Hebblethwaite et al., 1982).

Recent work (Hampton, 1983; Clemence and Hebblethwaite, 1984) has confirmed the suggestion of Spiertz and Ellen (1972) and Hebblethwaite and Ivins (1977), that vegetative tillers subtending developing fertile tillers compete directly with the growing seed for assimilates. Hampton (1983) found that in lodged crops of perennial ryegrass cv. S.24, assimilate movement from the flag and penultimate leaves was primarily down the plant to the subtending vegetative tillers. Clemence and Hebblethwaite (1984) recorded similar results and also showed that during stem elongation, the ear was a net exporter of assimilate, and that up to 10% of this assimilate was recovered from subtending vegetative tillers. Reciprocal transfer of assimilates between vegetative and parent tillers was limited, as vegetative tillers exported less than seven percent of the ^{14}C they fixed (Hampton, 1983).

Prevention of lodging, using the growth retardant paclobutrazol (PP333), has significantly increased perennial ryegrass seed yields (Hebblethwaite et al., 1982; Hampton et al., 1983; Hampton and Hebblethwaite, 1985) by increasing seed number per unit area, usually resulting from an increase in the number of seeds per spikelet (Hebblethwaite, et al., 1982). Hampton (1983) showed that in such non-lodged plants, there was an increased carbon allocation to the ear from both the flag and penultimate leaf at the expense of vegetative tillers, although the primary direction of assimilate movement was still down to the tillers. Prevention of lodging does not necessarily reduce vegetative tiller numbers (Hampton and Hebblethwaite, 1985), as PP333 reduces apical dominance (Froggatt et al., 1982) and may stimulate tiller production (Hampton and Hebblethwaite, 1985). Thus in some seasons, equal numbers of vegetative tillers were present in lodged and non-lodged crops (Hebblethwaite et al., 1982; Hampton and Hebblethwaite, 1985).

The presence of vegetative tillers in the crop poses further problems for seed production by increasing the difficulties of harvesting seed (Hampton and Hebblethwaite, 1982). Thus any treatment which would either suppress or at least slow down the formation of these tillers would be of benefit. Jewiss (1972) noted that application of gibberellic acid (GA_3) to *Phalaris tuberosa* L. reduced tiller numbers, and similar effects have been reported in wheat (Jewiss, 1972; Batch, et al., 1980; Hutley-Bull and Schwabe, 1982), barley (Kirby and Faris, 1972) and rice (Harada and

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Vergara, 1972). Trials in 1981 and 1982 examined the effects of GA_3, PP333, and a combination of the two on tiller numbers and seed yield in perennial ryegrass.

MATERIALS AND METHODS

Experiments were carried out at the University of Nottingham experimental farm, Sutton Bonington, Loughborough, Leics. on soil of the Astley Hall series. Certified basic seed of perennial ryegrass cv. S.24 was sown in the autumn of 1980 and 1981 at 12 kg. ha^{-1} with a row width of 15 cm. Details of experimental management are given in Table 1.

GA_3-Batch, et al., (1980) suggested that sequential low dose applications of high spray volume applied around the time of spikelet initiation were essential factors of any GA response in cereals, but failed to substantiate this in field experiments. However, Hutley-Bull and Schwabe (1982) and Koranteng and Matthews (1982) found that GA_3 application prior to spikelet initiation produced tiller responses in wheat and barley respectively. Accordingly, in 1981 and 1982, GA_3 as 90% gibberellin A_3 was applied to ryegrass plots at a concentration of 20 ppm in 1000 liters H_2O ha^{-1} (20 g ha^{-1}) for each application, in three sequential doses at double ridge and floret initiation (Table 1.).

Table 1: Experimental details.

	1981	1982
Sowing date:	4 Sept. 1980	18 Aug. 1981
Previous crop:	Winter wheat	Potatoes
Plot size:	2 × 1.5 m	12 × 1.5 m
Herbicide: Autumn-	2,3,6 -TBA 5.0 l ha^{-1}	Diacamba plus mecaprop 3.0 l ha^{-1}
	Ethofumesate 10.0 l ha^{-1}	Ethofumesate 10.0 l ha^{-1}
Spring-	2,3,6 -TBA 2.5 l ha^{-1}	2,3,6 -TBA 4.0 l ha^{-1}
Nitrogen: Rate-	160 kg N ha^{-1}	120 kg N ha^{-1}
Date-	19 Mar.	25 Mar.
GA_3 Application:		
Dates - (1st)	13, 16, 20 Feb.	15, 18, 22 Feb.
(2nd)	15, 17, 22 Apr.	16, 19, 22 Apr.
PP333 application date:	24 Mar.	30 Mar.
Seed harvest: Date -	16 July	7 July
Seed moisture content -	40%	40%

PP333-applied at 2 kg a.i. ha^{-1} at spikelet initiation (Table 1) in both years (Hampton and Hebblethwaite, 1985). Treatments in both years were: nil, GA_3 applied at double ridge and floret initiation = $2GA_3$; PP333 applied at spikelet initiation; PP333 plus $2GA_3$. The experiments utilized a randomized block design replicated five times. Growth analyses were carried out at regular intervals in both years (Hampton and Hebblethwaite, 1985) all plants being removed from an area of 0.05 m^2 in 1981, and 0.1 m^2 in 1982. Details of growth analysis techniques and lodging assessment have been previously published (Hebblethwaite, et al., 1978).

Harvesting was carried out when seed moisture content was at 40%. In 1981, fertile tillers from an area of 0.5 m^2 were hand cut from each plot, while in 1982 an area of 5.5 m^2 from each plot was cut with a reciprocating knife mower (Mayfield). The cut material was then placed in cotton bags and cool air dried to around 12-15% straw moisture content before the seed was threshed in a stationary thresher and cleaned (Hebblethwaite et al., 1978). Yield results are expressed as 0% moisture content.

RESULTS

Crop Development

Application of GA_3 at double ridge advanced crop development in both years (Table 2) e.g. spikelet initiation was advanced by 6 and 5 days in 1981 and 1982 respectively. PP333 application delayed crop development by four to five days but the combination of GA_3 plus PP333 delayed floret initiation and ear emergence by one or two days only (Table 2).

Table 2. The effect of growth regulator application on development of the ryegrass seed crop, 1981 and 1982.

Treatment	Date of development stage		
	Spikelet initiation[1]	Floret initiation[1]	First ear emergence
1981			
nil	23.3	13.4	4.5
GA_3	17.3	10.4	30.4
PP333	-	17.4	8.5
PP333 + $2GA_3$	-	15.4	6.5
1982			
nil	25.3	15.4	6.5
GA_3	20.3	10.4	1.5
PP333	-	19.4	10.5
PP333 + $2GA_3$	-	16.4	7.5

[1]date at which 70% of tillers examined were within each category (Hampton 1983).

Fertile tiller extension and lodging

Stem extension and lodging patterns were similar in both years - 1982 data are presented in Figure 1. In untreated and GA_3 plots, lodging was severe by anthesis (Fig. 1A) but was delayed until after anthesis in PP333 treated plots. Lodging was greater at all assessment dates in plots with GA_3 treatments.

GA_3 application increased stem length over that of untreated and PP333 treated plots (Fig. 1B), but after anthesis, differences were not significant.

Tiller Numbers

GA_3 application reduced vegetative tiller numbers in both years, but differences from untreated plots were significant only in May 1982 (Fig. 2). PP333 application promoted

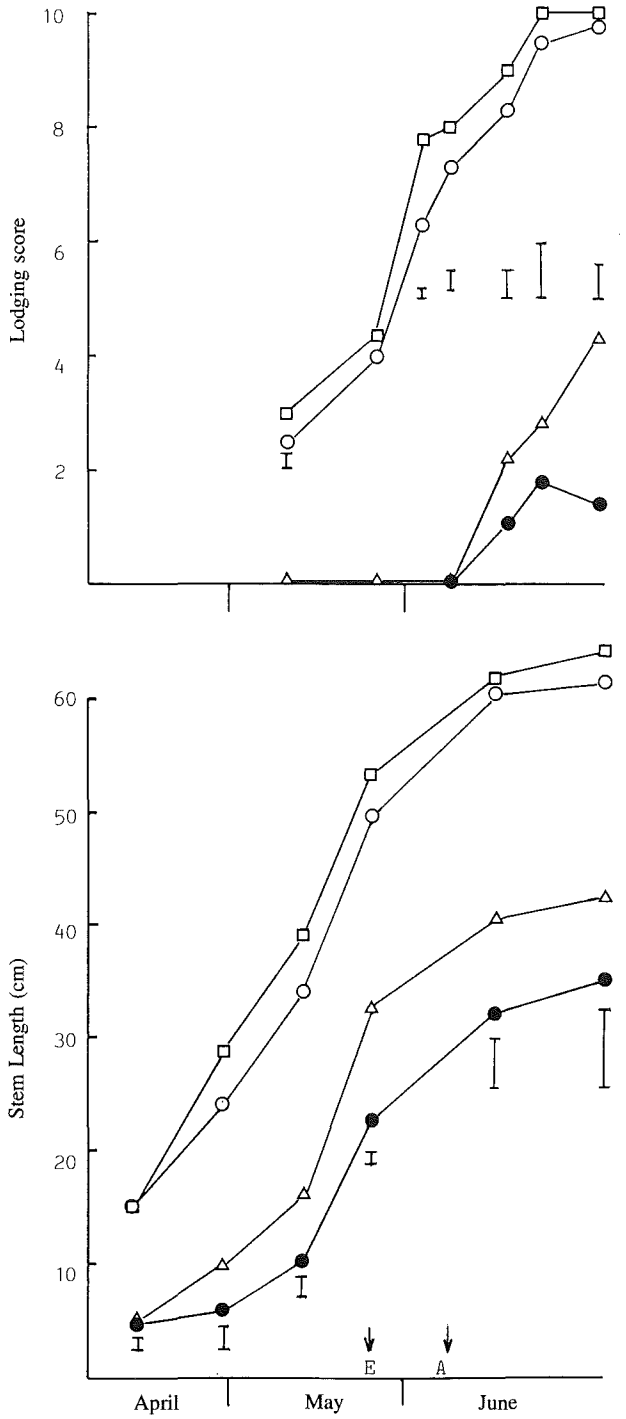


Figure 1. The effect of growth regulators on lodging and stem length of perennial ryegrass cv. S.24, 1982.

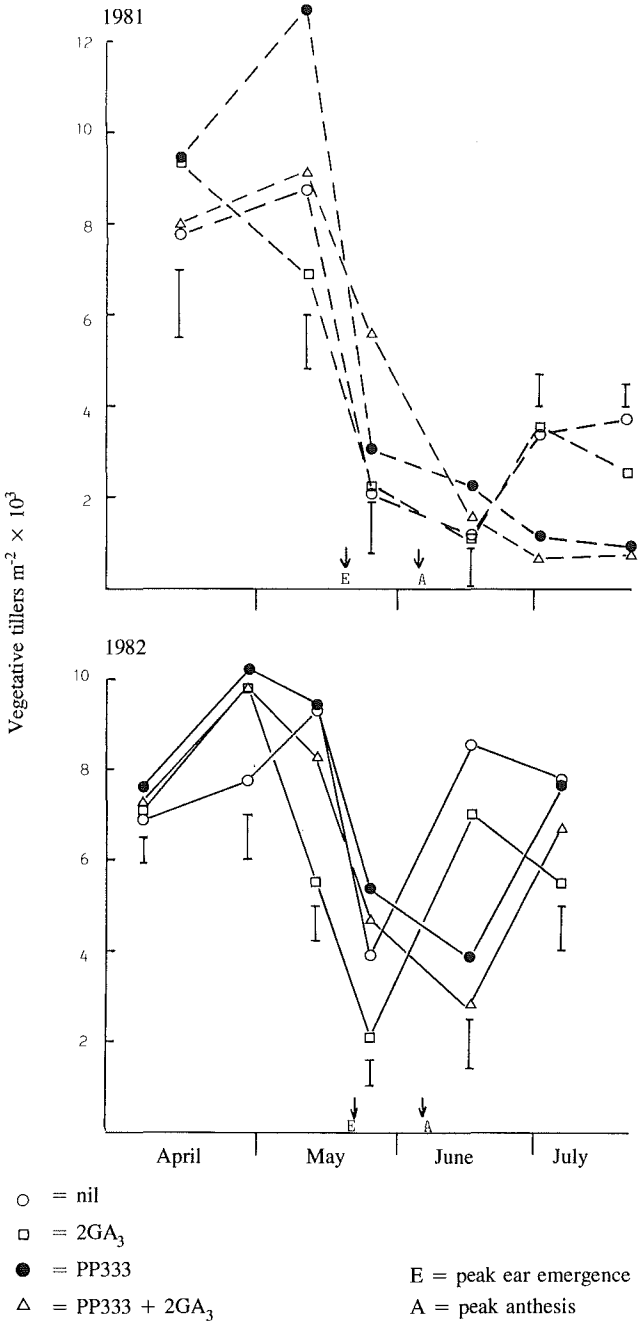


Figure 2. The effect of growth regulators on vegetative tiller numbers, 1981 and 1982.

tillering before ear emergence, particularly in 1981 (Fig. 2), whereas the combination of PP333 plus $2GA_3$ reduced the number of tillers produced.

Vegetative tiller numbers after ear emergence differed between treatments and years (Fig. 2). In 1981, vegetative tiller numbers in PP333 and PP333 plus $2GA_3$ plots continued to decline, whereas those in untreated and $2GA_3$ plots increased. Differences in tiller numbers between the former two treatments and latter two treatments were significant at the last two assessment dates (Fig. 2). In 1982, heavy rain after ear emergence stimulated vegetative

tiller production in all plots, and although the increase was delayed until after anthesis in PP333 and PP333 plus $2GA_3$ plots, by final harvest there were no significant differences between any treatments.

In both years, fertile tiller numbers in GA_3 treated plots did not differ from those in untreated plots (Fig. 3). PP333 significantly increased fertile tiller numbers over that of untreated plots from anthesis on in both years, while the combination of PP333 plus GA_3 produced more fertile tillers than PP333 alone, particularly in 1981 (Fig. 3). Seasonal effects on tiller production are reflected in the percentage of tillers which were fertile (Fig. 4). In 1981 at

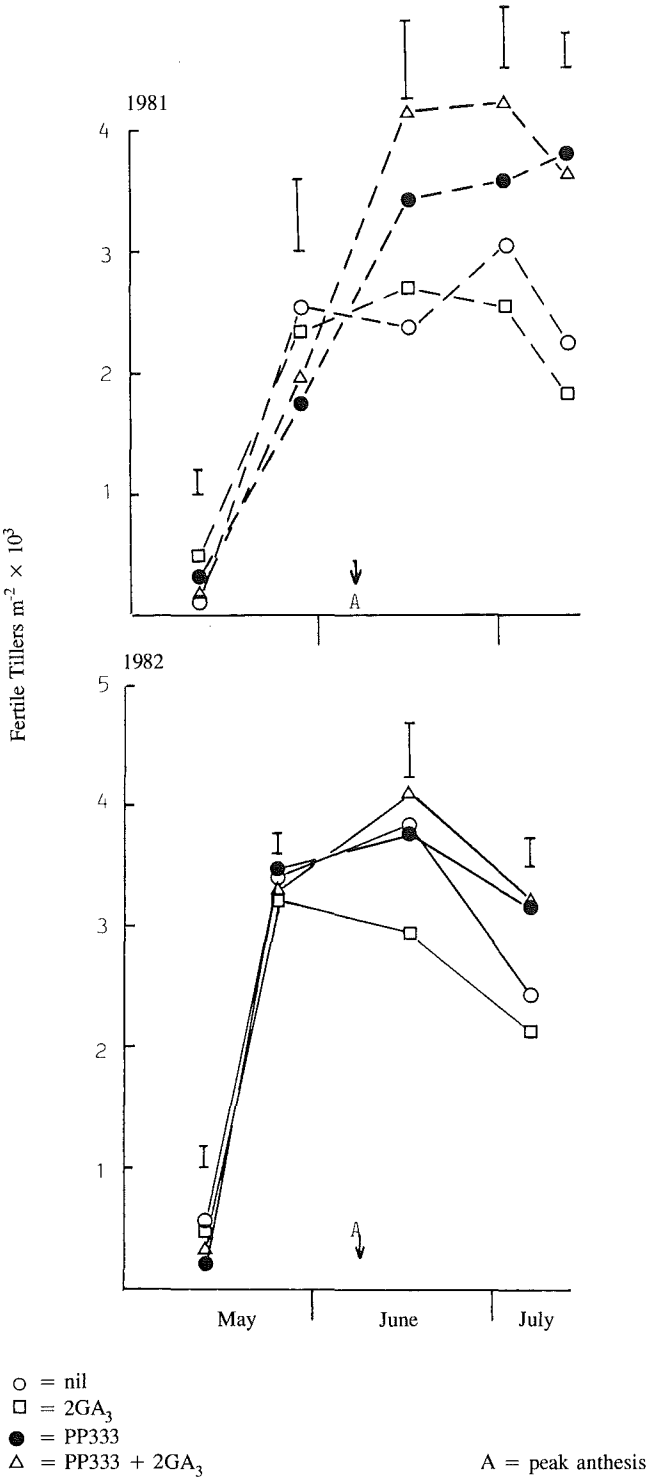


Figure 3. The effect of growth regulators on fertile tiller numbers, 1981 and 1982.

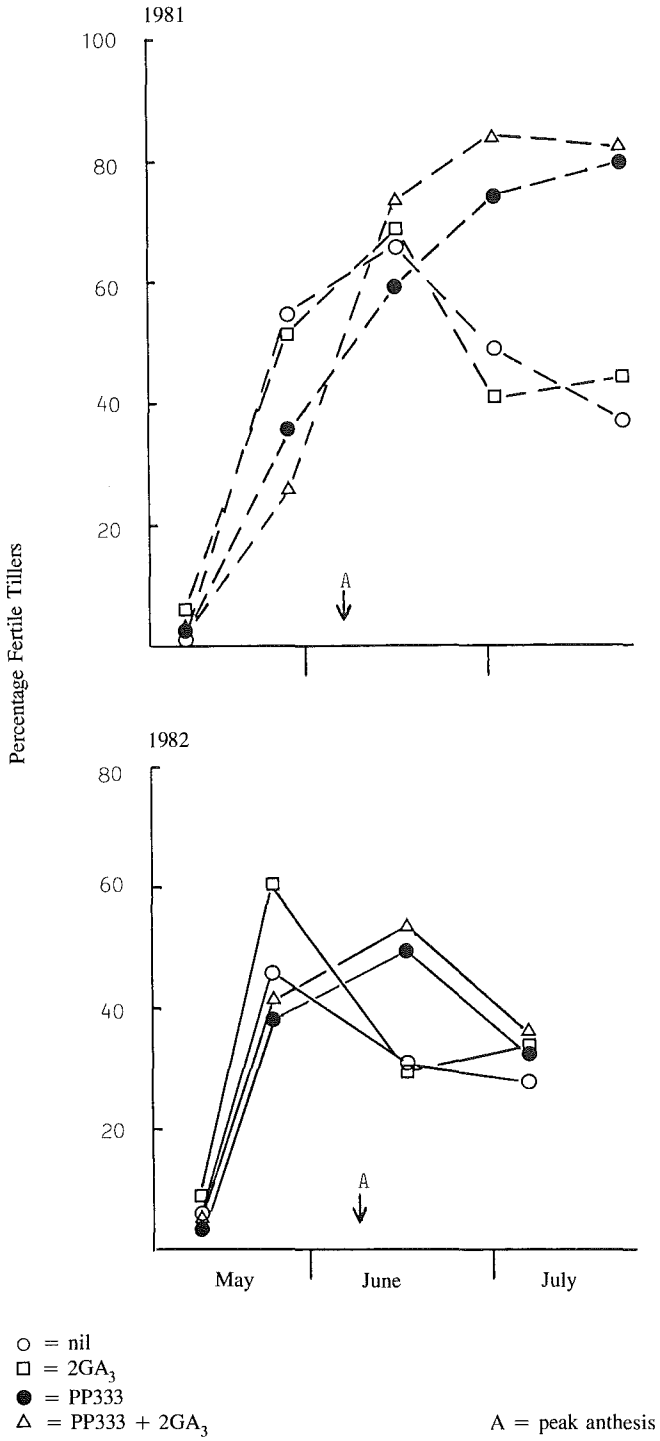


Figure 4. The effect of growth regulators on the percentage of fertile tillers, 1981 and 1982.

Table 3. The effect of growth regulator treatments on seed yield and yield components in perennial ryegrass cv. S.24, 1981 and 1982.

Treatment	Yield g m^{-2}		Harvest	Fertile tillers	Spikelets per	Seeds per	T.S.W.
	Seed	Straw	index	m^{-2}	tiller	spikelet (calc.)	(g.)
1981							
nil	116.1	921	0.11	2240	20.6	1.36	1.86
$2GA_3$	121.9	979	0.11	1850	21.3	1.62**	1.93
PP333	188.2**	757	0.20***	3840***	20.7	1.38	1.71*
PP333 + $2GA_3$	205.2***	833	0.20	3621***	20.6	1.55*	1.78
S.E.D. (12 d.f.)	17.0	71.7	0.001	310.7	0.53	0.07	0.05
1982							
nil	121.7	731	0.14	2459	20.2	1.24	1.98
$2GA_3$	118.8	736	0.14	2159	20.6	1.34	1.99
PP333	256.8***	659	0.28***	3415**	20.5	2.06***	1.77*
PP333 + $2GA_3$	263.1***	747	0.26***	3164*	21.3	2.00***	1.94
S.E.D. (12 d.f)	9.2	33.2	0.001	243.0	0.58	0.07	0.06

* = $P \leq 0.05$
** = $P \leq 0.01$
*** = $P < 0.001$

final harvest, PP333 plus $2GA_3$ treated plots had 82% of tillers fertile, compared with 78% for PP333, 44% for $2GA_3$, and 33% for untreated plots. In 1982, however, because of increased vegetative tiller production after ear emergence, all treatments had only between 28-36% of tillers fertile.

Seed yield and yield components

The seed yield from plots which received $2GA_3$ did not differ from that of untreated plots in either year (Table 3). PP333 application significantly increased seed yield, while the addition of $2GA_3$ to PP333 further increased yield in both years, but the differences were not significant from that of PP333 alone. PP333 reduced straw yield but other treatments did not differ from that of untreated plots. Harvest index and fertile tiller numbers were significantly increased in both PP333 treatments (Table 3), but no differences were recorded in the number of spikelets per tiller. In 1981, GA_3 treatments increased the number of seeds per spikelet, but in 1982 only PP333 treatments increased seeds per spikelet. PP333 decreased thousand seed weight in both years.

Crop Growth

In both years, dry matter accumulation and photosynthetic area index of $2GA_3$ treated plots did not differ from that of untreated plots. PP333 responses were similar to those previously reported (Hebblethwaite et al., 1982; Hampton and Hebblethwaite 1985) and responses of PP333 plus $2GA_3$ plots did not differ significantly from those of PP333 plots alone.

DISCUSSION

The potential for growth retardants to increase the yields of herbage seed crops is now well extablished (Hebblethwaite et al., 1980; 1982; Hampton, 1983; Albeke et al., 1983; Hampton and Hebblethwaite, 1985). A growth retardant such as PP333 may increase seed yield in perennial ryegrass by increasing fertile tiller numbers in some seasons (Hampton and Hebblethwaite, 1985) but more consistently by preventing or delaying lodging (Hebblethwaite, et al., 1982) which results in reduced seed abortion (Hampton, 1983), and an increase in the number of seeds harvested per spikelet (Hampton and Hebblethwaite, 1985).

Hutley-Bull and Schwabe (1982) suggested that in cereals, the manipulation of tiller production may also prove advantageous to seed yield. Various experiments (Batch et al., 1980; Hutley-Bull and Schwabe, 1982; Koranteng and Matthews, 1982) showed that GA_3 application could promote an increase in fertile tiller numbers. Koranteng and Matthews (1982) reported increased seed yields in glasshouse experiments, but field results were variable (Batch et al., 1980). However, Hutley-Bull and Schwabe (1982) showed that GA_3 application inhibited the growth and emergence of tiller buds, while accelerating the growth of tillers already emerging at the time of treatment. Those tiller buds which had not yet attained vascular status at the time of treatment suffered the greatest inhibition, and often failed to obtain this status. Only those tiller buds which carried differentiated leaves and which had begun elongation suffered little inhibition from GA_3 treatment (Hutley-Bull and Schwabe, 1982).

In perennial ryegrass, application of GA_3 alone did not significantly reduce the number of vegetative tillers produced after ear emergence, or increase the number of fertile tillers. Fertile tiller development was accelerated and lodging began earlier than in untreated plots. The application of GA_3 alone was of no benefit for seed production.

Significant seed yield increases were obtained from the use of PP333 alone, and the effects of this growth retardant on the growth and development of the ryegrass seed crop have been extensively discussed elsewhere (Hebblethwaite et al., 1982; Hampton and Hebblethwaite, 1985). However, further yield increases may be possible even in PP333 treated crops, as Hampton (1983) has shown that in such crops, vegetative tillers are in direct competition with the

developing ear for assimilate supply, although the degree of competition is less than in lodged crops. In some seasons (for example, 1981), PP333 treatment can reduce the number of vegetative tillers formed after anthesis, possibly because the upright growth habit of the crop restricts light penetration to the site of vegetative tiller production (Hampton, 1983). However, as occurred in 1982, heavy rain between ear emergence and anthesis (Hampton and Hebblethwaite, 1985) can stimulate vegetative tiller production. Although PP333 delayed the initiation of these vegetative tillers by three to four weeks in 1982, by final harvest vegetative tiller numbers were not significantly different from those of untreated plots.

PP333 application leads to a reduction of endogenous gibberellin levels within the ryegrass plant, and its retardant effects may be reversed by subsequent application of GA_3 (Shearing and Batch, 1982). However, Hutley-Bull and Schwabe (1982) suggested that in wheat, a stimulation of initial tiller production (by PP333), then a limitation in tiller production linked with a promotion in the development of existing tillers (by GA_3) tended to improve existing tiller survival while limiting further tiller production. This concept may not be applicable in a perennial crop such as ryegrass, where tiller production can continue virtually uninterrupted - although it is normally arrested after the reproductive phase has begun, usually at the onset of rapid stem elongation (Langer, 1979). In 1981, the application of GA_3 at floret initiation to plots treated with PP333 at spikelet initiation, significantly reduced vegetative tiller numbers before ear emergence. In 1982, although reduced, vegetative tiller numbers were not significantly different from that of PP333-treated plots. After anthesis, vegetative tiller numbers did not differ significantly between the two treatments. The timings of the GA_3 treatments used in these experiments were based on the cereal work of Batch et al., (1980) and Hutley-Bull and Schwabe (1982), and the results obtained have demonstrated that these timings were incorrect for perennial ryegrass. There was evidence of a response to GA_3 application at floret initiation in PP333 treated plots. Further work should consider GA_3 application at ear emergence to investigate the effects of such treatment on vegetative tiller production after anthesis.

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