Comparative Responses of a Perennial Ryegrass Seed Crop to Four Plant Growth Regulators

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ABSTRACT

The effects of CCC+CC, paclobutrazol, XE-1019 and ethephon on lodging, disease incidence, seed shedding, yield components and seed yield of perennial ryegrass (*Lolium perenne* L.) were investigated in two field experiments (Exp) at Elora, Ontario, Canada. Paclobutrazol consistently prevented lodging; XE-1019 showed a rate dependent activity, being ineffective at the lowest rates. CCC+CC and ethephon did not control lodging. Paclobutrazol and XE-1019 reduced the incidence of leaf rust (*Puccinia* sp.) at all rates applied, but paclobutrazol was more effective at the spikelet initiation application, whereas XE-1019 showed more activity following application at the boot stage. CCC+CC and ethephon had no effect on rust incidence. Paclobutrazol applied at spikelet initiation reduced 1000-seed weight (TSW) in Exp 2. All plant growth regulators (PGR), except paclobutrazol, increased seed shedding and significant PGR x rate x application time interactions occurred. Yield was not affected by PGR in Exp 1 but in Exp 2 paclobutrazol caused a yield reduction which may have been caused by increased seed retention.

Additional index words: **paclobutrazol, XE-1019, chlorocholine chloride, ethephon, lodging, seed shedding.**

INTRODUCTION

Yield in grass seed crops results from the integration of yield components (Hampton and Hebblethwaite, 1983). Season, management, and mineral nutrition interact to regulate development, shaping the contribution of yield components to potential yield achieved at anthesis. Subsequent physiological processes such as crop lodging, seed abortion, floret and seed abscission, and vegetative tiller production affect the eventual contribution of yield components to harvested yield (Marshall, 1985). The use of plant growth regulators (PGR) to control the growth, development, and yield of grass seed crops (Hebblethwaite, 1987) is a possible alternative to breeding for the various morphological and developmental traits associated with seed yield (Elgersma, 1985).

Numerous PGR are available. The main groups of synthetic PGR are ethylene-releasing compounds and inhibitors of the biosynthesis of auxins and gibberellins (Halmann, 1990). Ethephon is an ethylene-releasing chemical which reduces the height of the main shoot and stimulates tillering in cereals (Woodward and Marshall, 1988). CCC+CC, a blend of clormequat chloride (chlorocholine chlorine) and choline chloride, is a gibberellin biosynthesis inhibitor, widely used in Europe to prevent lodging in cereals (Jung, 1984). Paclobutrazol and XE-1019 are two triazole derivatives which inhibit gibberellin biosynthesis and also interfere with the biosynthesis of ergosterol (Davis, Steftens and Sankhla, 1988). The former effect explains their growth retardation activity and the latter is related to their fungicidal properties (Halmann, 1990).

Although PGR are currently used in a range of crops, their use in grass seed crops is not common practice. There are large quantitative and qualitative differences in the response of different plant species, and even cultivars, to a given PGR, preventing the generalisation of the biological effects (Halmann, 1990). Except for paclobutrazol, reports on the effects of PGR on ryegrass seed crops, and especially comparative studies, are scarce (Hebblethwaite, 1987). For paclobutrazol, consistent effects on lodging control but inconsistent effects on yield components, seed retention, and seed yield have been reported, the variability being attributed to interaction of the PGR with season and cultivar effects (Hebblethwaite, 1987). Work with CCC indicates similar inconsistencies of yield effects as described for paclobutrazol, but with a rather narrow range of variability, and a general lack of effect on lodging (Hampton, 1986). Reports concerning ethephon and XE-1019 effects on growth, development and seed yield of perennial ryegrass are limited.

The present study was conducted to evaluate and compare the effects of the abovementioned PGR, when applied at two rates and at two developmental stages prior to anthesis on a perennial ryegrass crop grown for seed.

MATERIAL AND METHODS

Two field experiments were conducted at the Elora Research Station, University of Guelph, on a silt loam (Typic Hapludalf-grey brown podsolic). Perennial ryegrass cv. Fiesta II, an early maturing turf type, was drilled at a rate of 6 kg ha^{-1} in 18 cm wide rows in 7 row plots, 7 m long. Experiment 1 was sown in August 1987 and Exp 2 in August 1988. The PGR paclobutrazol ([(2RS,3RS)-1-(4-chlorophenyl)-4,4-dimethyl-2-(1,2,4-triazol-1-yl) pentan-3-ol], CCC+CC [2-chloroethyl-trimethylammonium chloride + 2-hydroxyethyl-trimethylammonium chloride], ethephon [2-chloroethanephosphoric acid] and XE-1019 [(E)-(p-chlorophenyl)-4,4-dimethyl-2-(1,2,4-triazol-1-yl)-1-pentan-3-ol] were sprayed as treatments at two develop-

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mental stages. In Exp 1, all PGR were applied at spikelet initiation (4 May) and floret initiation (17 May). In Exp 2, paclobutrazol was applied at spikelet initiation (28 April) and floret initiation (19 May) whereas all other PGR were applied at spikelet initiation and the boot stage (5 June). Development was microscopically determined by the dissection of 25 tillers randomly and frequently taken from the experimental area. Applied rates, in kg active ingredient (ai) ha^{-1}, were: paclobutrazol (1.0, 1.5 and 2.0), CCC+CC (0.46, 0.92 and 1.38), ethephon (0.24, 0.48 and 0.72) and XE-1019 (0.03, 0.06 and 0.09 in Exp 1 and 0.1, 0.2 and 0.3 in Exp 2). Experimental units, including a control plot, were arranged as a randomised complete block design with four replicates. All plots received 120 kg N ha^{-1} split between autumn (early September, 30 kg ha^{-1}) and spring (25 April, 90 kg ha^{-1}) applications in both years.

Visual ratings of intensity and area affected of both lodging and disease were taken two weeks before harvest. Intensity was rated on a 1 (no lodging) to 5 scale whereas area affected was rated on a 1 (none) to 10 scale. Lodging and disease indices were obtained by multiplying intensity x area x 0.2. Plant height was measured at the same date. One week before harvest in both years, two 20 cm-long samples were taken from inner rows and the number of reproductive tillers in the two samples was counted. From the same samples, ten fertile tillers per plot were taken to determine the number of spikelets per tiller. In Exp 2, seed yield per sample was determined from the two 20-cm long samples per plot. From this sample yield, final seed numbers per spikelet and per tiller were determined. In Exp 1, number of seeds per spikelet and per tiller was calculated from the total plot yield. Twenty five phenologically comparable tillers per plot were tagged at anthesis. Five tagged tillers were sampled at day 2 after anthesis and florets were counted on one spikelet in each of the apical, intermediate and basal sections of the spike. Plots were direct-combined at 30% seed moisture content on 19 July 1988 (Exp 1) and 2 August 1989 (Exp 2). Immediately after harvesting Exp 2, shed seed was recovered from a 0.242 m^2 sampling area per plot, by means of a portable vacuum. Both harvested and shed seed were cleaned to commercial standard prior to weighing. Germination percentage and TSW were determined on samples of 200 seeds per plot for both the harvested and the shed seed.

Data analyses were performed by analysis of variance and least square regression.

RESULTS

Crop lodging

In both experiments, paclobutrazol reduced lodging at all rates and timing of application (Table 1). In Exp 1, the effect of paclobutrazol was similar among rates and it was equally effective when applied at spikelet or floret initiation. In Exp 2 the higher rate (2.0 kg ai ha^{-1}) provided a more effective control and the floret initiation application was less effective at the lower and intermediate application rates. In Exp 1, XE-1019 significantly reduced lodging when applied at the highest rate (0.09 kg ai ha^{-1}) (Table 1). However, the effect was not as large as paclobutrazol's and the difference was significant. In Exp 2, where application rates were increased three fold relative to rates in Exp 1, XE-1019 significantly reduced lodging at the intermediate and higher rates. The difference between these two rates was significant, the extent of control increasing with rate. XE-1019 at intermediate and highest rates had similar effectiveness as paclobutrazol at lower and intermediate rates respectively. In Exp 2 the two triazoles acted differently depending on the timing of application. Paclobutrazol was more effective the earlier the application, whereas XE-1019 was effective when applied at the boot stage but not when applied at spikelet initiation, except at the highest application rate (Table 1). CCC+CC and ethephon were ineffective in controlling lodging at all rates and timing of application tested.

Lodging control was related to reductions in plant height. In Exp 1, stand height was significantly reduced by 10-15 cm for paclobutrazol treated plots. In Exp 2, plant height was reduced by around 10 cm by both paclobutrazol and XE-1019. In both experiments, although the stem shortening effect of paclobutrazol occurred at all rates and timing of application, a greater reduction occurred following the earlier application (data not presented). XE-1019 application at both growth stages reduced plant height at the intermediate and high rates only, with a greater reduction coming from the floret or boot application times. Reduction in height resulted from the shortening of basal internodes since no differences in the length of either the uppermost internode or the spike were found. CCC+CC and ethephon had no effect on plant height.

Disease index

In Exp 2, an outbreak of leaf rust occurred. Paclobutrazol and XE-1019 significantly reduced the incidence of rust. The effect was rate independent. For paclobutrazol, the spikelet initiation application provided significantly better rust control whereas XE-1019 provided more control at the later application (Fig 1.). CCC+CC and ethephon did not reduce the incidence of rust.

Seed yield potential

Mean theoretical seed yield potential (florets m^{-2} x average seed weight) in Exp 1 was 11,819 kg ha^{-1} whereas the mean actual yield was 1,083 kg ha^{-1} or 9% of the potential yield. In Exp 2, mean values for potential and actual yield were 13,329 kg ha^{-1} and 1,177 kg ha^{-1}, respectively; actual yield representing again 9% of the potential. Neither PGR had any effect on potential yield in Exp 1 as yield components (fertile tillers, spikelets per tiller, florets per spikelet and seed weight) did not differ significantly. In Exp 2, a significant PGR x stage interaction occurred and

Table 1. Lodging control by PGR applied at three rates and two developmental stages (ST) to perennial ryegrass.

		Lodging index					
		Rate 1[1]		Rate 2[1]		Rate 3[1]	
Exp	PGR	ST1[2]	ST2[3]	ST1[2]	ST2[3]	ST1[2]	ST2[3]
				index (0.2-10.0)			
1	Control	5.28	5.28	5.28	5.28	5.28	5.28
	Paclobutrazol	0.20	0.28	0.26	0.20	0.22	0.28
	CCC+CC	4.60	3.03	2.70	5.08	3.33	4.63
	XE-1019	4.58	6.35	4.20	3.15	2.83	2.00
	Ethephon	5.73	4.33	6.03	3.50	3.78	5.23
2	Control	6.33	6.33	6.33	6.33	6.33	6.33
	Paclobutrazol	1.85	4.05	0.56	4.20	0.25	1.20
	CCC+CC	6.38	6.23	6.65	7.05	6.20	7.10
	XE-1019	6.38	6.55	6.13	3.70	3.18	1.71
	Ethephon	6.90	7.00	6.55	6.23	6.80	6.40

LSD ($P < 0.05$) PGR x Rate x Stage, Exp 1 = 2.84
LSD ($P < 0.05$) PGR x Rate x Stage, Exp 2 = 1.54
[1] See text - applies for all tables.
[2] ST1 = spikelet initiation in both experiments.
[3] ST2 = floret initiation for Exp 1 and paclobutrazol in Exp 2, but boot stage for other PGR in Exp 2.

potential yield was significantly increased by the highest rate of paclobutrazol applied at floret initiation (Table 2). Paclobutrazol significantly reduced TSW when applied at spikelet initiation, regardless of rate. Also, the number of florets per spikelet was increased by the intermediate and highest rate of paclobutrazol applied at floret initiation. A similar significant effect on number of florets per spikelet was produced by CCC+CC, XE-1019 and ethephon, particularly when applied at the high rate at the later stage (Table 2).

Shed seed

The quantity of seed recovered from the ground after harvest averaged 353 kg ha^{-1} which represented 30% of the mean yield. Significant PGR x rate x stage interactions occurred. All PGR, except paclobutrazol, increased the amount of seed shed at some or all the stages or rates applied. The increase was significant for CCC+CC at the highest rate, regardless of timing of application. The effect of XE-1019 was variable, whereas ethephon increased seed shattering at all rates (Table 3). The percentage of seed shed relative to seed yield was increased to 30-40% (from 18% for the control) by those PGR treatments which had a significant effect on seed shedding, so that the effect on the amount of seed shed was not proportional to any effect on seed yield.

TSW and percentage germination of shed seed

There was no effect of PGR on TSW of shed seed. The mean TSW of shed seed was 1.77 g which was 12% lower ($P < 0.001$) than the mean TSW of harvested seed. Standard germination of shed seed was 94% after seven days and no effect of PGR treatments was found.

Seed yield

Harvested yield was not affected by PGR application in Exp 1 (data not presented). In Exp 2, paclobutrazol-treated plots yielded 26% less seed than control plots (Table 3). Yield reductions occurred at all rates applied at spikelet initiation and for the intermediate rate applied at the floret initiation stage (Table 3). Harvested yield was also significantly reduced by XE-1019 at all rates of spikelet initiation, and by the high rate when applied at the boot stage. Mean reduction of harvested yield caused by XE-1019 was 24%, compared to the control plots. CCC+CC and ethephon had no effect on harvested yield (Table 3).

Total yield (harvested seed yield + shed seed) responded similarly in Exp 2 to harvested seed yield. Paclobutrazol treated plots yielded 25-35% less seed than control plots and the effect was significant at the spikelet initiation application. For XE-1019, total yield was significantly reduced by the earliest application of the lowest rate and the 18% reduction caused by the earliest application at the highest rate was marginally non-significant (Table 3). No effect of CCC+CC or ethephon on total yield was found.

DISCUSSION

Control of lodging of perennial ryegrass seed crops by paclobutrazol has been reported to increase with rate and

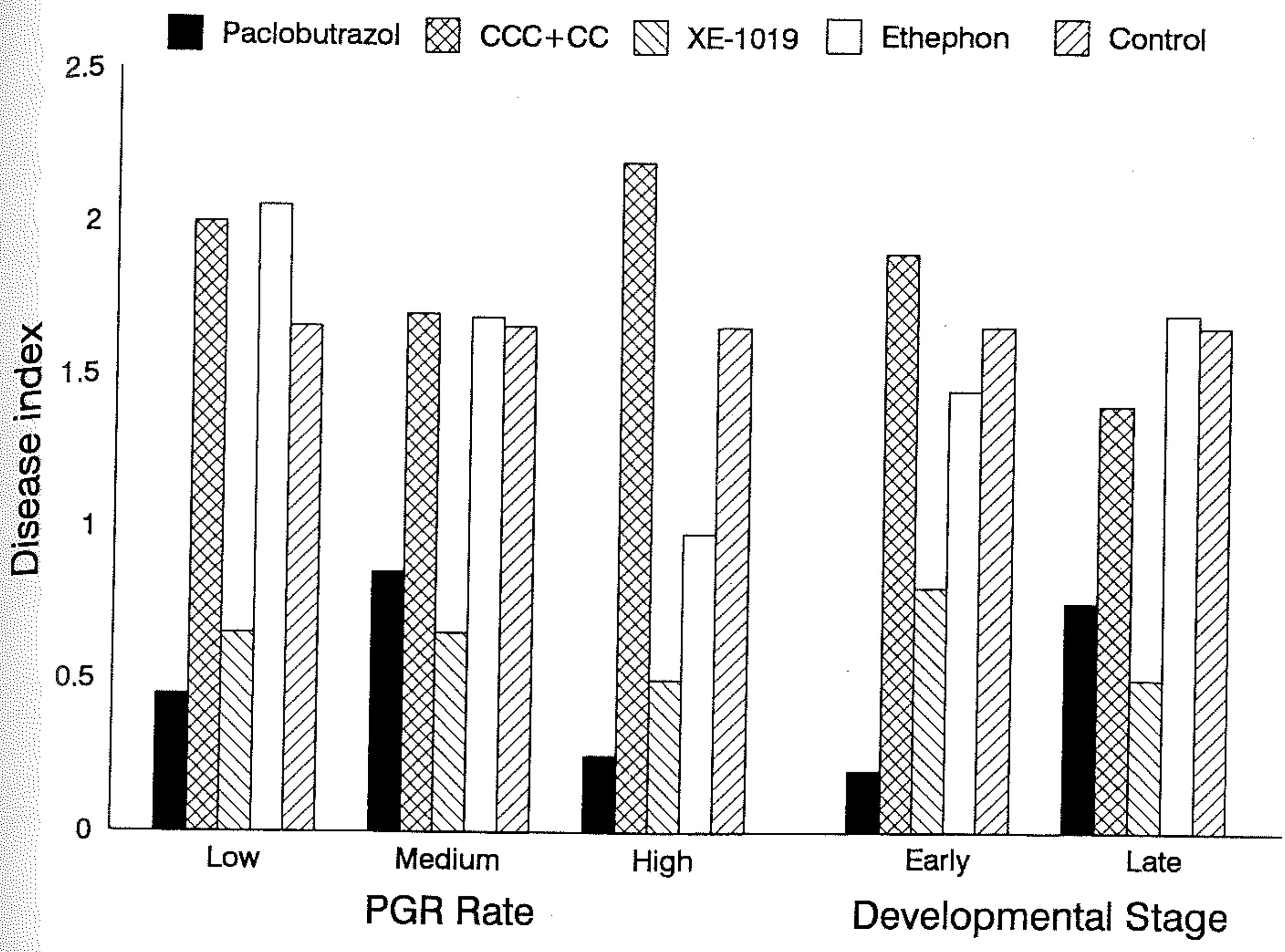

Figure 1
Disease index response to rate and developmental time of PGR application in Exp 2.
LSD ($P < 0.05$) PGR x Rate = 1.02
LSD ($P < 0.05$) PGR x Stage = 0.89

earliness of application for rates ranging from 0.5 to 2.0 kg ai ha^{-1} for a range of seasons, cultivars and nitrogen levels (Hebblethwaite, Batts, Barrett and Wiltshire, 1986; Hebblethwaite, 1987; Hampton, 1988). Our results concur with these reports. The stem shortening and lodging control effect of the two triazoles suggests that the timing and rates of application of XE-1019 were inappropriate in Exp 1. XE-1019 is more active than paclobutrazol in controlling stem elongation (Barrett and Nell, 1986), and the ratio of rates for the two PGR was 1:30 in Exp 1. However, lodging and stem height data from Exp 2 suggest that XE-1019 is about five times more active than paclobutrazol in perennial ryegrass.

The lack of effect of CCC+CC on lodging and stem height is consistent with observations by Hampton (1986) for chlormequat chloride (CCC) application to ryegrass at rates ranging from 1.5 to 4.5 kg ai ha^{-1}, which are higher than the rates we applied. In general, CCC has shown to be specific in its effects on different crops, controlling lodging and reducing stem elongation in some crops but not in others (Stoddart, 1964; Herbert, 1982; Hebblethwaite and Burbidge, 1976). This specificity is a function of differences in the rates of uptake, translocation to and from the sites of activity, and metabolism of the compound (Lord and Wheeler, 1981). Although the evidence suggests a physiologically based inefficiency of CCC+CC in ryegrass, it also appears that our rates of application, which were consistent with common usage, might have been too low. Recommended rates of application for paclobutrazol are 1:1000 that of CCC (Davis *et al.*, 1988). Although this ratio appears to be too high, it suggests that CCC rates tested in perennial ryegrass should be substantially increased.

Absence of effect of PGR on yield potential and their components in perennial ryegrass has been reported previously for paclobutrazol and flurprimidol (Hampton and Hebblethwaite, 1985b), for flurprimidol (Hebblethwaite, Hampton, Batts and Barrett, 1985), for paclobutrazol and CCC (Hampton, 1986), and for RSW0411 (Wiltshire, Hebblethwaite, Esslemont and McGilloway, 1989). However, our data suggest that seed yield potential might be increased by PGR application. The interaction with seasonal weather pattern might be a determinant factor. Exp 1 experienced a dry growing season whereas rainfall was not limiting for Exp 2.

Table 2. Mean response of components of potential seed yield to PGR applied at three rates and two developmental stages (ST) to perennial ryegrass for Exp 2.

	Rate 1		Rate 2		Rate 3	
PGR	**ST1[1]**	**ST2**	**ST1**	**ST2**	**ST1**	**ST2**
			Number of fertile tillers m^{-2}			
Control	4147	4147	4147	4147	4147	4147
Paclobutrazol	3693	3292	3613	4776	4222	4838
CCC+CC	2726	4893	3271	3226	3572	3601
XE-1019	3763	3167	3096	4522	3146	4380
Ethephon	3926	4159	4051	3524	4213	3876
			Number of spikelets/tiller			
Control	19.8	19.8	19.8	19.8	19.8	19.8
Paclobutrazol	22.0	20.0	20.8	18.9	21.5	21.7
CCC+CC	20.0	20.3	17.6	19.3	17.7	18.6
XE-1019	21.5	18.9	18.7	21.6	20.4	20.7
Ethephon	21.2	19.1	17.0	18.5	22.1	19.2
			Number of florets/spikelet			
Control	8.2	8.2	8.2	8.2	8.2	8.2
Paclobutrazol	8.1	8.6	8.5	8.9	8.8	9.2
CCC+CC	8.4	9.1	8.5	8.2	7.9	9.1
XE-1019	8.2	8.2	8.5	9.8	9.7	9.2
Ethephon	8.3	8.1	8.7	8.2	9.1	9.0
			Thousand seed weight (g)			
Control	2.11	2.11	2.11	2.11	2.11	2.11
Paclobutrazol	1.93	2.00	1.89	1.90	1.83	2.03
CCC+CC	2.05	1.94	2.02	2.11	2.06	1.95
XE-1019	1.97	2.07	1.94	1.99	1.90	2.06
Ethephon	2.12	2.13	2.15	2.03	1.95	2.00
			Potential yield (kg ha^{-1})			
Control	14437	14437	14437	14437	14437	14437
Paclobutrazol	15208	11450	9945	15405	14484	19638
CCC+CC	9461	17339	9799	10834	10588	11904
XE-1019	13135	10179	9516	19385	11852	17282
Ethephon	14071	13560	12879	10852	16604	13406

LSD ($P < 0.05$) PGR x Rate x Stage for fertile tillers m^{-2} = 995.65
LSD ($P < 0.05$) PGR x Rate x Stage for spikelets/tiller = 2.799
LSD ($P < 0.05$) PGR x Rate x Stage for florets/spikelet = 0.642
LSD ($P < 0.05$) PGR x Rate x Stage for TSW = 0.1706
LSD ($P < 0.05$) PGR x Rate x Stage for potential yield = 4996.14
[1] See Table 1.

Data of floret dynamics from Exp 2 showed that paclobutrazol, CCC+CC and XE-1019 increased early floret retention (Mares Martins and Gamble, 1993). The data discussed in the present paper suggest that the early increase in seed retention brought about by paclobutrazol lasts longer than any retention caused by CCC+CC or XE-1019, whose effect reversed to a fragile seed retention at harvest. Not withstanding any involvement of ABA, the consistent increase in seed shedding brought about by ethephon suggests a concomitant involvement of ethylene. We did not

Table 3. Mean amount of seed shed, harvested seed yield, total seed yield, and number of seeds per fertile tiller for perennial ryegrass as affected by the rate of PGR applied at two developmental stages (ST) in Exp 2.

PGR	Rate 1		Rate 2		Rate 3	
	ST1[1]	ST2	ST1	ST2	ST1	ST2
	Amount of seed shed (kg ha^{-1})					
Control	251	251	251	251	251	251
Paclobutrazol	225	165	344	339	306	308
CCC+CC	197	256	147	337	383	511
XE-1019	278	475	464	235	335	487
Ethephon	411	420	480	368	448	558
	Harvested seed yield (kg ha^{-1})					
Control	1364	1364	1364	1364	1364	1364
Paclobutrazol	824	1302	870	1053	742	1285
CCC+CC	1199	1205	1307	1474	1373	1328
XE-1019	984	1370	957	1229	992	955
Ethephon	1231	1292	1354	1353	1198	1177
	Total seed yield (kg ha^{-1})					
Control	1615	1615	1615	1615	1615	1615
Paclobutrazol	1049	1467	1214	1392	1048	1593
CCC+CC	1397	1462	1454	1811	1756	1839
XE-1019	1262	1845	1422	1464	1327	1443
Ethephon	1641	1712	1834	1722	1646	1735
	Number of seeds/fertile tiller (calculated)					
Control	27.1	27.1	27.1	27.1	27.1	27.1
Paclobutrazol	14.6	19.1	16.9	28.3	16.3	22.9
CCC+CC	21.2	29.3	30.7	23.4	25.9	26.0
XE-1019	20.9	29.3	19.9	23.1	24.1	23.2
Ethephon	27.2	19.6	30.1	24.0	26.5	25.5

LSD ($P < 0.05$) PGR x Rate x Stage for amount of shattered seed = 125.09
LSD ($P < 0.05$) PGR x Rate x Stage for harvested seed yield = 266.12
LSD ($P < 0.05$) PGR x Rate x Stage for total seed yield = 289.33
LSD ($P < 0.05$) PGR x Rate x Stage for number of seeds/tiller = 6.1
[1] See Table 1.

determine the position on the spikelet from which most shed seed came. However, as shed seed was lighter than harvested seed, it is plausible that most shedding would have occurred at the apical third of the spikelet, which has been shown to produce lighter seed than either the basal or intermediate floret positions (Hampton and Hebblethwaite, 1985a). A higher incidence of seed shedding at the apical end of the spikelet could be due to increased exposure to mechanical stress and less support provided by the glumes, compared to the basal location.

Since the trends of harvested yield and total yield were similar, no differences in harvested yield can be attributed to differences in seed shedding. It appears that yield reductions were caused by reductions in TSW. However, the calculated number of seeds per fertile tiller was concomitantly reduced, particularly by paclobutrazol (Table 3). As both seed set (Mares Martins and Gamble, 1993) and seed yield potential were similar for all treatments, the reduction in the number of seeds per spike suggests that a stronger seed retention which restricted seed threshing, and/or seed abortion were involved as determinants of harvested yield in paclobutrazol treated crops. Delayed harvest maturity is probably not a factor because the number of seeds per spike were obtained from dried tiller samples. Seed retention in the spike at harvest, caused by paclobutrazol, could partially explain the reduction in yield recorded in Exp 2. Hampton and Hebblethwaite (1985c) have determined that a single direct combining of a paclobutrazol treated crop was not able to harvest all the available seed. On the other hand, our data on early seed abortion (Mares Martins and Gamble, 1993) for Exp 2 showed that paclobutrazol, XE-1019 and CCC+CC significantly increased abortion, compared to the control, during the first 10 days of seed development. In Exp 1, both CCC+CC and paclobutrazol significantly reduced early seed abortion (Mares Martins and Gamble, 1993). These abortion data are consistent with the yield responses to paclobutrazol reported here. Variable responses of perennial ryegrass seed yield to the application of growth regulators, particularly paclobutrazol and CCC have been reported (Hebblethwaite, 1987; Hampton, 1986). The reasons for the inconsistency of results are not fully elucidated, particularly for results within a given cultivar. However, our data suggest that seed abortion, seed retention and seed shattering are major determinants of seed yield, and that PGR affect those factors. Timing and method of harvesting appear to be of utmost importance to realise any effect of PGR.

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