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Title: TILLERING, LODGING, DRY MATTER PARTITIONING, AND SEED YIELD IN RYEGRASS (Lolium spp.) AS AFFECTED BY THE PLANT GROWTH REGULATOR PACLOBUTRAZOL.

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Seed yield in ryegrass (*Lolium* spp.) is the product of the number of fertile tillers per unit area and seed weight per spike at maturity. These components of yield develop through a series of growth stages beginning with tiller bud initiation and finishing with seed filling. Environmental conditions during plant growth control potential yield development and the efficiency with which it is utilized.

Lodging in ryegrass can have dramatic effects upon the utilization of potential yield. It occurs when culm strength is inadequate to maintain the spike in its vertical position. High moisture and fertility stimulate vegetative growth, stem elongation, and produce premature or early lodging. The timing and severity of lodging directly determine its impact upon seed yield and its components.

In these experiments, the effects of the plant growth regulator paclobutrazol upon tillering, lodging, dry matter partitioning, and seed yield were investigated under controlled environment and field conditions.

Linn and Pennfine perennial ryegrasses under dry conditions (1982) lodged after anthesis with no significant effect upon yield. In 1983, Caravelle and Pennfine perennial ryegrasses lodged prior to the completion of anthesis which resulted in yield reductions when compared to unlodged plants.

The plant growth regulator paclobutrazol delayed lodging by restricting stem elongation. This effect was concentrated in the basal internodes where both internode length and weight were reduced. In Pennfine and Caravelle perennial ryegrasses the strength of the internodal segments were found to be related to the dry weight per unit length of stem. Paclobutrazol increased the dry weight per unit length of stem, stem strength, and seed yield. Yield increases were attributed to increased number and weight of seeds per spike and larger number of fertile tillers.

Paclobutrazol was found to influence plant growth in several ways. Paclobutrazol applied to annual ryegrass at the vegetative growth stage increased tiller number, decreased leaf length, and decreased leaf area. Treatment at the floret initiation stage decreased tiller length and increased the number of florets in the top spikelet. Tiller number was not significantly increased. This indicates that paclobutrazol had a variety of potential effects upon ryegrass development depending upon the growth stage at application and the rate applied.

Tillering, Lodging, Dry Matter Partitioning, and Seed Yield in Ryegrass (*Lolium* spp.) as Affected by the Plant Growth Regulator Paclobutrazol

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INTRODUCTION

Seed yield in ryegrass (*Lolium* spp.) is developed during several stages beginning with tillering and ending with seed filling. During this time cultural and environmental factors may influence both the potential yield developed and the efficiency with which it is utilized.

Tillering is the process of axillary bud initiation, elongation, and emergence which occurs mainly during vegetative and early reproductive growth. It is controlled by mineral nutrition and the level and balance of endogenous plant hormones.

As the developing tiller bud expands and elongates, meristematic tissues produce leaf primordia and other tissues from which the stem and its structures originate. When the proper conditions are present the apical meristem produces spikelet and floret primordia which give rise to the final components of potential yield. The number of primordia produced is controlled by endogenous plant growth regulators, assimilate supply, and environmental conditions.

Potential yield represents the biological capacity of ryegrass for seed production. Since actual seed yield is a fraction of the biological potential, various factors restrict the full realization of potential yield.

The realization of potential yield is dependent upon tiller survival through maturity and successful flower pollination, ovule fertilization, and seed development. These processes are all influenced by environmental conditions. Temperature, humidity, and wind speed can effect pollination and fertilization by reducing pollen dispersal and interception. Sub-optimal light and nutrient supplies can reduce seed development and cause embryo abortion and tiller mortality. These factors can all be influenced by the orientation and density of the canopy. If lodging occurs, with consequent canopy compression, dramatic reductions in the utilization of potential seed yield can occur.

Lodging is a major problem in a range of crops and is especially serious in susceptible crops such as ryegrass. Lodging occurs frequently under the high moisture and fertility conditions associated with seed production. Plant growth regulators have been examined as a means of increasing the efficiency of grass seed production by preventing lodging and allowing better utilization of potential yield.

Paclobutrazol and other similar plant growth regulators may have a wide range of effects on plant growth and development beyond lodging control. The following two papers look at the effects of the plant growth regulator paclobutrazol upon tillering, lodging, dry matter partitioning, and seed yield in the ryegrass plant.

Tillering, Lodging, Dry Matter Partitioning, and Seed Yield in Ryegrass (Lolium spp.) as Affected by the Plant Growth Regulator Paclobutrazol

REVIEW OF LITERATURE

INTRODUCTION

Seed yield in ryegrass (Lolium spp.) is the product of yield components which develop over the life of the plant and its tillers. Hebblethwaite, Wright, and Noble (1980) divided this process of seed yield development into two basic stages:

1) establishment of the yield potential;

2) utilization of the yield potential.

Each of these stages is the result of developmental processes which are influenced by a plant's genome and environment.

Seed yield potential is developed through the division of meristematic tissues in the leaf axils and shoot apices. Apical meristems produce primordial tissues that give rise to spikelets, florets, and other floral organs and determine the yield potential of an individual fertile tiller (Jeater, 1956). Axillary meristems may produce buds which can elongate and produce either a vegetative or reproductive tiller. These tissues together produce the organs or structures which contribute to the following components of seed yield:

1) number of fertile tillers;

2) spikelets per fertile tiller;

3) florets per spikelet.

The utilization of potential yield is dependent upon the survival of fertile tillers until pollination, fertilization, and seed filling are complete. This literature review examines the development and utilization of yield potential as it relates to tillering, and lodging.

TILLERING

Tillering is the process by which a grass plant produces multiple stems, each capable of continued vegetative and reproductive growth. The number of tillers developed per plant and the timing of tiller emergence is influenced by a variety of factors such as soil fertility, light intensity, and plant density. Kirby and Faris (1972) found that there are three stages of tiller development in barley:

1) tiller bud initiation;

2) tiller bud elongation and emergence;

3) tiller survival.

Jewiss (1972) describes the developmental events leading to the formation of the tiller bud. First, leaf primordia are formed from the terminal meristem in acropetal succession. Early in the continued division and enlargement of the leaf primordia, cell divisions in the growing point give rise to axillary buds which can give rise to tillers. These tiller buds first must further develop in size and differentiate to form vascular connections, and then elongate past their subtending leaf sheaths.

Williams and Langer (1975) examined the controlling mechanisms for tillering in wheat. They felt that

> tillering in cereals should be seen as the resultant of determinants at several levels within the hierarchy which is the living plant. These levels related to the action of hormones and inhibitors, to competition for nutrients and energy substrates, and to the incidence of dynamic physical constraint between organs within the shoot-apical system.

The implication is that tillering and its control are complex processes with major influences upon the development of seed yield potential. Plant hormone levels and assimilate competition are the most important control mechanisms.

Hormonal Control of Tillering

Hormones control tiller number by regulating the following two processes:

1) tiller bud initiation;
2) tiller bud elongation.

Tiller bud initiation can be defined as the transition between a quiescent bud and one which is actively undergoing cell division and growth. It is the stage prior to elongation during which the bud is developing vascular connections and increasing in cell number. Sharif and Dale (1980) examined the effects of IAA, GA, and cytokinin upon barley tiller buds. They found that IAA and GA had no effect upon tiller bud growth in the absence of either cytokinins or mineral nutrients. Cytokinins stimulated a dramatic increase in tiller bud weight in the absence of mineral nutrients, GA or IAA. Cytokinins in conjunction with GA produced twice the rate of tiller bud growth compared to cytokinin alone. This indicates that tiller bud initiation can be stimulated by mineral nutrients and by the presence of cytokinins and that GA can stimulate rapid growth of tiller buds once intiated. Thus, these two compounds at least partially control tillering.

Hormonal and Environmental Control of Tillering

In Michael and Beringer's (1980) review of the role of hormones in the formation of yield they suggested that IAA plays an unknown role in the apical control of tillering. It was also recognized that cytokinin plays a role in tillering. They felt that any factors which influence root growth have an indirect effect upon tillering because of the association of root growth with cytokinin production. Thus, root growth might have an indirect effect upon tiller bud initiation.

Spiertz and Ellen (1972) found that tillering was stimulated by increased light intensities and reduced by shading. If cytokinin is necessary to stimulate the initiation of tillers then the increased growth of roots under high light conditions might also increase cytokinin production and stimulate tillering. Kirby and Faris (1972) reported that tillering was reduced at higher plant densities in barley. They attributted this to higher levels of endogenous giberellin in the shaded environment. They felt that GA has an inhibitory effect upon tillering. Their results could also be explained by decreased root growth under shaded conditions which occur in high density plantings with an attendant decrease in cytokinin production. If GA levels are elevated under the shaded conditions present at high plant densities, the growth of existing tillers and initiated buds would be stimulated and compete for assimilates with the roots. This hypothesis is in agreement with observations by Ryle (1970) upon the importance of lower leaves in providing assimilate to roots and tillers. High density plantings or other low light situations have more intense competition for light and assimilate with less being partitioned to root growth.

TILLER SURVIVAL

The first phases of tiller development are tiller bud initiation and elongation. Both phases are directly controlled by hormonal levels and indirectly by assimilate production. The last phases of tiller development are tiller emergence and survival. Tiller emergence and survival are controlled by many of the same factors controlling earlier phases of development. Tiller emergence occurs earlier at high plant densities than in low density stands (Kirby and Faris, 1970). Tiller survival appears to depend upon its ability to compete for light (Kirby and Faris, 1972) and its time of emergence. Hill and Watkin (1975) found that the earlier a tiller of perennial ryegrass was initiated the lower its rate of vegetative mortality. Tillers initiated during the four months following autumn sowing or during the post-harvest period made the major contribution to seed yield. Under conditions of environmental stress, recently formed tillers usually die first. Ong (1978) found that if plants were subjected to acute nutrient stress or reduced rates of photosynthesis, either would lead to the death of some tillers. The smallest tillers regardless of position tend to die first. These tillers usually had no more than two leaves and no independent roots. Thus, they are dependent upon their parent tillers for both water and nutrients. Tiller death in a grass sward arises from a variety of causes. Ong and Sagar (1978) found that physiological stresses are the most important causes of tiller mortality. Grazing by slugs or rodents is more important as a cause of death than damage by stem boring insect larvae. They also found that if a tiller is defoliated during early reproductive growth it can import assimilate from an undefoliated adjacent tiller. Defoliation of a tiller at anthesis usually leads to its death since undefoliated tillers at this point retain their assimilate.

Thus, tillers are subject to hormonal and environmental influences which control the number of tillers initiated and how many survive to maturity. The utilization of the reproductive potential established by fertile tiller emergence begins with tiller survival from anthesis to harvest, and the pollination, fertilization, and filling of the embryos borne by the fertile tillers.

LODGING

Stand orientation plays a critical role in determining the efficiency of potential yield utilization. If lodging occurs, dramatic yield losses can result. Lodging was defined by Pinthus (1973) as, "...the state of permanent displacement of the stems from their upright position." Lodging often limits the development of optimum yields. Pinthus (1973) states, "... favorable growing conditions promoting crop development and grain yield, will evoke lodging and increase its severity." Consequently he regarded lodging as an "abundance disease" which restricts the exploitation of otherwise yield-promoting factors.

Lodging is caused by a wide variety of conditions ranging from disease to excess amounts of water or nutrients. Mulder (1954) states that,

> favorable growing conditions prevailing during the first part of the growing period of the plants, particularly during the period of elongation of the lower culm internodes give rise to a crop with a high tendency to lodging.

He also observed that,

> Since tendency to lodging depends on a disproportionality between the height of the aerial parts of the plant and resistance to bending or breaking of the basal culm internodes and the roots, it can be concluded that a high liability to lodging may in different cases, be due to different causes.

Lodging is difficult to predict or anticipate. While there are grass and cereal varieties susceptible to lodging, there is a broad range of resistance to lodging. The degree of lodging also depends on the many variables associated with growing and management conditions. Lodging may occur even in a lodging-resistant variety if environmental conditions are sufficiently favorable. Grass or cereal varieties can be described as being resistant to lodging, in a relative sense, based upon their frequency and severity of lodging. Atkins (1938) found that the breaking strength of straw and the weight per unit length of culm were two means of measuring the resistance of a variety to lodging. For 129 varieties of hard and soft winter wheats these two parameters were highly correlated. Welton and Morris (1931) in studying lodging in oats and wheat found

> the low carbohydrate content, whether induced by hypernutrition, shading, or high temperature, resulted always in a relatively low percentage of dry matter. The difference in content of dry matter between erect and lodged plants becomes even more marked if the constituents are calculated for a given length per culm.

Thus, it appears that a lack of dry matter partitioned into the lower culm appears to account for some lodging. Practices or conditions which alter the partitioning of dry matter into the stem may either increase or decrease lodging.

The Effects of Lodging

Lodging in cereals can be a problem causing 21% to 44% reductions in yield in summer wheat and 15% to 69 % in oats (Mulder, 1954). Pendleton (1954) mechanically supported oats and then artificially lodged them at different times. He found that losses caused by lodging varied depending on its time and severity of lodging. Plots lodged to 90° four days after heading yielded 51% of the unlodged plots versus 76% for plots lodged twenty days after heading. In plots lodged to 45^{o}, yields were 83% and 97% of the unlodged plots for the two lodging dates. Weibel and Pendleton (1964) studied the effect of artificial lodging on winter wheat grain yield and quality. They found that lodged plots had yield reductions of 31% if lodged at heading, 25% at milk stage, 20% at soft dough, and 12% at hard dough. Yield reductions were due to reduced test weight and kernal weight.

One effect of lodging in cereals is an increase in self-shading and decreased light penetration. Judel and Mengel (1982) found that shading plants after the onset of anthesis reduced grain yield by 17%. This yield decrease was the result of fewer grains per ear and a reduction in single grain weight. Ear number was constant, indicating that no tiller mortality occurred. The 70% light reduction in this experiment produced a smaller yield reduction than expected because of the plant's ability to mobilize non-structural carbohydrates in the stem and leaves. Control plants were found to have as much as 10% non-structural carbohydrate left in vegetative organs. Thus, it appears that low light is partially compensated for by greater utilization of stored carbohydrates, reducing the effects of low light on seed development.

The effects of lodging in ryegrass follow the same general pattern as in cereals except that lodging has greater chance for disrupting pollination and fertilization since cereals are self-pollinated and ryegrass is cross-pollinated. Hebblethwaite, Burbidge, and Wright (1978) examined lodging in perennial ryegrass and its effects upon seed yield and yield components. They found that lodging reduced seed yield by 25% to 30%, reduced seeds per unit area (resulting from fewer seeds per spikelet), and in some cases reduced numbers of fertile tillers per unit area. This indicates that lodging in perennial ryegrass affects the utilization of yield potential by either reducing pollination and fertilization, or by increasing embryo abortion and tiller mortality. Momma (1981) studied the effects of lodging on Lolium multiflorum by mechanically supporting control plants and preventing their lodging. Lodging at early anthesis reduced yield 33% to 36% and lodging at late anthesis reduced yields 9% to 18% with significant variation between varieties. Lodging reduced 1000 seed weight, weight of seeds per ear, and the numbers of seeds per ear. Ears per unit area was reduced most for two late varieties but in all cases early anthesis lodging significantly decreased ear number. There seems to be a broader range of lodging effects in this study than in Hebblethwaite, et al. (1978).

Lodging appears to have a wide range of effects including reductions in tiller number, seed number, and seed weight. Cultural practices have been examined as a means of reducing lodging but results have been variable. For this reason, extensive interest has been shown in controlling lodging through chemical means. The earliest compounds were either unreliable in their activity or too expensive for practical use. Wright and Hebblethwaite (1979) examined the effects of the plant growth regulator ancymidol on lodging. They found that ancymidol was effective in reducing culm length and delaying lodging in perennial ryegrass. It had no effect on tiller number in one year (1976) but increased fertile tiller number in the next (1977). Ancymidol increased seed yield by increasing seeds per unit area and seeds per spikelet. This is similar to what was found when perennial ryegrass was mechanically supported and lodging prevented.

In a recent article Hebblethwaite, Hampton, and McLaren (1982) discussed the effects of the new plant growth regulator paclobutrazol (PP333). Paclobutrazol was found to have effects similar to ancymidol upon lodging and seed yield. Yield increases from applications of paclobutrazol at the floret initiation stage resulted in 27% to 50% increases in seed yield with respect to the check. Increased seed yield was again attributed to an increased number of seeds per unit area and per spikelet. Increased fertile tiller number did not seem to account for a significant amount of the yield increase. This suggests that delaying lodging may only delay tiller mortality and not increase fertile tiller number at maturity. Straw weight was not significantly affected by paclobutrazol but harvest index was increased which implies a more efficient partitioning of dry matter into seed yield.

Albeke (1983) found that paclobutrazol reduced culm length as much as 29% and delayed lodging. Seed yield was increased 40% to 74% with significant increases in seeds per spikelet and in some cases increased numbers of fertile tillers. He attributed increased yield in the cultivar Pennfine to increases in fertile tiller number, while in a later maturing cultivar, Caravelle, the bulk of the yield increases came from increased numbers of seeds per spikelet.

Hampton, Clemence, and Hebblethwaite (1983) investigated the influence of nitrogen rates and paclobutrazol upon seed yield. Nitrogen application increased the number of fertile tillers in one study (1981) but spikelets per tiller were reduced as nitrogen applications increased. Seed number per spikelet usually decreased with increased nitrogen applications. Seed yield increased by the same amount in paclobutrazol treated plots regardless of nitrogen levels when compared to untreated plots at the same nitrogen rate.

CONCLUSIONS

Crop lodging can have major ramifications on yield by decreasing the efficiency with which potential yield is utilized. Lodging results from the development of tillers which have insuffficent stem strength to support their own weight. The stem strength of a tiller is controlled by genetic, environmental and cultural factors.

Lodging can reduce yield by increasing fertile tiller mortality, reducing the number of seeds per spike, and reducing seed weight. Plant growth regulators such as ancymidol and paclobutrazol can stimulate increases in seed yield by delaying lodging and reducing subsequent yield reductions. Paclobutrazol may have other potential effects upon the growth and development of perennial ryegrass through its alteration of dry matter production and light penetration in the canopy.

Chapter One

Tillering, and Dry Matter Partitioning in Annual Ryegrass (*Lolium multiflorum* Lam.) as Affected by the Plant Growth Regulator Paclobutrazol

ABSTRACT

The plant growth regulator paclobutrazol has been shown to be a means of chemically retarding plant growth and preventing lodging in perennial ryegrass seed production. The effects of paclobutrazol upon plant development have not been thoroughly studied.

This research examines the effect of paclobutrazol upon tillering and dry matter partitioning in annual ryegrass when applied at the vegetative or floret initiation stages of development.

Paclobutrazol applications of .50 and 1.00 kg/ha to vegetative annual ryegrass increased tillering by 100% and decreased leaf area by 30%. The weight of the root and shoot portions of the plant were not significantly affected.

Applications at the .75 kg/ha rate to annual ryegrass during the floret-initiation stage of development produced no significant change in tiller number. Tiller height was reduced by 25% and internode length decreased 15% to 50%. Internode dry weight

decreased 16% to 42% with nonsignificant increases in specific stem weight (SSW).

The effects of paclobutrazol treatment differed between the two experiments. This is probably due to differences in source-sink relationships and levels of endogenous hormones at the vegetative and floret-initiation stages of development.

Additonal key words: tillering, dry matter partitioning, paclobutrazol, plant growth regulator

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Tillering and Dry Matter Partitioning in Annual Ryegrass (*Lolium multiflorum* Lam.) as Affected by the Plant Growth Regulator Paclobutrazol

INTRODUCTION

The plant growth regulator paclobutrazol has been examined as a means of chemically controlling or delaying lodging in perennial ryegrass. Lodging is delayed by reducing plant height and increasing stem strength (Hunter, 1984).

The plant growth regulator paclobutrazol is an inhibitor of GA (giberellin) biosynthesis. It can cause significant reductions in internode elongation (Albeke, 1983; Hunter, 1984), dry weight (Hebblethwaite, Hampton, and McLaren, 1981; Hunter, 1984), and tillering (Hebblethwaite, et al., 1981). This reflects the wide role GA plays in controlling plant growth.

Tiller bud release, elongation and emergence are all steps which are critical in the development of yield potential in grass seed crops. Hebblethwaite, Wright, and Noble (1980) described the developmental processes for potential and actual seed yield components of perennial ryegrass as consisting of four stages:

1) tillering;
2) apical development;
3) pollination/fertilization;
4) seed growth.

The two experiments reported here seek to describe the affects of paclobutrazol upon the first two of these stages of development. Tillering in grasses is an important process controlled by a variety of factors. Williams and Langer (1975) state that the development of axillary buds is controlled by the interaction of hormones and inhibitors, the competition for energy and substrates, and the physical constraint of the axillary bud by the enclosing leaf sheath.

Plant hormones have long been identified as factors which control or influence tillering. Sharif and Dale (1980) found that IAA (Indole acetic acid) and GA could neither promote or inhibit tillering in barley. They also found that mineral nutrients or cytokinins are required for tiller bud stimulation. Thus, cytokinin availability may be the determining factor in tiller bud growth.

Cytokinins are known to stimulate cell division and protein synthesis. Jewiss (1972) found that local application of kinetin (a cytokinin) stimulated bud growth. Cytokinins appear to be produced in areas of meristematic activity. The lower axillary buds are likely to be stimulated by cytokinins produced by the root apices. Jewiss (1972) stated

> presumably the greater root growth produced under high light condtions will result in more cytokinin production. This in turn will change the balance between auxin and cytokinin, and therefore result in a reduction in the ability of apical meristems elsewhere in the plant to suppress lateral bud

development.

This suggests that the effect of GA upon tiller bud development might be indirect via its stimulation of the growth of competitive sinks which can in turn influence the supply of assimilates for active root growth and cytokinin production.

MATERIALS AND METHODS

Two experiments were performed under controlled conditions with annual ryegrass cv. Gulf. Light intensities for both experiments ranged from 250-300 microeinsteins $sec^{-1}m^{2}$ with controlled temperature and photoperiod condtions.

Experiment One

This experiment examined the effects of paclobutrazol upon tillering and dry matter partitioning in pre-reproductive plants. Seeds were pre-germinated on blotter paper and seedlings selected for even germination and vigor. After the first two true leaves had developed the selected seedlings were transplanted to three galvanized metal trays each 15 x 50 x 140 cm in size. These trays were filled with pre-moistened perlite and fitted with a drain. Twenty seedlings were planted in each tray in two rows with plants approximately 10 cm apart within the row and 30 cm between rows. The growth chamber was operated at a constant temperature of 65^{o} F and eight hour daylength. Plants were watered as needed with .25 strength Long-Ashton's nutrient solution. When four to six tillers had been formed by all the plants, paclobutrazol was applied at the 0, 0.50, and 1.00 kg/ha rates as a slow release .25% granular formulation. Plants were allowed to grow for four weeks following application and then the experiment was terminated. Tiller number, leaf area, and the dry weight of the root and shoot portions of the plant were determined at that time.

<u>Experiment Two</u>

This experiment examined the effects of paclobutrazol upon tillering and dry matter partitioning when applied to annual ryegrass plants at the floret-initiation stage of development. Three seeds were planted per pot in soil consisting of a mixture of sandy river loam and peat moss. After seed germination and seedling emergence the seedlings were thinned to one per pot with the most uniform seedlings being retained. Pots were placed in the greenhouse under short daylengths and about 65° F until 15-20 tillers per pot had developed. At this point the plants were transferred to the growth chamber where they were exposed to 14 hour daylengths and 75° F days and 65° F nights. Apical development was followed by dissecting representative tillers from extra pots until the majority (four of five) tillers dissected were at the floret-initiation stage. At this point 24 of the 48 pots were randomly selected and labelled with a marker and arranged in a completely random fashion. The pots were treated with 50 ml of an aqueous solution of paclobutrazol at a rate equivalent to 0.75 kg/ha. This rate is equivalent to that being reccomended for use on perennial ryegrass under field conditions.

Plants were supported with bamboo stakes when there was danger of lodging. Plants were terminated following anthesis but before seed maturity so that seed head shattering could be avoided.

Three representative tillers were severed at the soil surface and separated into internodes, leaves, and spikes. The inflorescences were examined, and the number of spikelets per spike and florets per spikelet were determined. The data was analyzed as a completely randomized design with 24 replications and two treatments.

RESULTS AND DISCUSSION

Experiment One

Paclobutrazol had a variety of effects upon the growth and development of vegetative annual ryegrass. Paclobutrazol increased the number of tiller buds which initiated growth, reduced leaf expansion, and decreased stem elongation.

Tillering was stimulated in paclobutrazol treated annual ryegrass plants. A large number of tiller buds were initiated producing many very small tillers (Table 1.1). These tillers originated from axillary buds on the five tillers present at the time of treatment. In some cases, late developing tiller buds were observed to pierce the subtending leaf sheath instead of emerging in a normal fashion. This behavior was only observed in treated plants.

As tiller number increased, average tiller height was reduced by 80%. This resulted from the inhibition of pseudostem elongation by paclobutrazol and from an increased number of short tillers. The psuedostems consisted of unelongated or partially elongated culms surrounded by a series of overlapping leaf sheaths.

Paclobutrazol inhibited the expansion and elongation of the leaf sheath and blade. Leaf widths were observed to increase slightly with decreased leaf blade elongation. This resulted in a net decrease in leaf area of 30% despite the increased number of leaves. The overlapping leaf sheaths on treated plants had a smaller effective leaf area than on untreated plants (Table 1.1).

Root and shoot weight were not significantly affected by paclobutrazol treatment. Root growth did not appear to affected by paclobutrazol. Root length appeared to be the same in treated and untreated plants. The reduced elongation of leaf tissues resulted in a decreased amount of dry matter partitioned per tiller. Increased tiiler bud initiation in treated plants produced large numbers of small tillers which competed for assimilate with the roots. This could account for the lack of a significant alteration in the root-shoot ratio of treated plants. However, paclobutrazol might increase root development and increase the root-shoot ratio if plants were grown under low moisture and fertility conditions. Under these conditions root growth would be stimulated and compete for assimilate with initiated tiller buds.

Table 1.1 - Tiller number and length, leaf area, and dry matter partitioning as affected by paclobutrazol.

Treatment	Tiller		Leaf area	Root weight	Shoot weight	Root:shoot
	Number	Length				
(kg/ha)	(/plant)	(cm)	(cm^2/plant)	(g)	(g)	
0	9.3	5.5	161	.086	.422	.204
0.50	15.5	1.6	105	.080	.328	.243
1.00	20.4	0.9	103	.085	.344	.247
$LSD_{.05}$	5.1	0.8	30	n.s.	n.s.	n.s.

n.s. = not significant

Experiment Two

In experiment two, paclobutrazol was applied to annual ryegrass just initiating reproductive growth. The effects of paclobutrazol treatment were detectible within ten days to two weeks. The first signs were a reduction in leaf expansion, stem expansion, and a darker green color in leaf tissues. Tiller number was not significantly affected by paclobutrazol treatment. Growing conditions in this experiment favored root growth more than those present in experiment one. All plants were raised in soil without the application of excess water or nutrients. This was done so that the effects of mineral nutrition upon tillering could be minimized so the effects of paclobutrazol treatment could be studied while reducing any interaction with high fertility levels.

Tiller height for untreated plants was within the normal range for this cultivar of annual ryegrass. Plant height was reduced by paclobutrazol application (Table 1.3). The internodes which expanded during and immediately after treatment were affected more than those which developed later (Table 1.2). Internode length was significantly reduced in all sections of the stem. Internode dry weight was significantly reduced for the second, third, and fourth internodes below the spike. The ratio of internode weight to internode length reflects the impact of paclobutrazol treatment upon the partitioning of dry matter within a particular internodal segment. This ratio can be regarded as the dry weight per unit length of stem. The term specific stem weight (SSW) was created to represent this ratio. It quantifies dry matter partitioning for the purpose of treatment comparisons. No significant changes in SSW were found in this experiment.

Paclobutrazol had no effect upon floret or spikelet number except for a slight increase in the number of florets per spikelet in the top of the spike (Table 1.3). This indicates that under these conditions the development of potential yield was not significantly increased.

Table 1.2 - Internode weight, length, and specific stem weight as affected by paclobutrazol.

Treatment	In1[1]			In2			In3			In4			In5		
	DW[2]	Lth[3]	SSW[4]	DW	Lth	SSW	DW	Lth	SSW	DW	Lth	SSW	DW	Lth	SSW
(kg/ha)	(g)	(cm)	(mg/cm)	(g)	(cm)	(g/cm)	(g)	(cm)	(g/cm)	(9)	(cm)	(g/cm)	(g)	(cm)	(g/cm)
0	.104	34	2.88	.086	19	4.44	.069	13	5.31	.079	12	6.29	.070	10	7.09
0.75	.087	29	2.92	.058	11	5.53	.044	7	6.34	.046	6	7.93	.048	6	8.02
	n.s.	*	n.s.	**	**	n.s.	**	**	n.s.	**	**	n.s.	n.s.	**	n.s.

*Significant at P = .10

**Significant at P = .05

n.s. = Not significant

[1] = First internodal segment below the spike

[2] = Internode dry weight

[3] = Internode length

[4] = Internode specific stem weight

Table 1.3 - Tiller height, number, and yield components as affected by paclobutrazol.

	Tiller			Florets/spikelet		
Treatment	Height	Number	Spikelets/spike	Top	Middle	Bottom
(kg/ha)	(cm)	(/pot)				
0	122	17.7	22.3	9.0	10.1	9.2
0.75	84	19.3	22.6	9.8	10.6	9.6
	**	n.s.	n.s.	*	n.s.	n.s.

*Significant at P = .10

**Significant at P = .05

n.s. = not significant

CONCLUSIONS

Paclobutrazol has been shown to increase seed yields in perennial ryegrass by delaying lodging. These two experiments indicate that paclobutrazol may be able to alter the components of yield by stimulating the production of additional tillers, or by altering the production of florets in a spikelet. Further research needs to be done to investigate the effect of soil fertility and application dates upon tillering and growing point differentiation.

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Chapter Two

Lodging, Dry Matter Partitioning, and Seed Yield in Perennial Ryegrass (*Lolium perenne* L.) as Affected by the Plant Growth Regulator Paclobutrazol.

ABSTRACT

The plant growth regulator paclobutrazol has been identified as a means of chemically delaying lodging. For this reason, the effects of paclobutrazol upon lodging, dry matter partitioning, and seed yield were studied over a two year period (1982 and 1983).

Stem strength, length, and dry matter partitioning were all observed with respect to their impact upon the date and severity of lodging. The number of fertile tillers per unit area, spikelets per spike, and florets per spikelet were measured to determine the yield potentials of treated and untreated Caravelle, Linn, and Pennfine perennial ryegrasses.

It was found that paclobutrazol significantly delayed lodging, reduced stem length and in some cases reduced stem dry weight. In some instances, significant increases in specific stem weight and stem strength were observed. The results varied widely between years and varieties.

Yield differences were observed in 1983 which were attributable to earlier and more severe lodging of the untreated plots. Paclobutrazol treatments in 1983

delayed lodging and reduced tiller mortality which caused more fertile tillers at harvest in treated plots.

These results indicate that paclobutrazol has promise as a means of increasing seed production efficiency in areas subject to early and severe lodging of perennial ryegrass grown for seed. Positive results will be obtained only under certain environmental conditions.

Additional key words: Lodging, dry matter partitioning, specific stem weight,stem strength.

Lodging, Dry Matter Partitioning, and Seed Yield in Perennial Ryegrass (Lolium perenne L.) as Affected by the Plant Growth Regulator Paclobutrazol.

INTRODUCTION

The lodging of crop stands is a widespread problem. It is associated with crop production under conditions which would otherwise favor rapid plant growth and high yields. Lodging has been described as an "abundance disease" by Pinthus (1973), since it often poses an obstacle to the achievement of higher yields through additional inputs of nutrients and water.

The lodging of cereal and grass crops has been extensively studied. It is widely reported that lodging can reduce crop yield and quality. Pendleton (1954) reported that spring oats which were artificially lodged at 4 and 20 days after heading yielded 17.2 and 10.2 bushels less than upright plots. Plots lodged to 90° from the vertical yielded 63% of the check plots versus 86% for plots lodged to only 45°. Thus, both the time and severity of lodging influence the impact of crop lodging upon yield. Weibel and Pendleton (1964) reported similar results with winter wheat. Weather conditions following lodging can influence the degree of yield reduction. Lodging prior to anthesis results in the largest yield losses if weather conditions are adverse.

If dry sunny weather follows pre-anthesis lodging some recovery may occur through the expansion of the intercalary meristems (Mulder, 1954). Thus, environmental conditions have an important role in determining the timing and severity of lodging and the magnitude of post-lodging yield reductions.

Lodging is a major problem in perennial ryegrass (*Lolium perenne* L.) seed production. Comparing mechanically supported stands with lodged ones indicate that lodging can decrease yields 30% to 49% (Hebblethwaite, Burbidge, and Wright, 1978; Momma, 1981). Therefore controlling lodging does produce significant yield increases. Several chemicals have been used as a means of chemically delaying lodging in perennial ryegrass (Burbidge, Hebblethwaite, and Ivins, 1978; Wright and Hebblethwaite, 1979; Albeke, 1981). Seed yield increases from 0% to 100% have been obtained depending upon the cultivar and the season.

Paclobutrazol and other similar plant growth regulators have been shown to reduce lodging by altering the pattern of internode elongation, plant height and partitioning of dry matter in the plant. The resistance of a cultivar to lodging has been attributed to a variety of factors ranging from the deposition of lignin in the culm to the thickness of the culm. Plant characteristics such as basal internode length have been examined and found to have little correlation with stem strength. However, a positive correlation was found between the amount of dry matter per unit length of culm and stem strength (Atkins, 1938; Welton, 1928). The dry matter partitioned per unit length of stem appears to be an important determiner of stem strength, and consequently of lodging. The partitioning of additional dry matter per unit of stem length in the lower internodal segments would have the greatest impact upon lodging in ryegrass.

The objective of this experiment was to determine the effects of paclobutrazol treatment upon lodging, dry matter partitioning in the stem, yield components, and seed yield in perennial ryegrass (Lolium perenne L.).

MATERIALS AND METHODS

This experiment was conducted over the course of two years (1982 and 1983) on second year stands of perennial ryegrass cv. Pennfine and Linn. The stands were located on a Willamette silt loam soil at Oregon State University's Hyslop Research Farm.

In 1982, paclobutrazol was applied on March 26 at the floret initiation stage of development. The stage of development was determined by microscopic examination of the growing point. Floret initiation treatments were applied when four or more of the five primary and secondary tillers sampled had growing points with clearly defined floret primordia.

Paclobutrazol was applied at 0.75 kg a.i./ha in 400 l/ha water using a bicycle wheeled sprayer powered with a compressed air. The application was followed by 5.6 mm rainfall within 24 hours which insured root uptake. Plots were fertilized with diammonium phosphate at a rate equivalent to 50 kg/ha of actual nitrogen in the fall with a spring application of ammonium nitrate on March 9 at a rate equivalent to 100 kg/ha of nitrogen. Fungicide applications were made as required to control rust. Because of abnormally dry conditions, 5 cm of irrigation water was supplied May 27 and again on June 17.

Fertile tiller number, stem length, internode length and weight, and other components of yield were determined from 0.30 m samples of row taken June 21. Seed yield and 1000 seed weight were determined from 1.4 m samples of row harvested June 29. Samples were placed in large burlap sacks, air dried, and placed in a forced air drier for 12 hours prior to threshing with a belt thrasher. Threshed seed was scalped and run through an air screen machine to remove chaff. Clean seed was weighed for the determination of yield, then divided using a seed divider to produce a random seed sample. This sample was used to determine 1000 seed weight by using an electronic seed counter and scale.

In 1983, paclobutrazol treatments were applied at the spikelet and floret initiation stages of development on March 23 and April 8 to two year old stands of Caravelle and Pennfine perennial ryegrasses. The six treatments consisted of 0, 0.5, and 0.75 kg/ha applications at the spikelet and floret initiation stages. Treatments were arranged in a randomized block design with six replications.

Paclobutrazol treatments were applied using a Cooper-Pegler backpack sprayer and a hand-held spray boom. Application pressure was 17 psi with 8002LP nozzles. The spikelet and floret initiation treatments were followed by 1.5 cm and 0.4 cm of precipitation within 24 hours.

Plots were fertilized in the fall with 30 kg/ha of nitrogen as ammonium diphosphate and a total of 120 kg/ha nitrogen applied as a split application on March 4 and March 21.

Samples were removed at the spike-emergence stage to evaluate tiller population composition prior to anthesis for each of the treatments. Two 10 cm sections of row were removed from each treatment in four of the six replications. The tillers in each of these sections were cut at ground level and removed from the sod. The tillers were then separated into groups based upon their basal tiller diameter.

Samples consisting of 8 tillers per plot were removed at anthesis and the stem strength of four cm segments were measured from the culm base to the base of the spike. The length and weight of the internodes and leaves were determined at this time.

Stem strength was measured by determining the highest bending resistance using a Kiya Seisakusho straw fracture tester model EO-3. The maximum bending resistance was recorded by taking the maximum resistance before five degrees of stem deflection occured. Stem strength for each internode was calculated by determining the mean bending resistance for each of the four centimeter sections contained within each node. When a fraction of a four segment was included in the internode, the value for that portion of the internode was adjusted for its length.

Larger samples, 929 cm^2, were removed and the tillers separated into classes based upon their maturity. Tillers were described as fully-emerged reproductive, late-emerged reproductive, or vegetative based upon their height, thickness, and relative maturity. The number of florets per spikelet, and spikelets per spike was determined from a subsample of the late-emerged and fully-emerged reproductive tillers.

Seed yield was determined by harvesting 5 m^2 area into burlap bags using a small-plot harvester. Samples were handled in the manner described for 1982.

RESULTS AND DISCUSSION

Lodging

The timing and severity of lodging is a major factor which determines the value of chemical lodging control in enhancing seed yield. The yield increase resulting from paclobutrazol treatment will be greatly influenced by the interaction of the plant with its environment.

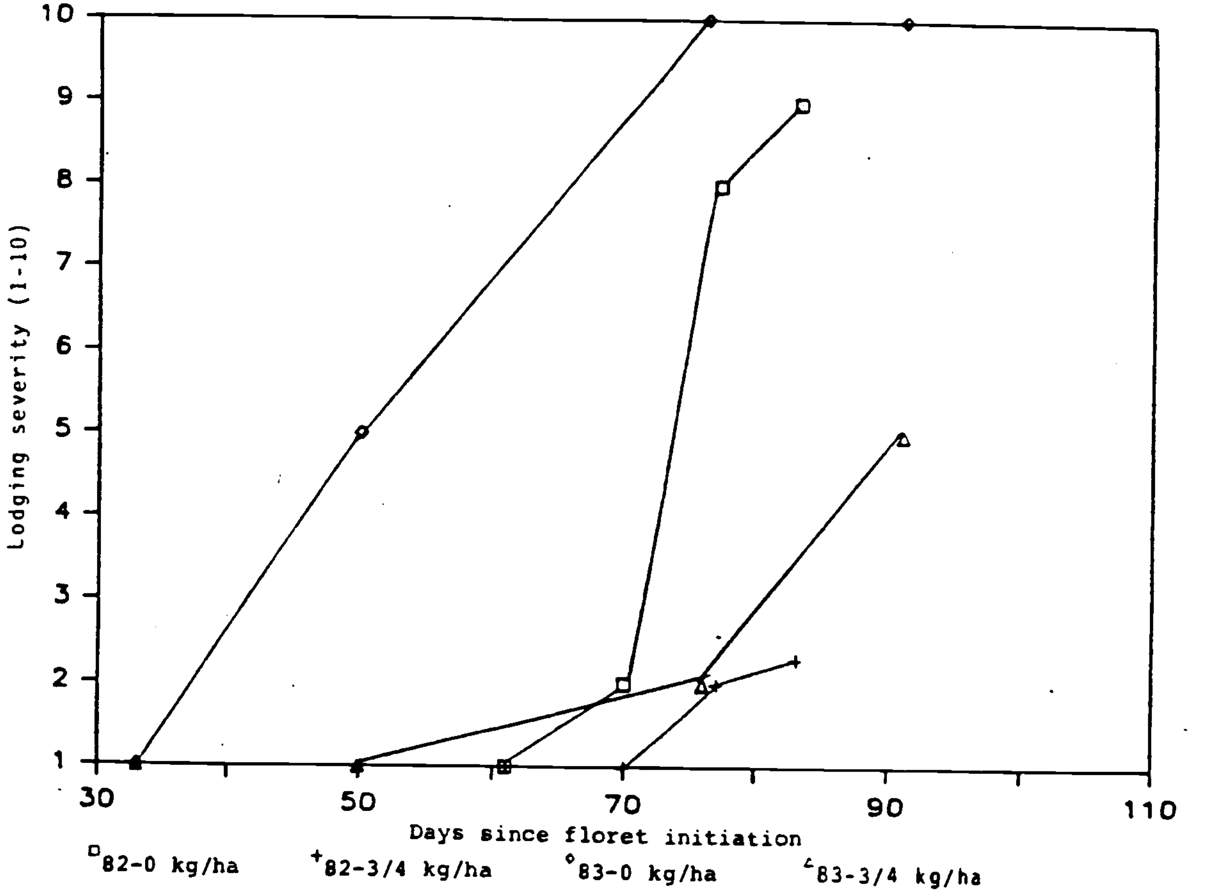
Pennfine perennial ryegrass grown in 1982 and 1983 was exposed to differing amounts of rainfall and it developed in different light and temperature environments (Table 2.1). The most important factor influencing lodging was the variation in rainfall between these two years. In May of 1982 a total of 10.9 mm of rainfall was measured in the plot area while in 1983 a total 38.4 mm was recorded. During the same periods, 176 mm and 127 mm of pan evaporation were measured. Thus, a much greater moisture deficit was present during culm elongation in 1982 than in 1983. This deficit probably reduced plant water potential and decreased cell elongation, thus having similar results as paclobutrazol application. This explains the variation in the date and severity of lodging for Pennfine (Figure 2.1).

Variation in lodging severity between varieties is also large because of genetically controlled patterns of development. The timing of tiller bud initiation and elongation, pollination, and seed filling all vary widely between varieties. In these experiments the early maturing varieties (Linn and Pennfine) seemed to benefit more from paclobutrazol treatment than the later maturing variety (Caravelle).

Table 2.1 - Average monthly solar radiation, temperature, and rainfall for Corvallis, Oregon during the spring of 1982 and 1983

Date	Solar radiation	Temperature	Precipitation
	(ly/day)	(°F)	(mm)
1982			
March	265	45.0	90
April	376	47.0	116
May	483	55.4	12
June	417	62.7	38
1983			
March	186	49.3	223
April	366	50.1	76
May	536	57.0	38
June	476	59.4	35
Mean			
March	241	44.9	118
April	337	49.0	62
May	451	54.7	49
June	494	60.4	31

Figure 2.1 - Lodging in Pennfine perennial ryegrass in 1982 and 1983 as affected by paclobutrazol.



Tiller Height

Lodging occurs when tillers are produced which have inadequate strength to support their own weight. In perennial ryegrass, lodging occurs because of the bending of the lower segments of the culm. This curvature is a function of the height of the culm, the weight of the spike, and the rigidity or strength of the affected internodal segments. Plant height is consistently decreased by paclobutrazol treatments in the range used in these experiments (Table 2.2). The height reduction occurs as the result of the inhibition of cell elongation in the tissues composing the stem. The effect of paclobutrazol treatment upon internode development is determined by the timing of application with respect to the degree of elongation for a particular internodal segment. Internodes that are almost completely elongated are affected less than those which are just starting rapid growth. The spikelet and floret initiation treatments reduce the length of the lower two or three internodal segments the most. The growth of the later developing internodes is inhibited less than earlier developing internodes. This occurs either because paclobutrazol levels in the soil gradually decrease following treatment or environmental conditions naturally retard the elongation of the top internodes so there is a smaller response to an application (Table 2.3).

Tiller height reduction in Pennfine perennial ryegrass was greater in the second year of the study (1983) than for the first (1982). In 1982, untreated tillers were abnormally short because of low moisture conditions during culm elongation. Untreated tillers in 1983 were 20 cm taller than those from 1982. The height of tillers treated with the same rate of paclobutrazol varied insignificantly between years (Table 2.2). The 1982 growing season was a low lodging year with no major lodging occuring until irrigation was applied. Thus in 1982 environmental conditions reduced plant height just as paclobutrazol would have, but to a lesser degree.

Table 2.2 - The effect of paclobutrazol on tiller height for Caravelle, Linn, and Pennfine perennial ryegrasses in 1982 and 1983.

Variety	Year	Treatment	Height
		(kg/ha)	(cm)
Caravelle	1983	0	86.8
		0.5	65.2
		0.75	61.5
$LSD_{.05}$			11.5
Pennfine	1982	0	78.3
		0.75	67.5
$LSD_{.05}$			2.9
Pennfine	1983	0	99.1
		0.5	68.5
		0.75	65.5
$LSD_{.05}$			5.1
Linn	1982	0	82.3
		0.75	70.5
$LSD_{.05}$			3.0

Table 2.3 - Internode length, dry weight, and specific stem weight, as affected by paclobutrazol.

Treatment	IN 1[1]			IN 2			IN 3			IN 4			IN 5		
	Lth[2]	DW[3]	SSW[4]	Lth	DW	SSW	Lth	DW	SSW	Lth	DW	SSW	Lth	DW	SSW
(kg/ha)	(cm)	(mg)	(mg/cm)	(cm)	(mg)	(mg/cm)	(cm)	(mg)	(mg/cm)	(cm)	(mg)	(mg/cm)	(cm)	(mg)	(mg/cm)
Caravelle-1983															
0	20.0	99	5.0	12.4	91	7.5	10.5	86	8.1	10.0	87	9.1	8.2	84	10.2
0.5	21.0	100	4.9	10.5	87	8.3	5.7	64	11.3	4.4	56	13.0	3.2	45	14.4
0.75	19.9	93	4.7	10.3	82	8.2	5.3	60	11.6	4.0	53	13.7	3.8	43	14.5
$LSD_{.05}$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	2.7	n.s.	n.s.	3.1	33	4.0	3.5	21	n.s.
Pennfine-1982															
0	26.4	73	2.8	15.9	84	5.3	10.3	80	7.8	7.4	72	10.3	-	-	-
0.75	26.8	86	3.2	13.1	86	6.7	6.7	65	10.0	3.3	43	7.7	-	-	-
$LSD_{.05}$	n.s.	n.s.	n.s.	1.3	n.s.	1.0	1.7	n.s.	n.s.	1.7	18	0.9	-	-	-
Pennfine-1983															
0	24.7	115	4.6	16.7	97	5.8	16.1	99	6.1	10.7	76	7.2	4.9	40	8.3
0.5	24.7	93	3.8	10.6	63	6.4	4.5	43	10.2	5.3	38	9.7	3.5	27	10.1
0.75	24.1	106	4.4	7.9	63	8.4	3.4	42	23.7	2.8	35	12.9	3.8	32	10.8
$LSD_{.05}$	n.s.	19	n.s.	2.5	22	1.7	1.0	18	1.7	3.9	15	3.1	n.s.	12	n.s.
Linn-1982															
0	23.1	77	3.4	16.8	93	56.0	13.3	90	6.8	9.9	89	6.9	-	-	-
0.75	16.7	96	3.6	15.1	97	64.6	7.7	80	10.7	1.9	32	16.8	-	-	-
$LSD_{.05}$	1.6	14	n.s.	1.5	n.s.	n.s.	1.5	n.s.	1.7	1.9	53	2.8	-	-	-

[1] Internodal segment starting at the base of the spike.
[2] Internodal segment length.
[3] Dry weight of segment.
[4] Specific stem weight.

Dry Matter Partitioning

A reduction in tiller height results from the decrease in length of the individual internodal segments (Table 2.3). As the length of the internodes is reduced, the relative distribution of dry matter among the different portions of the stem is altered. A shorter internode usually is also lighter than a longer internode of equivalent thickness. The reduction in internode length resulting from paclobutrazol treatment is not linearly related to the reduction in dry weight. In most cases, it appears that as internode length decreases, the dry weight decreases more slowly. Thus, the amount of dry matter partitioned into the stem per unit of length increases. The ratio of stem dry weight to the length of stem can be described as the specific stem weight (SSW), which is the dry weight of stem per unit of length (Table 2.3).

The magnitude of internode length and dry weight reduction and the magnitude of specific stem weight increase can vary between different varieties and years. Caravelle perennial ryegrass is a later maturing variety than Pennfine and usually is 10 to 15 cm shorter. Caravelle treated with 0.75 kg/ha of paclobutrazol had an increase in SSW of 43% and 50% for the third and fourth internodes below the spike. Pennfine in 1983 had a 108% and 79% increase for the same internodes. However, Pennfine in 1982 had 28% and -26% for the same internodes. The smaller relative increases in SSW for Caravelle in 1983 and Pennfine in 1982 demonstrates the variation in SSW between varieties and years. Significant increases in SSW with paclobutrazol treatment are most likely to occur with varieties which develop under the high moisture and fertility conditions which favor severe lodging.

Stem Strength

The amount of dry matter partitioned per unit length of stem (SSW) is of special importance because of its positive relationship with stem strength. A significant increase in SSW indicates that as the length of a stem segment decreases, the segment dry weight does not decrease a comensurate amount (Table 2.3). This increased partitioning of dry matter per length of stem appears to increase the bending-resistance moment and stem strength and decrease stem bending and lodging (Table 2.4). This indicates that stem strength may not always be increased by paclobutrazol treatment if the plant has developed under restrictive conditions where SSW is not increased. Paclobutrazol may still delay lodging by reducing plant height even in the absence of increased stem strength.

Table 2.4 - Specific stem weights and average stem strength for internodal segments from Caravelle and Pennfine perennial ryegrass treated with paclobutrazol.

Treatment	IN 1[1]		IN 2		IN 3		IN 4		IN 5	
	SSW[2]	SS[3]	SSW	SS	SSW	SS	SSW	SS	SSW	SS
(kg/ha)	(mg/cm)	(g/cm)	(mg/cm)	(g/cm)	(mg/cm)	(g/cm)	(mg/cm)	(g/cm)	(mg/cm)	(g/cm)
Caravelle										
0	5.0	18.4	7.5	32.3	8.1	39.1	9.1	46.4	10.2	48.5
0.5	4.9	17.9	8.3	35.1	11.3	44.4	13.0	44.5	14.4	45.2
0.75	4.7	18.8	8.2	34.7	11.6	43.6	13.7	44.8	14.5	44.4
$LSD_{.05}$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	4.0	n.s.	n.s.	n.s.
Pennfine										
0	4.6	11.0	5.8	15.8	8.1	17.6	7.2	20.0	8.3	18.5
0.5	3.8	10.3	6.4	20.3	11.3	24.9	9.7	28.0	10.1	28.2
0.75	4.4	12.0	8.4	22.8	11.6	28.6	12.9	33.1	10.8	33.8
$LSD_{.05}$	n.s.	n.s.	1.7	6.9	2.7	6.8	3.1	9.1	n.s.	n.s.

[1] Internodal stem segments starting below the spike.

[2] SSW - specific stem weight = internode weight/internode length.

[3] Stem strength.

Tiller Mortality

The delay or prevention of lodging occurs because of a reduction in tiller height and an increase in stem strength. The yield increases observed in 1983, were due in part to an increase in fertile tiller number at maturity in the treated plots. The increase in fertile tiller number at maturity in treated plots resulted from either an increase in tiller initiation or a decrease in tiller mortality.

In 1982, lodging was delayed until after anthesis and then it was not present to an extreme degree. Because of the relatively late and low severity of lodging, tiller number at harvest was the same for both the untreated and treated plots.

In 1983, the tiller populations for Pennfine and Caravelle were followed from spike-emergence through harvest (Table 2.5). In both varieties, total tiller number decreased from spike-emergence through harvest until only 20% to 30% of the original tiller population remained. The tiller population at harvest was composed of mostly fertile tillers. The spike-emergence tiller population consisted of a greater number of tillers varying in height, stem thickness, and maturity (Table 2.6). The largest, most mature tillers had the best chance of survival.

Table 2.5 - Tiller numbers for Pennfine and Caravelle perennial ryegrass at three growth stages following paclobutrazol treatment.

Treatment	Spike emergence	Anthesis	Harvest
(kg/ha)		(930 cm^2)	
<u>Pennfine</u>			
0	685	225	190
0.5	814	254	252
0.75	811	265	238
$LSD_{.05}$	n.s.	n.s.	27
<u>Caravelle</u>			
0	613	305	243
0.5	963	308	313
0.75	736	325	288
$LSD_{.05}$	225	n.s.	35

Table 2.6 - Tiller number and tiller stem base size distribution, at spike emergence, from stands of Pennfine and Caravelle perennial ryegrass treated with paclobutrazol.

Treatment	Total tillers	1mm tillers		2mm tillers		3mm tillers	
(kg/ha)	(930 cm^2)						
Pennfine	(No.)	(No.)	(%)	(No.)	(%)	(No.)	(%)
0	685	166	24.2	499	72.8	20	2.9
0.5	815	195	23.9	507	62.2	113	13.9
0.75	812	176	21.6	499	61.4	137	16.9
$LSD_{.05}$	n.s.	n.s.		n.s.		68	
Caravelle							
0	613	190	31.0	383	62.5	40	6.5
0.5	963	319	33.1	481	49.9	163	16.9
0.75	736	215	29.2	373	50.7	148	20.1
$LSD_{.05}$	225	128		n.s.		87	

Paclobutrazol appeared to significantly increase the number of 3 mm tillers while holding the number of 2 mm tillers constant. In Caravelle there was a significant increase in the number of 1mm tillers. This might indicate that the Caravelle applications were applied prematurely. Research has shown that paclobutrazol applied at the vegetative growth stage can stimulate the production of tillers. In this case, the increased number of tillers at spike-emergence may be attributed to increased production of 1 mm and 3 mm tillers.

The larger number of tillers at spike-emergence in treated plots was greatly reduced by anthesis (Table 2.7). This was largly due to the death or mortality of the vegetative tillers i.e. 1 mm tillers. At anthesis only about 10% of the smallest tillers remained alive. In general, there was no significant difference in the number of fully-emerged and late-reproductive fertile tillers at anthesis. There was a small increase in the number of fully-emerged tillers at the 0.5 and 0.75 kg/ha application rates at the spikelet initiation stage for Pennfine. The fertile tiller population was approximately the same for each of the other treatments.

The fertile tiller number at harvest was slightly less than at anthesis. The competition for light increased as the grass stand developed. This resulted from a general increase in stem height, leaf number, and area. Thus, the weakest, least developed tillers were lost as the stand matured. The effects of light competition were especially intense under lodged conditions. In the lodged canopy, less efficient photosynthetic tissues such as the lower stem and leaves became essential for assimilate production since the primary photosynthetic structures were not exposed. Under these conditions competition was intensified and tiller mortality accelerated. If lodging occurs close enough to maturity, non-structural carbohydrates may be mobilized for tiller survival and seed filling. Tillers from erect treated plants were also under competitive pressure but were able to sustain a larger fertile tiller population because of more efficient light interception (Table 2.5).

Table 2.7 - Tiller numbers at different maturity stages in Pennfine and Caravelle perennial ryegrass after treatment with paclobutrazol.

Treatment	Total tillers at spike emergence	Number of different class tillers and total at anthesis: Fully emerged spikes		Late reproductive spikes		Vegetative tillers		Total tillers	
(kg/ha)	(/930 cm^2)								
Pennfine		Sl[1]	Fl[2]	Sl[1]	Fl[2]	Sl[1]	Fl[2]	Sl[1]	Fl[2]
0	685	176	202	18	17	28	33	214	236
0.5	815	227	207	16	13	12	16	271	237
0.75	812	260	207	19	14	13	17	293	238
$LSD_{.10}$	n.s.	32	n.s.	n.s.	n.s.	12	12	39	n.s.
Caravelle									
0	613	254	240	21	18	34	44	308	302
0.5	963	239	245	24	24	42	43	305	311
0.75	736	248	266	30	29	39	37	317	334
$LSD_{.10}$	225	n.s.	n.s.	7	7	n.s.	n.s.	n.s.	n.s.

[1]paclobutrazol treatment at spikelet initiation stage of development.

[2]paclobutrazol treatment at floret initiation stage of development.

Components of Yield

The development of the florets and spikelets seem to be unaffected by paclobutrazol treatment. This was shown by the non-significant effect of paclobutrazol upon floret number or spikelet number (Table 2.8). In some cases the number of caryopsis produced per spikelet appears to increase. This could reflect either improved pollination in an unlodged canopy, improved seed filling, or decreased embryo abortion (Table 2.9). Some combination of these factors may contribute to a yield increase but this experiment does not allow the relative contributions to be evaluated. The 1000 seed weight measurements were made after the seed had been cleaned using an air screen machine. This could potentially mask differences in seed filling by removing the lighter seed from a sample and producing misleading 1000 seed weight data.

Potential Yield Utilization

The observed yield increases were mostly attributable to the presence of significantly more fertile tillers at harvest. Both decreased tiller mortality and increased tiller production can increase yield. Tiller mortality varied widely between 1982 and 1983 as did lodging severity and environmental conditions.

Table 2.8 - Seed yield and its components as affected by paclobutrazol.

Treatment	Fertile tiller no.	Spikelets/ spike	Florets/ spikelet	1000 seed weight	Seed yield
(kg/ha)	(/930 cm^2)			(g)	(kg/ha)
Caravelle-1983					
0	243	24.2	6.68	1.82	773
0.5	313	24.0	6.79	1.74	922
0.75	288	23.9	6.63	1.75	833
$LSD_{.05}$	35	n.s.	n.s.	0.03	84
Pennfine-1983					
0	190	25.1	6.11	2.06	749
0.5	252	24.6	6.23	1.92	1397
0.75	238	25.5	6.52	1.93	1596
$LSD_{.05}$	27	n.s.	n.s.	0.02	159
Pennfine-1982					
0	226	2.47	5.38	1.57	1483
0.75	223	2.61	5.60	1.60	1470
$LSD_{.05}$	n.s.	n.s.	n.s.	n.s.	n.s.
Linn-1982					
0	233	2.36	5.29	2.16	1617
0.75	225	2.31	5.87	2.08	1671
$LSD_{.05}$	n.s.	n.s.	n.s.	n.s.	n.s.

Table 2.9 - Floret site utilization, seeds/tiller, and fertile tiller survival as affected by paclobutrazol

	FSU	Seeds/tiller	Fertile tiller survival
	(%)		(%)
Caravelle			
0	10.5	17.0	83.9
0.50	09.5	15.8	103.5
0.75	09.9	15.6	91.2
$LSD_{.05}$	n.s.	n.s.	n.s.
Pennfine			
0	12.0	18.1	87.5
0.50	17.9	27.1	100.8
0.75	20.3	33.2	92.3
$LSD_{.05}$	03.6	5.1	n.s.

n.s. = not significant

There were significant differences in floret site utilization (FSU) in 1983 for Pennfine. This also appears as an increased number of seeds per tiller at harvest (Table 2.9). This together with the significant increase in fertile tiller number at harvest resulted in large yield increases in Pennfine and smaller increases in Caravelle (Table 2.8).

CONCLUSIONS

The treatment of perennial ryegrass with plant growth regulators such as paclobutrazol can prevent or delay lodging. This effect results from reduced plant height, increased partitioning of dry matter per length of stem, and stronger culms. These modifications in plant growth do not directly increase seed yield, but instead allow for the maintenance of naturally produced yield potential by reducing lodging. The prevention of lodging results in increased floret site utilization (FSU), more seeds per spikelet, and more fertile tillers per unit area at harvest. The results of paclobutrazol treatment will be directly dependent upon the severity and earliness of lodging. Increased yield may result from several sources, each controlled by environmental and genetic factors.

The ancillary effects of lodging or lodging control need to be further identified. The effects of lodging upon pollenation and seed filling need to be investigated in additional studies.

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