1986

The Role of Plant Hormones in Grass Tiller Development

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HONORS PROJECT IN RANGE SCIENCE:
THE ROLE OF PLANT HORMONES IN
GRASS TILLER DEVELOPMENT

Marit Snow
June, 1986

A REPORT SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE
HONORS DEGREE
IN
RANGE SCIENCE

Approved:
HONORS PROJECT IN RANGE SCIENCE:
THE ROLE OF PLANT HORMONES IN
GRASS TILLER DEVELOPMENT

Marit Snow
June 1986
PREFACE

The two papers presented here represent two research projects I have undertaken to explore the effects of plant hormones in grass plants. The first paper entitled "The Effects of Kinetin, Gibberellic acid, and Auxin on Two Agropyron Species" explains the results of a research project I conducted at the Green Canyon Ecology Center in June 1985. It represents my final senior project for the Honors program.

I have also included another paper, "Effects of Two Plant Hormones on Tiller Production and Growth in Bluebunch wheatgrass", which I presented at the Society for Range Management meetings in Salt Lake City, 1985, and at the Honors Day presentations here at USU in 1986. This paper covers research I conducted in March 1984 in a greenhouse setting. The results of this research were unclear and, therefore, I decided to conduct further study the next year to see if I could improve the clarity of my results. My senior project paper is the result of that continued research, which includes a more detailed statistical analysis of the findings of the experiment.

I learned from both projects: the techniques of scientific investigation and technical writing, as well as knowledge about plant hormones. I have included the two reports separately because they represent two different, though related, projects and because I feel I have learned more about scientific research, which is reflected in two different styles of reporting.
THE EFFECTS OF KINETIN, GIBBERELLIC ACID, AND AUXIN ON TWO AGROPYRON SPECIES GROWN IN THE FIELD

Submitted as partial fulfillment of the requirements for the Honors degree in Range Science

Marit Snow
2 June 1986

Dr. James H. Richards, advisor
ABSTRACT

Two bunchgrass species commonly found in the Intermountain West, *Agropyron spicatum* and *A. desertorum*, are morphologically similar but respond to defoliation very differently. *A. desertorum* produces more daughter tillers and is more hardy than *A. spicatum*. Hormones were applied to experimental plants to observe changes in tillering rates, growth rates, and response of plants to the stress of exogenous hormone application. Gibberellic acid treatments were related to increased tiller height in both species, but also a decrease in daughter tiller production in *A. desertorum* and an increase in senescence in *A. spicatum*. Kinetin increased senescence in *A. desertorum*. Auxin showed no significant response in either species or in any of the treatments. *A. spicatum* plants showed higher levels of senescence than *A. desertorum* plants and appeared unhealthy and stressed in subjective observations.
INTRODUCTION

Grazing tolerance is an desirable attribute of grasses grown in the Intermountain West. Grasses with a high grazing tolerance retain their vigor under heavy livestock pressure. This helps maintain good soil cover and prevents undue erosion and range degradation.

Two bunchgrass species commonly found in the Intermountain West, *Agropyron spicatum* (Pursch) Scribn. and Smith, and *A. desertorum* (Fisch ex. Link) Schult., are morphologically very similar, but respond very differently to grazing. *A. spicatum*, a native of the Intermountain Region, is sensitive to grazing and declines under heavy use (Caldwell et. al. 1981). *A. desertorum* was introduced from Russia in 1906. It evolved with grazing pressure from herbivores and is very grazing tolerant (Provenza Dept. of Range Science, USU, personal communication 1983). It has been the major grass species used in range seedings because of its vigor under high grazing pressure, its suitability to arid conditions, and its longevity (Asay and Knowles 1985).

Research to explain the differences in grazing tolerance of these two apparently similar grasses has been conducted at Utah State University for several years. Studies have included work on the roles of resource acquisition from photosynthesis and carbohydrate pools, the rates of photosynthesis in defoliated versus entire plants (Caldwell et. al. 1981, Richards 1984, Richards and Caldwell 1985, Nowak and Caldwell 1984), as well as the influence of apical dominance, and the importance of the
ratio of red and far-red light reaching tiller buds (J.H. Richards, B. Olson, unpubl.).

This paper describes the results of research conducted using three plant hormones on *A. spicatum* and *A. desertorum* plants. The three hormones; cytokinin, gibberellic acid, and auxin, have been used in previous research with greenhouse and hydroponically grown cereals (Johnston and Jeffcoat 1977, Langer et. al. 1973, A. Leopold 1949). This past research on annual plants has indicated that auxins and gibberellins suppress development of basal buds while cytokinin can be used to increase the number of active basal buds. Both cytokinins and gibberellins increase cell division and daughter tiller growth in several species (Johnston and Jeffcoat 1977, Salisbury and Ross 1978). These two hormones have also been shown to affect the rate of senescence by postponing (Salisbury and Ross 1978), or hastening its onset (Mishra and Gaur 1985), depending on the phenology of the plant. These findings were tested in a field experiment using perennial rangeland grasses to observe whether hormone effects on field grown plants can be correlated with reactions in artificial environments.
MATERIALS AND METHODS

Site information:

The study site was located at the Green Canyon Ecology Center, 4 km northeast of Logan, Utah, at 41° 45' N., 111° 48' W. Elevation at the site is 1460 m a.s.l. Mean annual precipitation is 46.8 cm, although in 1985, when the experiment was conducted, precipitation was 113% of normal. Most precipitation falls as snow, with warm, dry springs, as was the case in May and June 1985 when the study was conducted.

The study plot was in a natural setting with only incident precipitation and sunlight reaching plants. A competitive atmosphere was maintained by transplanting Agropyron spicatum, A. desertorum, and Artemisia tridentata ssp. vaseyana (Rydb.) Beetle into a 8 * 8 m² plot in a regular pattern at a 50 cm spacing so that each plant was surrounded by the other two species. Transplanting occurred four years prior to the experiment.

Neighboring plants of the two grass species were selected for equal size and vigor. Five replicate plant pairs were randomly assigned to each of six treatments. Eight tillers per plant were measured for total height, green leaf length, stem and sheath length, and developmental state at the beginning and end of the experiment. Four tillers were chosen from the outside and four from the inside of the bunch in each of the cardinal directions. These values were pooled and the mean values per plant were used in the statistical analysis.
Hormone treatments:

The six hormone treatments were prepared in a concentrated 50% ethanol solution and stored in a freezer. The treatments and final concentrations were: low kinetin, (5 ppm kinetin, a synthetic cytokinin, in a 50:50 kinetin:kinetin-riboside mixture), high kinetin (25 ppm of the same kinetin mixture), GA₃ + kinetin (25ppm gibberellic acid and 25 ppm kinetin mix), GA₃ alone (25 ppm gibberellic acid), NAA (50 ppm napthalene acetic acid, a synthetic auxin), and distilled water as a control. When hormones were to be applied, they were warmed to room temperature and diluted using distilled water with a dissolved wetting agent, Triton-x (Fischer Scientific). Final concentrations of the additional substances in the hormone solutions were 1% ethanol, and 0.4 % Triton-x. Control solutions used 2% ethanol and 0.4% Triton-x the first four treatments and 1% ethanol and 0.4% Triton-x the last two treatments. Ten to 12 drops of glacial acetic acid were added with a Pasteur pipet to the high kinetin and GA₃ + kinetin spray solutions at each hormone application to keep the hormones in solution.

On May 16, five plant pairs were randomly chosen and data on vigor, average plant height, and individual tiller height were taken. Plants were then clipped to within 6 cm of the ground, measured from the center of the plant, to remove elevating apical meristems. Plants were reclipped to the same height directly before the first three hormone applications.

On May 20, hormones were sprayed onto plant bases until runoff using an all-purpose sprayer bottle. This averaged about
50 ml per plant. Hormones were reapplied five more times on May 23, 27, 29, 30, and June 2. Hormones were applied in early evening when sunlight and temperature were less intense. Subjective observations on plant condition and growth were also made at each hormone application.

Final tiller data were collected on June 13 and 14. Data were analyzed using one-way and two-way analysis of variance for total daughter tiller height, percentage of parents producing daughter tillers, and percentage of all tillers showing more than 50% and more than 75% senescence. The LSD ($P = .05$) was used to identify which treatments were significantly different within the analysis. All figures expressed as percentages were arcsine transformed before analysis.
RESULTS

Daughter tiller production:

Agropyron desertorum and A. spicatum showed different responses when analyzed for the percentage of parents producing daughter tillers. A. spicatum produced fewer daughter tillers per parent tiller than A. desertorum (fig. 1). This difference was not significant when analyzed in a two-way analysis of variance due to the large difference in treatment effects in A. desertorum. However, when control plants were compared between species, there was a significant difference in the number of daughter tillers produced in control plants of each species (fig. 1).

The two species responded differently to hormone treatments. A. spicatum showed no difference between treatments while A. desertorum produced significantly more tillers per parent in control plants than in GA3 + kinetin or GA3 treated plants. All other hormone treatments showed low tillering rates, but were not significant at P<.05.

Growth in height of daughter tillers:

Height growth of daughter tillers increased in GA3 treatments for both species (fig. 2). Agropyron spicatum grew less than A. desertorum in all treatments. There was a significant increase in height between GA3 treatments and kinetin, auxin, and control treatments in A. spicatum (P<.05). A. desertorum responded with a significant height increase in GA3
Figure 1: Percentage of parents producing daughter tillers.
Data for both species, collected on 13, 14 June 1985.

Treatments:
1= low kinetin
2= high kinetin
3= GA₃ + kinetin
4= GA₃
5= NAA
6= control

Species and treatment: Agropyron desertorum, Agropyron spicatum
Figure 2: Height of daughter tillers (cm). Data for both species, collected on 13, 14 June 1985.

Treatment: 1= low kinetin, 2= high kinetin, 3= GA₃ + kinetin, 4= GA₃, 5= NAA, 6= control
+ kinetin over kinetin, auxin, and control plants (P<.10). There was no significant difference between GA₃ and GA₃ + kinetin treatment responses in either species.

**Senescence:**

There was no significant difference in hormone treatments at the 50% senescence level, although treatment effect was significant at the 75% senescence level. Species responded differently at both levels with *A. spicatum* showing a higher proportion of senescent tillers in both cases (fig. 3 & 4).

Treatment effects at the 75% senescence level indicated that high kinetin treatments were related to high senescence in *A. desertorum* (P<.025). All other treatments showed significantly less senescence than high kinetin treated plants. There were no other significant differences between other treatments.

*A. spicatum* showed the highest proportion of senescent tillers in the GA₃ + kinetin treatments (P<.25). Due to the high alpha level, Bonferoni's test of significance was used. Only controls were significantly different than GA₃ + kinetin treatments using this test, although GA₃ treatments also showed a high level of senescence.
Figure 3: Percent of tillers showing ≥ 50% senescence. Data for both species, collected on 13, 14 June 1985

Treatments:
1= low kinetin
2= high kinetin
3= GA$_3$ + kinetin
4= GA$_3$
5= NAA
6= control

Species and treatment:

Agropyron desertorum

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Agropyron spicatum

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Figure 4: Percent of tillers showing ≥ 75% senescence. Data for both species, collected on 13, 14 June 1985.

Species and treatment:

Treatments: 1 = low kinetin, 2 = high kinetin, 3 = GA₃ + kinetin, 4 = GA₃, 5 = NAA, 6 = control.
DISCUSSION

Both species showed a statistically significant height increase when exposed to GA₃ and GA₃ + kinetin. This result is supported by several studies (Johnston and Jeffcoat 1977, Salisbury and Ross 1983). GA₃, a synthetic gibberellin, increases shoot length first by stretching the cell by water loading and later by increasing cell structural components (Salisbury and Ross 1978). Visual inspection of GA₃- and GA₃ + kinetin-treated plants showed that many tillers exposed to these treatments had long, though very slender, light green leaves. This indicates that these plants had a higher rate of linear leaf growth than other plants, which may have affected some of the results described above.

Although GA₃ increased tiller height, it was also associated with increased senescence in A. spicatum (P<.25) and a decrease in daughter tiller production in A. desertorum (P<.025). Johnston and Jeffcoat (1977) found that stem elongation of GA₃-exposed plants inhibited basal bud growth, causing a decrease in tiller number. Mishra and Gaur (1985) found that barley plants showed increased senescence if GA₃ was sprayed on plants before the flag leaf began to senesce. Plants in the current experiment were clipped well before the boot stage. These results are in contrast with evidence presented in Salisbury and Ross (1978) which indicated that GA₃ and kinetin decrease senescence. The increased growth rate associated with GA₃ application may have upset a nutrient balance in the exposed plants. There may have
been a reallocation of assimilates away from the older parent tillers in *A. spicatum* or away from other basal buds on observed tillers of *A. desertorum*.

Richards (1984) found that although carbohydrate pools were similar in both species, *A. desertorum* was more efficient in allocating its root carbohydrate reserves to the growing shoots. This inefficiency and loss of assimilates due to reallocation to growing shoots might have stressed *A. spicatum* plants enough to cause an increase in senescence and tiller mortality.

*A. desertorum* showed the highest senescence rate in high kinetin treatments. Several factors may explain this result. First, 25ppm kinetin is a high application level. Johnston and Jeffcoat (1977) found that root growth diminished with kinetin exposures above 6 ppm. Mortality was also increased at high rates of kinetin application in their experiment.

There is also evidence that kinetin increases migration of nutrients from sites low in kinetin to those high in kinetin. This pathway is generally open only from older to younger tissue and not vise versa, preventing young tissues from exporting the hormone (Johnston and Jeffcoat 1977). Senescence occurred almost exclusively in parent tillers, indicating that a loss in needed energy or nutrients may have occurred in these tillers.

Neither plant species showed a significant increase in tiller production in any hormone-treated plants. It was hypothesized that kinetin would increase tiller bud formation. Johnston and Jeffcoat (1977) and Langer et. al. (1973) found that cytokinins such as kinetin might cause bud enlargement, but buds
did not always develop into fully productive tillers. This project did not examine individual tiller bud sizes to observe whether kinetin exposed plants had significantly larger buds.

Another factor in this experiment that would decrease the effectiveness of kinetin treatments is the natural level of the hormone in the plant. Salisbury and Ross (1978) noted that the addition of kinetin to plants with an adequate supply produced little reaction. Richards (Dept. Range Science, USU, personal communication 1986) notes that there is a high genetic variation in A. spicatum plants. This variation shows up in daughter tiller production and may have covered up significant differences in treatment effects due to large standard deviations.

The two grass species, A. desertorum and A. spicatum, reacted differently to the same hormone treatments. A. spicatum tended to be inhibited while A. desertorum responded positively to hormone treatments. This indicates that A. spicatum is more sensitive to environmental changes, such as defoliation or chemical sprays, than is A. desertorum. No conclusions could be drawn explaining why the species reacted differently, but this research indicated that hormone applications would not be effective in overcoming the slow recovery and low tillering rates of A. spicatum plants subjected to defoliation. The source of difference between the two grasses does not appear to be due to inadequate levels of cytokinins, gibberellins, or auxins.
LITERATURE CITED


Mishra SD, Gaur BK (1985) Modification of flag leaf senescence and yield characteristics in barley (Hordeum vulgare) by gibberellic acid and kinetin. J Plant Growth Regul 4: 63-70


EFFECTS OF TWO PLANT HORMONES ON TILLER PRODUCTION AND GROWTH IN BLUEBUNCH WHEATGRASS

presented by:
MARIT SNOW

for Honors Day, April 3, 1986
INTRODUCTION

Tillering in grasses is the development and growth of basal buds on a grass plant. This method of vegetative reproduction is a chief means of maintaining and enlarging many bunch grass plants. Reproduction by tillering is especially important in the grazing situation. Plants that produce tillers rapidly after grazing can more quickly utilize the newly formed leaf area for photosynthesis and assimilate production (Caldwell et al., 1981). Because of this ability to rapidly regenerate photosynthetic tissue, grasses with high tillering rates are better able to compete for sunlight, nutrients, and water after being grazed than species that produce tillers more slowly.

In the Great Basin, an important native bunchgrass species, *Agropyron spicatum* (Pursh) (Scribn. and Smith) is less tolerant than a morphologically similar introduced bunchgrass, *A. desertorum* (Fisch. ex Link) Schult. Although many factors contribute to *A. desertorum*'s increased tolerance to grazing, one important factor is tiller production rate and the related total leaf area available for photosynthesis. Caldwell et al. (1981) found that *A. desertorum* plants produced more tillers than *A. spicatum* plants, and therefore had a larger leaf surface area exposed to the sun. Also, because leaves of *A. desertorum* plants were thinner, less energy was invested in producing each leaf, an adaptation that would be beneficial in an environment where grazing regularly occurs.
Mechanisms controlling tillering rates have been studied in the past, but none have produced conclusive evidence to explain why some grasses are more prolific than others. Two main ideas have been introduced: 1) that hormones play a chief role in allowing tiller development (Leopold 1949), and 2) that assimilate supply also controls tillering rates (Johnston and Jeffcoat 1977).

In wheat tillers, apical dominance is strong during stem elongation and floret development (Langer et al. 1973). During this time, tiller buds normally show little development. By removing apical meristems, suppressed buds have been shown to grow into tillers (Leopold 1949). The same effect has been noted upon application of the auxin inhibitors, NPA (naphthylphthalamic acid) (Isbell and Morgan 1982), and TIBA (2,3,5-tri-iodobenzoic acid), (Langer et al. 1973). The response time for the initiation of tiller growth was similar for the auxin inhibitors and meristem removal (Isbell and Morgan 1982), implying that auxins coming from the meristem are directly involved with the suppression of tillering.

Cytokinin, another plant hormone, has also been found to act as an auxin inhibitor. Benzyladenine, a synthetic cytokinin, increases tillering rates when applied to grass plants (Isbell and Morgan 1982). At least part of this is due to cytokinin's ability to increase assimilate supply to buds. One study using wheat tillers, exposed one leaf to $^{14}$CO$_2$ and found that application of kinetin, another cytokinin, increased the amount of labeled carbon reaching buds (Langer et al. 1973).
To further test this assimilate theory, the same researchers reduced assimilate supply in two ways. Some plants had leaves removed, and others plants were exposed to DCMU (3-3,4,-dichlorophenyl-1-dimethyl urea), a photosynthetic inhibitor, thereby reducing assimilate supply. Early in this experiment tiller production was lower in these plants. The addition of kinetin alleviated this, however. Late in the experiment, after floral emergence, plants with DCMU still produced fewer tillers than control plants, but defoliated plants produced more than controls. Kinetin did not increase tillering at this time. It appears that after floral emergence, defoliation encourages tillering more than the addition of cytokinin (Langer et al. 1973).

Some researchers, such as Johnston and Jeffcoat (1977) have found that tillering in wheat and oat plants can be controlled by nutrient availability only, and that the role of hormones is only minor. When the floret emerges, the flag leaf is developed and supplies most of the energy needed for the developing flowers. Perhaps this is why grasses are freer to tiller after floral emergence (Johnston and Jeffcoat, 1977). Before floral emergence, cytokinins can aid in increasing tillering rates, perhaps through the ability to increase assimilate supplies to tiller buds.

Most researchers feel that defoliation, nutrient availability, hormones, temperature, light quality, daylength, and phenology are all important. This study is an observation of tillering responses of A. spicatum when it is exposed to
defoliation and hormonal treatments in a greenhouse situation. Field results will be used for comparison.

METHODS

Twenty-one bunches of *Agropyron spicatum* were transplanted in mid-November from a native stand in a sagebrush-bunchgrass community on the benchlands above Logan, Utah. Transplanting in fall allowed vernalization to occur. Plants were placed in peat pots with a 50-50 mix of Bacto potting mix and perlite and placed in a greenhouse. Plants were watered every 2 to 3 days and fertilized weekly until the experiment began in late February. Plants were rated 1 to 3 for vigor, height, and phenology before the experiment, then distributed evenly among treatments based on these characteristics. Each plant had between 60 to 120 tillers; 7 tillers per plant were marked with wire rings around the tiller base and observed for 8 weeks. Tiller observations included total height, greenleaf number, reproductive state, and new tiller production.

There were 3 clipping treatments, coupled with 2 hormone treatments, and controls. Each treatment was replicated 3 times. Treatments were: 1) control - unclipped, 2) severe defoliation by clipping to 2-4 cm, and 3) apical meristem removal by clipping out growing tips from grass shoots. The hormones Auxin (indole-3-acetic acid) and cytokinin (zeatin) were applied at a $1 \times 10^{-5} \text{ M}$ solution to unclipped and defoliated plants. A
hormone-water solution with 0.4% Tween-20 wetting agent was used to spray around plant bases until runoff. Control plants were sprayed with water and wetting agent.

A companion project was run in the field from mid May to mid June 1985 at the Green Canyon Ecology Center, near Logan. Plants were established in a sagebrush (Artemisia tridentata Nutt.), crested wheatgrass (Agropyron desertorum), bluebunch wheatgrass (A. spicatum) matrix in native mollisols. Only natural precipitation reached plants, although this was 150% of normal. All plants were defoliated. Auxin was applied at 50 ppm, while kinetin a cytokinin, was applied at 5 and 25 ppm and gibberellic acid was applied at 25 ppm alone and in a 50-50 mixture with the 25 ppm kinetin solution. Preliminary data indicate similar responses to auxin and cytokinin treatments in the field.

RESULTS

Daughter tiller production

Data showed that plants with leaves intact produced the largest number of daughter, or second generation tillers (Fig. 1). 1.48 daughter tillers were produced per parent, or first generation tiller, in control plants. Plants with meristems removed produced 1.52 daughter tillers per parent, while defoliated plants produced only 0.81 second generation tillers by the end of the experiment. Auxin treated plants produced almost the same number of tillers as controls (1.52 for auxin
treatments, 1.48 for control treatments) while cytokinin treated plants produced fewer; only 1.19 tillers per parent (Fig. 2). When hormones were applied to defoliated plants, both auxin and cytokinin increased tillering levels above those of defoliation controls. Auxin applied to defoliated plants produced 1.14 tillers per parent and cytokinin produced 1.1 tillers per parent on defoliated plants in comparison to the 0.81 tillers per parent produced on defoliation controls (Fig. 3). Although auxin treated plants showed reduced tiller numbers when defoliated, cytokinin treatments were basically unchanged by defoliation.

Tiller Mortality

Plants exposed to clipping had the highest tiller mortality rates (see Fig. 4). Defoliated plants had a 33 percent mortality rate; meristem removal plants, a 14 percent mortality rate; and no tiller deaths occurred in control and hormone control treatments. When hormone treatments were coupled with defoliation, their mortality rates were equal to (33 percent, cytokinin) or approaching (23 percent, auxin) mortality rates of straight defoliation.

Growth in Height

Cytokinin-treated parent tillers grew more than those of other treatments (see Fig. 5). This is partly due to the fact that over 50 percent of the parent tillers in this treatment reached the reproductive, floret-producing stage. Only 25
percent of auxin treatments and controls reached this stage and none of the defoliated plants became reproductive (see Fig. 6).

Growth in height of daughter tillers was nearly opposite. Defoliated plants produced the highest growth rates while control plants and straight hormone treatments showed less growth. Apical meristem removal plants and hormone treatments coupled with defoliation had the smallest height growth (see Figs. 7 & 8). However, hormone treatments on defoliated plants produced nearly the tallest plants because their original heights were greater than other treatments. Defoliation treatments and cytokinin control treatments produced the tallest plants.

Comparison with field experiment

Preliminary results indicate that fewer daughter tillers were produced per parent in the field experiment. Percentage of tillers greater than 50% senescent was slightly higher for the high level cytokinin treatment and the cytokinin/giberellic acid mixture. These differences are not significant at the 95% level, but may be significant if complete mortality is measured, rather than senescence. Heights were not significantly different for any treatment.

DISCUSSION

Many factors affect tillering rates in grass plants. Results of this experiment indicate that hormones play a part, as
was shown by their ability to increase tillering rates in
defoliated plants. However, apical dominance appears to play a
minimal role, as it had little effect on tillering in either
experiment. Factors other than hormones also influence tillering
rates, and may even override hormonal effects. Plants grown in
the greenhouse produced more tillers than any treatment grown in
the field, but even in these ideal conditions, no treatment
increased tillering rates above those of controls. It appears
that hormone treatments may improve tillering in injured plants,
but not in healthy, whole individuals.

Factors affecting tillering rates include photoperiod, light
intensity, moisture, competition with other plants, and plant
phenology. Langer et al. (1973) found that few defoliated plants
were induced to tiller until after ear emergence. In our
greenhouse study, over 1/3 of the marked tillers reached the
reproductive stage, while none of those measured in the field
study, which was done during the grass' natural reproductive
cycle, completed this growth stage. This was probably due to
moisture stress and more complete meristem removal.

Mortality of first-generation tillers increased on
treatments that involved stress, such as defoliation and meristem
removal. However, greenhouse data showed that height growth of
daughter tillers was increased in defoliated plants, suggesting
that second-generation tillers were growing at less than their
potential rates in undefoliated plants. These effects were less
obvious on apical meristem removal plants.
This study cannot conclude that hormones are more important than other factors in their effect on tillering. However, this study does suggest that hormones affect a grass plant's development, and that other factors unique to the greenhouse, such as light intensity, lack of competition, and moisture level can also act to improve the low tillering rates naturally found in *Agropyron spicatum* plants.
Daughter Tiller Production

Legend:
- △ Control
- × Ap Mer Removal
- ○ Defoliation

Days from Start of Experiment vs. # of Daughters Per Parent
Daughter Tiller Production

Legend

△ auxin
X control
□ cytokinin

Days from Start of Experiment

# of Daughter Tillers Per Parent Tiller
NO. OF DAUGHTERS PER PARENT

Days from Start of Experiment

Legend

- Control
- Auxin defoliation
- Cytokinin defoliation
- Defoliation
Average Total Height of Daughters for Control, Apical Meristem Removal, and Defoliation Treatments

![Graph showing the average total height of daughters over days from the start of the experiment. The legend indicates different treatments: Control (△), Apical meristem removal (X), and Defoliation (□).](image-url)
Average Total Height of Daughters for Defoliation and Hormone Treatments

Legend:
- Δ Auxin & Defoliation
- X Cytokinins & Defoliation
- □ Defoliation

Height of daughters in mm vs. Days from Start of Experiment.
LITERATURE CITED


