SEED-HEAD DEVELOPMENT IN TALL FESCUE AS INFLUENCED BY DATE OF APPLICATION OF 3 CHLORO IPC

by

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INTRODUCTION

The influence of various environmental factors on the reproductive processes of seed producing plants remains a source of constant and intense interest to plant scientists the world over. Numerous investigations have been carried out and many comprehensive reports published on this subject. More than being a source of interest to curious researchers, factors affecting the reproductive processes in plants are of vital importance to the agricultural wealth of Oregon. An ideal combination of climate, cultural practices and techniques has established the production of forage seed as a major industry in this state. Therefore, many problems relating to the forage seed industry have received special attention.

Tall fescue is one of Oregon's most valuable seed crops. It is grown for seed production purposes in 21 of the 36 counties of the state. The value of this crop ranked second highest of Oregon's grass-seed crops during the period of 1948 to 1951. This state accounted for approximately one fourth of the total U. S. production of tall fescue seed from 1949 to 1951. Since 1953, there has been a decline in total acreage of Oregon's tall fescue seed crop which has been largely due to over production and strong competition from the southern states. However, favorable climatic conditions and superior handling and production practices have enabled Oregon to produce high quality seed at lower cost and thus hold its place in the competitive market.

In the face of stiff competition from other areas, Oregon has initiated a program to further improve quality and reduce the cost of seed production in tall fescue. Work has been initiated to gain fundamental knowledge of various factors affecting seed-head development in this crop. A number of experiments dealing with the influence of different cultural conditions on seed production have been carried out in connection with this problem. Studies involving rates and dates of application of 3 Chloro IPC (O-Isopropyl N-3-Chloro Phenyl Carbamate) revealed that applications after October could practically eliminate seed production by tall fescue in the Willamette Valley of Western Oregon (8, p. 26). The effectiveness of 3 Chloro IPC in preventing seed-head formation in tall fescue has made it a valuable tool for studying floral development in this species.

The application of 3 Chloro IPC made it possible to observe the development of the shoot apex at specific periods and to relate these findings to floral development. This experiment was designed to stop seed-head formation at approximately monthly intervals from October 15 to February 18. The object was to observe certain factors affecting seed-head development from the date that the plants were treated until the time of seed-head formation.

REVIEW OF LITERATURE

Many experiments have been conducted to study the effect of various cultural practices and climatic conditions on the development of the seed head in grasses. The physiological and morphological conditions which of necessity may precede or accompany floral development have been found to be profoundly influenced by the environment under which the plant grows.

CULTURAL PRACTICES AND CONDITIONS

A number of workers have studied the influence of cultural practices on seed-head production in grasses. Tall fescue has received special attention in Oregon. Investigations conducted along these lines include the works of Richardson (56, pp. 1-84), Bayer (8, pp. 1-61), Whitesides (70, pp. 1-38) and Schoth (60, pp. 88-94), (61, p. 104) and (62, p. 108).

Age and Density of Stand

It is a generally accepted fact that with an increase in age of grass stands there usually occurs a corresponding decrease in the rate of seed yield. Many theories have been advanced in an attempt to explain this phenomenon. Sod-bound conditions and studies of root development found in old stands have received much attention in seeking a solution to this problem (74, pp. 108-118), (71, pp. 189-209) and (56, pp. 1-84). Richardson (56, pp. 1-84) found that under field conditions there was a correlation between maximum root content and

the development of sod-bound conditions. Further studies by Richardson (56, pp. 20-23) revealed that plants growing in larger pots produced more seed heads than those growing in smaller pots under greenhouse conditions and under a 10 hour photo-period.

The age of stand has also been found to have a definite effect on the time of transition from the vegetative to the reproductive phase of the shoot apex (21, p. 13) and (79, pp. 1-38). Whitesides (79, pp. 29-30) found that the growing points of tall fescue in young stands (1 to 5 years old) changed to the reproductive phase a few days earlier than those of old stands (7 years and older). This was found to be true under both greenhouse and field conditions. The young stands were much more vigorous than the old stands and were considerably more advanced in vegetative growth in the fall. Evans (21, pp. 13-14) noted that as timothy meadows grew older there was a general tendency for the number and also the per cent of fertile shoots per unit area to become smaller from year to year. The per cent of sterile shoots was found to be much greater in old meadows.

Richardson (56, p. 51) found that sod-binding seemed to be due to density of stand rather than age of stand. He observed that thinly seeded stands of tall fescue produced more seed than those established by heavy rates of seeding. It then follows that the increase in sod-boundness and the subsequent reduction in seed head development is not necessarily due to the increase in age, but due to the density of the plant population and the other environmental conditions that usually accompany the increase in age of a stand.

Available space also had an important bearing on the proportion of fertile to sterile shoots in an established timothy meadow (21, pp. 14-15). By reducing the tiller population within a unit area it was possible to raise the proportion of tillers producing seed heads from 43 to 57 per cent. In row stands where the competition for space was less than in solid stands, there was usually a higher proportion of seed heads formed and also an increase in seed yields over solid stands (60, p. 87) and (83, p. 4). Tall fescue grown in rows has produced consistently higher seed yields than when grown in solid stands (56, p. 17). Evans (21, p. 15) also found that when timothy was given sufficient space in row plantings, the plants produced fertile shoots in a proportion of 99.4 per cent as compared to a sterile-shoot production of 0.6 per cent. Whitesides (79, pp. 20 and 24) studied the effect of width between rows and the time of transition of the shoot apex to the reproductive phase, but found little significant difference between the treatments used.

Renovation

To over-come the adverse conditions that are usually found in old stands, various methods of renovation have been studied. Experiments carried out in Oregon (61, p. 104), (62, p. 108), (56, pp. 1-84) and (79, pp. 1-38) indicated that highly significant increases in the production of seed in old and sod-bound stands of tall fescue could be achieved. Renovation by chemicals has also been

successfully used (56, p. 51).

By mechanical means, Richardson (56, p. 18) almost tripled the production of seed when ten-year-old solid stands of tall fescue were reduced with a garden roto-tiller. This marked increase in production was attributed to an increased supply of available nutrients as well as to a stimulation in the production of seed-head primordia. Whitesides (79, p. 19) tested the effect of renovation on the date of transition from the vegetative to the reproductive phase and found no significant difference between renovated and non-renovated treatments. Schoth and Rampton (62, p. 108) got marked increases in seed yields when they reduced old stands of tall fescue by plow renovation.

Burton (14, pp. 523-529) successfully used burning to renovate aged stands of several species of southern grass. Burning was also found to hasten certain phases in the development of the inflorescence when this treatment was used on tall fescue (79, p. 17) and also to increase seed yields (61, p. 104). Partial destruction of sod-bound tall fescue stands by chemicals resulted in a great increase in seed yields the following year (56, pp. 51-55). Richardson (56, pp. 67) found that TCA was the most effective method of renovation. Stands renovated with this chemical produced increases in seed yields that were considerably above those obtained from stands that were reduced by mechanical means.

Soil Fertility

The application of fertilizers, either alone or in combination

with other treatments, has probably been one of the most effective methods of increasing seed production in old grass stands, and nitrogen has been found to be the key element in fertilizer programs for grass seed production. In 1934, North and Odland (46, pp. 941-942) discovered that the yield of seed of Rhode Island Colonial bent was influenced chiefly by the amount of nitrogen applied, and that phosphorus and potassium had little effect. In fact, potassium without the application of nitrogen depressed seed yields.

Working in the British Isles, Evans (20, p. 207) found that nitrogen increased seed yields in such leafy species as orchard grass, timothy, and perennial ryegrass. Similar results were reported in Oregon by Schoth and Rampton (60, p. 88) where applications of nitrogen to tall fescue stands gave marked increases in seed yields. Sprague (72, p. 152) found that pot-bound plants when given adequate nutrients and exposed to the proper environmental conditions would produce seed heads. Southern species of grass seemed equally responsive to nitrogen. Burton (14, pp. 523-529) studied 10 southern grasses from 1937 to 1940 and found that seed-head formation was influenced little by the application of potassium. However, there were significant increases when nitrogen was added to the basic applications of phosphorus and potash.

The time of fertilizer applications can be critical in the production of grass seeds. Generally, spring applications are recommended (54, pp. 15-16) and (33, p. 644). However, Whitesides (79, p. 26) found that fertilizers applied in the fall were responsible for advancing

the period of transition of the growing point from the vegetative to the reproductive phase by several days. Another study (48, p. 38) made on bluegrass showed that nitrogen applied in the fall stimulated vegetative growth and increased the number of flower heads to approximately five times those of unfertilized plants and that fall clipping completely eliminated the formation of flowering shoots on plots that did not receive nitrogen. Schoth and Rampton (60, p. 94) found that there was usually no significant increase in total seed yield when nitrogen was split between fall and spring dates of application. However, there was a measured increase in seed yields of fall applications over those applied in the spring.

Age of stand was also an important factor in determining the response in seed yield to nitrogen applications. Investigating the reaction of tall fescue to fertilizers as influenced by age of stand, Schoth and Rampton (62, p. 108) noted that there was a steady decline in yield as age increased. This crop was grown in rows that were 3½ feet apart and the fertilizer treatments ranged from 50 to 400 pounds of nitrogen applied annually. Some response was shown when fertilizer applications were doubled in the 6th year but seed yields did not show any appreciable increase.

Benedict (9, pp. 1108-1109) attempted to support a theory which proposed that as grass stands aged there was a build up in the roots of a toxic or inhibiting substance that was responsible for the "so called" sod-bound condition that reduced seed yields in grasses. However, other workers (43, pp. 77-773) were able to show that the

toxic substance referred to by Benedict was actually a nitrogen deficiency created by the excess carbonaceous material that was added to the soil.

The interaction of fertility and cultural conditions such as method of seeding, density of stand, soil texture, moisture, and rate of seeding have an important bearing on seed production in grasses. Explorations involving solid versus row plantings and their response to nitrogen are now in progress at the Southern Oregon Experiment Station (83, p. 4) and (84, p. 9). The relative effectiveness of these trials is shown by the increase in net returns from nitrogen applied to solid and row stands of tall fescue and several other leafy grass species grown for seed production in Jackson and Josephine Counties by Yungen (83, p. 4). In timothy, Evans (21, p. 16) discovered that the proportion of fertile shoots to sterile shoots was larger in meadows where the cultural conditions were favorable for vigorous growth. This experiment also indicated that timothy responded to the application of commercial fertilizers in terms of vegetative vigor and with an increase in the per cent of fertile shoots.

CLIMATIC CONDITIONS

It has been long established that certain plants pass through separate and distinct phases in order to fulfil the requirements of floral development (41, pp. 111-112). These phases are known to require specific climatic conditions for their successful completion.

More than this, it appears that it is necessary for the plants to be in a certain state of morphological and physiological readiness in order to respond to a favorable environment which may be critical for the respective phases.

Temperature and light have been discovered to have remarkable effects on the development of the inflorescence in many plants. Grasses native to northern latitudes and temperate climate are known to be particularly receptive to these environmental factors. Other conditions may also play an important part in determining the ultimate outcome of the reproductive processes in plants. Richardson (56, p. 59) noticed that tall fescue became dormant during the summer due to a deficiency of water. When moved into the greenhouse and given sufficient moisture, it flowered profusely. From this it appears that a combination of a number of factors both cultural and climatic, may interact to effect the flowering condition of the plants.

Phases of Floral Development

Substantial evidence has been presented (31, pp. 201-217); (44, pp. 417-424) and (48, pp. 31-41) indicating that there are three principal phases of flowering (1) induction of the flowering condition, (2) initiation and early growth of the inflorescence and (3) complete development of the inflorescence. Each of these phases represents a separate stage in the cycle of the developing seed head and, therefore, the environmental conditions required for each may be completely different. These phases were discovered to be especially sensitive to

light and temperature requirements. Gardner and Loomis (31, pp. 202-212) defined these phases of flowering as follows:

1. Floral induction, the chemical or hormonal differentiation resulting from the fulfilment of certain thermo-photoperiodic requirements.

2. Floral initiation, the morphological transformation of an induced growing point from a vegetative to a floral primordium.

3. Further floral development, processes resulting in the production of macroscopic flowers.

The conditions necessary for floral induction were set forth by Peterson and Loomis (48, pp. 31-41). Evidence was given that both short days and cool temperatures are necessary for floral induction and subsequent flowering in Kentucky bluegrass. Induction of the flowering condition occurred during fall under normal cool temperatures and short photo-periods. Gardner (31, pp. 201-217) and others who also studied this problem found that when certain grasses native to northern latitudes did not receive low temperature treatments under short photo-periods the plants produced no seed heads or flowered only sparingly, even though subjected to favorable conditions in the spring. Gardner and Loomis (31, p. 210) found that the light and temperature conditions responsible for floral induction could be applied separately; however, there was one restriction -- the photo-period had to precede the thermo-period. Thus if all short days occurred at warm temperatures and were then followed by long days at low temperatures, floral induction was effected. However, when the low thermo-period preceded the period of short days, induction did not

occur. The fact was also established that two weeks of long-warm days between short-warm and the cool-day period prevented induction. Evidence (31, p. 210) pointed to the photo-periodic reaction as the basic one, and that the low temperature effect was necessary to complete the short day reaction to insure induction.

A number of grasses that are native to northern latitudes do not require short days and cool periods in order to produce seed heads (56, p. 59, (30, pp. 59-71), (3, p. 194) and (72, p. 153). Grasses that are native to southern latitudes have generally been found to be independent of short-day and low-temperature requirements (31, p. 214).

The initiation of floral primordia was established as the next phase in the development of the inflorescence. Photo-period has a striking effect on the initiation of floral primordia. Favorable temperature also seems to play an important role in this process. Whitesides (79, pp. 14-16) concluded that floral primordia in tall fescue became evident during the first two weeks in February. This season of the year is characterized by intermittent periods of cool and warm days and increasing length of day. According to Allard and Morgan (3, pp. 226-227) the increase in length of day affected either flowering or stem elongation or both.

The investigations of Evans (22, pp. 182-187) emphasized the importance of photo-period on floral primordia initiation. The conclusions reached are based on observations made on a single clonal line of timothy that grew at various stations extending from Alaska

in the north to Georgia in the south. Evans' findings indicated that most of the plants at the northern stations bloomed at a decidedly shorter period of time in the spring than the southern grown clones. The season of blooming progressed from south to north at a constant accelerating rate due to the gradual increase in length of day from south to north during the spring. In a later experiment (23, pp. 571-586), Evans found that there was usually a minimum length of day required for floral initiation. As the length of day increased above the minimum at which blooming occurred, the total period necessary for blooming was decreased up to an 18 hour maximum. No additional response was obtained beyond this photo-period.

Date of blooming seems to be determined largely by the adjustment of the respective biotypes to the photo-periods. Short-day plants are early while strains with longer photo-periods do not bloom until long days arrive later in the growing season. Sprague and others (72, pp. 144-154) and (23, pp. 571-586) concluded that a 12 hour photo-period appears to be the approximate minimum needed for floral initiation in the majority of the grass species adopted to northern latitudes. Festuca elatior and five other grass species of the north gave best response to a photo-period of 16 hours. A 10 hour day plus 1 to 2 hours in the middle of the night were approximately equal to a 16 hour day of continuous light (72, p. 148). Sprague noted also that light intensity above 75 ft-candles had no effect on the flowering condition of the grasses studied (72, p. 145).

Macrodevelopment of the floral parts is the culminating phase

in seed-head formation. This period of further development of the floral primordia is favored by increasingly longer days, warmer temperatures and high levels of nutrients (31, p. 212) and (72, pp. 144-154).

As partly adopted from Gardner and Loomis, (31, 213) the three phases of seed-head development may be summarized according to the following table.

Phase	Requirements	Season
Induction	1. Low temperature 2. Short days	Fall
Initiation	1. Warmer temperatures 2. Longer days	Late Winter
Macrodevelopment	1. Warm days 2. Long days 3. Abundant nutrients	Early Spring

Maturity of the Vegetative Shoot Apex

As far back as 1918, Klebs (41, pp. 128-151) described three phases in the development of the inflorescence. These were postulated to be (1) the onset of "ripe-to-flower", (2) formation of floral primordia and (3) the development of the inflorescence. The last two proposed by Klebs are essentially the same as those described above by Gardner and Loomis. However, the first phase proposed by Klebs, "ripe-to-flower", seems to indicate a certain capacity or state of readiness that is

necessary for further progress toward the development of an inflorescence.

Klebs (80, p. 22) was of the opinion that the ripe-to-flower condition was characterized by intense carbohydrate assimilation with an accompanying limited uptake of nutrient elements. In other words, the condition of "ripe-to-flower" was pictured as being favored by an increase in carbohydrate assimilation and the hindrance of the counter reaction of vegetative growth. Under conditions that allow vegetative growth to accompany assimilation, "ripe-to-flower" condition may be prevented. This condition may also be destroyed by any relation of temperature and light which may favor vegetative activity. Therefore, high temperature when balanced by high light intensity may not adversely affect the condition of "ripe-to-flower". However, when light intensity decreases, high temperature can be deleterious to this process.

The "ripe-to-flower" state as postulated by Klebs is an expression of the internal physiology of the plant. However, Purvis and Gregory (52, pp. 935-936) and (53, p. 580) attached morphological significance to this condition. Evidence was presented to show that a minimum number of leaves were necessary before the "ripe-to-flower" condition could be attained. The minimum number of leaves was variable and subject, within limits, to vernalization and photo-period.

It is generally recognized that in many of the Gramineae a certain minimum vegetative growth must occur before "ripe-to-flower" is reached (52, pp. 919-955), (53, pp. 569-591), (65, p. 208), (68, p. 25), (55, pp. 361-377), (30, pp. 59-71), and (42, pp. 413-438). Sharman

(65, p. 208) indicated that some sort of minimum internal requirement had to be satisfied before the change of the shoot apex from the vegetative to the reproductive condition could be achieved. Further suggestions were made that the number of leaves could be used as an indicator of the maturity of the shoot apex before any morphological signs of floral primordia were evident. After additional investigations, this author (68, p. 25) concluded that the minimum number of leaves formed on a tiller before floral primordia differentiated was attained while the photo-period was still favorable for floral initiation in the species.

Rice (55, pp. 361-377) also investigated the relation of leaf number on a shoot as an indicator of floral maturity. This investigator studied five species of native range grass in Oklahoma and found that four indicated a correlation between the number of expanded leaves and the state of floral development. His analysis gave evidence that culms which did not have the number of leaves required for the particular species did not initiate an inflorescence.

Lamp (42, pp. 413-438) noted that the number of exserted leaves on undeveloped shoots during late summer and early fall was, in part, determined by the age of the shoot. A count of exserted leaves during the fall showed that fertile tillers had consistently more leaves than those which did not initiate an inflorescence during the following spring. However, the highly fertile clones that had exserted only a few leaves in the fall initiated an inflorescence the next spring. The shoots of clones that were relatively sterile, usually initiated

floral primordia when the leaf number was high, but only a few tillers with relatively few leaves formed an inflorescence the following spring. In 80% of the flowering tillers, the range in leaf number was found to be fairly constant and fell within a relatively narrow range.

CARBAMATES AS HERBICIDES

Various carbamate compounds are now being used as selective herbicides for the control of annual weedy grasses. The history of these compounds as herbicides dates back to the experiments of Templeman and Sexton (76, p. 630). These workers used ethyl phenylcarbamate at the rate of 50 mg per square foot and discovered that oat seedlings were killed but there was little or no damage to certain broad leaf plants.

Ennis (18, p. 823) and (19, pp. 15-21) studied the mode of action of these chemicals on certain plants and noted that they acted mainly as mitotic poisons. This damage to plants was characterized by blocked metaphases, giant cells with multinuclei and increased chromosome numbers which were present in meristematic tissue of both the root and shoot. Cells capable of further growth became greatly enlarged before maturing. Specialized cells that were mature showed no response to the chemical.

These carbamate compounds are known to be easily fixed by the soil and move with great difficulty. Freed (28, pp. 25-26) determined that it takes approximately an inch of water to leach IPC

into the soil to a sufficient depth where it could be effective. The persistance of 3 Chloro IPC and other carbamates in the soil largely depends on the climatic and environmental conditions to which they are exposed (45, pp. 393-397). According to Freed (28, pp. 25-26) the average field applications of 4 pounds per acre of 3 Chloro IPC per acre will last approximately six weeks under the climatic conditions of the Willamette Valley in Oregon. Freed (29, p. 2) also reported that micro-organisms were responsible for the breakdown of the carbamates in the soil and that conditions most favorable for the activity of soil organisms were most effective in reducing the longevity of these compounds.

These carbamates have been successfully used to control many of the weedy annual grasses found in perennial seed crops (7, p. 90) Bayer (8, p. 56) achieved marked success with 3 Chloro IPC in controlling annual grasses in tall fescue. However, this study indicated that when 3 Chloro IPC was applied after October there was a striking reduction in seed yields.

This reduction in seed yield has been of major concern to workers and researchers associated with this problem. Freed and Bierman (8, p. 12) observed that after the grass plant tillered it became more tolerant to the action of IPC. Taylor (75, pp. 620-629) found that when IPC was applied to wheat at low concentrations it stimulated tiller formation.

Bayer (8, p. 52) proposed three possible explanations as to why the action of Chloro IPC reduced or prevented seed production by

tall fescue when it was applied after October. The first of these indicated that applications after October did not allow sufficient time for adequate regrowth to produce seed. There was also the feeling that the seed bud primordia were not laid down until November, and therefore, applications of 3 Chloro IPC at this formative period was lethal. Bayer also proposed that 3 Chloro IPC probably could act as an inhibitor of enzymes that control seed-head development in tall fescue.

MATERIALS AND METHODS

An experiment was planned which consisted of two genotypes of tall fescue (Festunca arundinancea, Schreb.) in a randomized block design. There were six treatments and five replications. The treatments were made up of a control and five dates of applications of 3 Chloro IPC at the rate of 4 pounds per acre with the object of observing certain factors affecting seed-head development in tall fescue during the period from October 15 to March 17.

Plant Material

The plant material used in this experiment came from two clonal lines of fine-leaf selections of tall fescue that were lifted from the nursery in 1954 to establish greenhouse polycross trials. The highest and lowest seed-yielding clones were chosen in order to have more variability in fruitfulness between the genotypes studied. The genotypes were 258 and 254, as designated in the polycross trials.

On June 1, 1955, the root systems of the clones were uniformly pruned and the shoots rooted in fertile greenhouse potting soil contained in "2 x 2½" "Vita-Bands". These were grown in the greenhouse in plant flats with a capacity of 50 bands each. By August 3rd, the plants had practically filled the bands with shoots and were then transferred to six inch clay pots that contained approximately 1900 grams of air dry soil. The plants remained in the greenhouse until September 17th. On this date, the plants were transferred

to Hyslop Agronomy Farm, graded for uniformity of size and the inferior plants discarded. Each pot selected for the experiment was randomly assigned as an entry for the respective genotype. Randomization was achieved by arranging 135 squares into a table of 9 x 15 squares for each genotype. The entries for the particular genotype was then drawn and systematically recorded in the prepared table. The pots were later tagged according to their positions in the table. In a similar manner, tags were randomly drawn to select entries to complete a map of each block.

Field Experiment

Each block contained 88 pots, 54 of which were entries that were surrounded by a single row of 34 border pots. The pots that made up the main body of each block, those containing the entries, were placed in a 6 x 9 arrangement. This, with the border pots, made a complete block arrangement of 8 x 11 pots. In addition to the main experiment, an extra block of 88 plants was grown for a more intensive study of the plants during the early spring. Treatments selected for this special study were plants of the check, and those treated in October and November. The pots were embedded in sawdust contained in a rectangular bed that measured 7 x 44 feet and was approximately one foot above the ground, (Fig. 1).

The six treatments consisted of a check and 3 Chloro IPC, applied at the rate of 4 pounds per acre on October 15, November 18, December 18, January 15 and February 18. The chemical

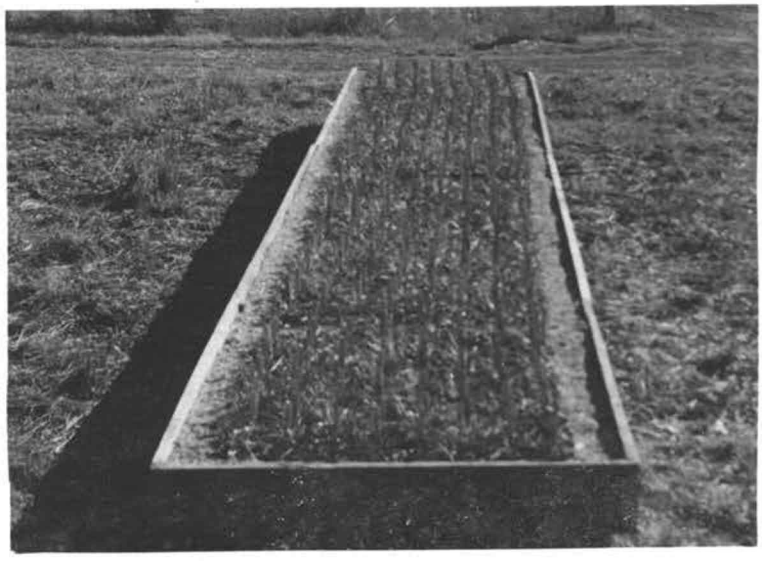

Figure 1. Arrangement of plants in the field. Rectangular bed (7' x 44') containing potted plants embedded in sawdust.

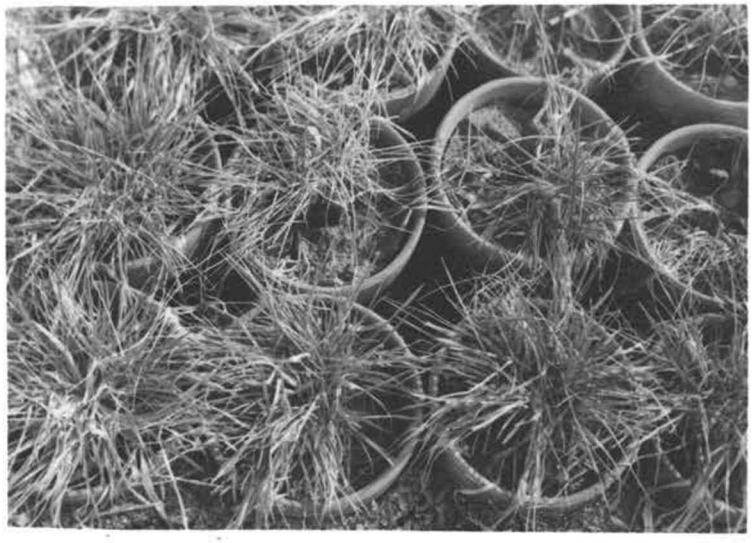

Figure 2. Close up of the plants on the last date samples were taken in mid-March.

material was measured out by pipette. Seventeen and one-tenth ml. of a solution containing an equivalent of 4 pounds 3 Chloro IPC per gallon were put into a container and brought up to one liter in volume. This was enough to treat 100 pots, using the top surface of the soil contained in the pot as the unit of measurement. A 100 ml. aliquot of the original solution was taken and made up to 10 liters. One hundred ml. of the latter solution were applied to the surface of the soil in each pot which gave a rate 4 pounds of 3 Chloro IPC per acre.

Random sampling of mother shoots for study, started with the control treatment on October 15 and on the succeeding month following application of 3 Chloro IPC for each of the other treatments. Once started, the sampling of all treatments continued at monthly intervals until March 17. The sampling of the special block continued at various intervals until April 16.

The plants were watered as often as it was judged necessary and fertilized by applying nitrogen, P_2O_5, and lime to the potting soil at the rate of 160 pounds, 200 pounds and 4 tons per acre respectively. An additional application of nitrogen in the form of ammonium nitrate was applied on October 1st. Spring applications of 100 pounds per acre of nitrogen were made, on February 4 and April 2 with final addition of 50 pounds per acre on May 19.

Collecting Samples

On each harvest date, three shoots were randomly sampled from

each replication and stored in 50% FAA (Formalin-Aceto-Alcohol) so that all treatments could be studied and compared from October 15 until the initiation of the inflorescence.

To obtain the plant samples, a predetermined quarter of the plant in each pot sampled was randomly selected. This was accomplished by tossing a coin to choose the right or left hand section of the pot and a second time to choose the upper or lower quarter. The particular plant section was removed by making deep cuts across the center of the pot in vertical and horizontal directions, and then lifting out the quarter section of the plant. The shoots were labeled, secured with a rubber band, and placed in a plastic bag to maintain their freshness while being transported; after which, the shoots were torn apart, washed and made ready for sampling. These shoots were then evenly spread between two boundaries as wide as a section of hair comb that was used to section them off. The comb had been modified by having every other tooth of the coarse section removed. The shoots were selected according to the section occupied nearest the number drawn. If two sections were equidistant, the section on the right received priority.

Harvesting Of Plant Materials

As the seed neared maturity, the panicles were counted and bagged. Bagging was done to insure no loss of seed. Vegetable parchment bags that are commonly used in forage breeding were used for this purpose. The bags were placed over the heads of the plants and tied at the bottom. They were then secured to galvanized iron

rods by means of aluminum wire which ran through an eyelet in the corner of the bag.

The seed was harvested on July 7 by clipping the culms just below the end of the parchment bag, rubbed out by hand and sacked for weighing. On July 7, all pots representing treatments were placed in individual gallon containers for soaking. The following day, soil was washed from the roots and a count made of the tillers. The plants were placed in cloth bags with their tops and roots intact and dried. When drying was completed, the whole plant was weighed and then the roots and tops were separated. The roots were weighed and top weight determined by difference.

Examining Technique

Examination of the plant material was done visually by studying collected material with the unaided eye and with a binocular dissecting microscope. Two shoots from each replication were prepared for microscopic study. The plant material was prepared for embedding by removing several of the outer leaves, washing in three changes of 50% ethyl alcohol, infiltrating and embedding according to the tertiary butyl alcohol method, (39, p. 41).

The following schedule was used according to Smith (69).

1. 50% FAA
2. Wash in 50% alcohol, 2-4 changes in 4 hours.
3. Tertiary butyl alcohol; 100% ethyl alcohol (1:1), 3 changes, 12 hours.
4. Tertiary butyl alcohol - 3 changes, 12 hours.

5. Tertiary butyl alcohol; paraffin oil (1:1), 1-4 hours.

6. Pour into vial with parawax. Leave cork off and place in 50 degree oven. Leave 1-2 hours after material has sunk to the bottom of vial.

7. Parawax, (2 changes in 6-12 hours in a 60 degree oven).

8. Tissuemat - (54-56 degrees) 4-12 hours.

9. Tissuemat - 2-4 hours. Fill vial.

10. Embed.

The material was embedded in paper embedding trays about one inch square and approximately 1/4 inch deep. The paper tray was placed on a warm plate so that the plant material could be arranged before the paraffin became cool. By using a binocular dissecting microscope and also by means of the unaided eye, the specimens were arranged so that they rested with their distichous planes parallel to the bottom of the embedding tray. The paraffin block was then cooled as rapidly as possible in running water. In addition to the 10 longitudinal sections prepared for each treatment per genotype for each particular date of sampling, one to two specimens were prepared for transverse sectioning. The material for transverse sectioning was embedded vertically. All paraffin blocks were cut and soaked overnight before sectioning.

Each specimen was identified by the particular block on which it was mounted. All ribbons from a single block were placed on a transparent strip of wax paper about three inches wide and a foot long.

These were identified by number and as many as 72 stored in the refrigerator to be mounted on slides later. The refrigeration allowed the ribbons to be stacked upon each other without causing them to stick to the sheet of wax paper above.

The median section of each stem was picked out by examining the ribbons on the sheet of wax paper with the aid of substage lighting and the medium power objective of a binocular disecting microscope. The binocular disecting microscope used had a large stage and was particularly adapted for this procedure. The ribbon was moved across the stage by drawing the front end of the wax paper strip across the stage. The ribbons had sufficient affinity for the wax paper that the over hanging front or rear ends seldom lost their sections. The sections were affixed to the slides with Haupt's adhesive. Formalin used for floating out the ribbons contained one drop of a 1% aqueous solution of safranin to 25 cc of solution (66, p. 105). This made it easy to further examine sections under a microscope or with the disecting microscope. Both specimens from the same pot were mounted together on a slide. The sections were allowed to dry on a covered warming plate for several hours and then placed in slide boxes with the lids removed to permit further air drying.

Three staining schedules were used during preliminary staining trials. These were Foster's (39, p. 91) tannic acid-iron chloride-safranin method, Popham's (50, pp. 185-190) safranin-hematoxylin-analine blue schedule and Sharmon's tannic acid-iron alum-safranin-orange G procedure. The complete schedules of Sharmon

(66, pp. 105-111) and Popham (50, pp. 185-190) gave excellent results and were used, therefore, to the same extent in studying the plant material of the experiment. Sharman's staining schedule proved superior for bringing out the contents of the cytoplasm. Starch granules and plastids were made quite distinct, and the vacuoles could be more clearly seen. The schedule of Popham gave a clear definition of the nucleus, with the nucleoli being quite well defined. Provascular tissue and necrotic areas were also shown best by this stain.

The photomicrographs were taken with a 35 mm Leica 1c camera with Micro-ibso attachment and a Leitz Ortholux microscope setup. The film used was Adox KB-17 which required an orange filter with Sharman's tannic acid-iron alum-safranin-orange G schedule and a combination of wratten G no. 15 and a wratten K-2 no. 8 with the procedure of Popham (23, p. 185). Figures 8, 9, 10, 11, 18, 19, 24 and 25 were photographed on Kodak's Contrast Process Pan and developed for 2½ minutes with EK-D 60A. The photomicrographs were then contact printed.

EXPERIMENTAL RESULTS

The phytotoxicity of 3 Chloro IPC at the relatively low rate of four pounds per acre was found to have had gross morphological as well as pronounced cytohistological effects on tall fescue. There was a direct effect of 3 Chloro IPC on meristematic tissues such as apical and intercalary meristems and provascular strands. Cells in these areas became greatly enlarged and their nuclei lobed and tended to have an increased number of nucleoli. The cells of parenchyma of relatively mature tissue usually became greatly swollen and highly vacuolate with the cytoplasm generally being arranged in a finely netted pattern in these cells. Mature vascular elements did not appear to be affected. However, the phloem elements of treated plants stained darker or contained a darker deposit than those of the controls.

GROSS DAMAGE OF 3 CHLORO IPC

Effect on Leaves

The leaves of plants treated with 3 Chloro IPC became swollen in their intercalary regions and were highly brittle. A close examination of older leaves that were fully expanded showed little effect of the chemical treatments; however, closer scrutiny often revealed a slight distortion of the veins of the lamina just above the leaf collar. As the treated plants grew older, these mature or expanded leaves often became necrotic near the base of the sheath. The blades of leaves that were only partly exserted at the time of treatment

generally became tightly rolled and tended to die back from their tips. The whole exposed portions of these blades eventually became necrotic. Older leaves often remained green and little affected even after the unexpanded leaves appeared dead.

The month following fall applications of 3 Chloro IPC there usually appeared a bulb-like swelling at the base of the mother shoots. This enlargement became so pronounced that the outer most leaf would be pried open near the base of its sheath by the pressure of the expanding tissues beneath (Fig. 3). Besides this swollen area near the base of the shoot, there was often a second knot-like swollen area on the shoot about halfway between its base and the collar of the oldest expanded leaf. Handling the plant while it was in this condition could easily shatter the laminae of the partly exserted leaves or cause the shoots to snap in the region between the base and the lowest expanded leaf.

Effect on Roots

The root tips and young roots usually showed a relatively early response to the treatment of 3 Chloro IPC. This response was shown by a pronounced swelling of the root tips. Mature roots seemed little affected and close examination did not reveal any damage. However, young roots in the vicinity of the crown became noticeably enlarged (Fig. 4). When a study was made of roots in the bottom of the pots, it was found that the roots were able to translocate the 3 Chloro IPC relatively long distances through root tissue to affect the most

distant tips on the bottom of the pot. These were found to be much enlarged and distorted when examined one month after the plants were treated.

The over all effect of 3 Chloro IPC on the root system of the plants showed that it was quite restrictive to root development. Figures 6 and 7 and tables I and II show the striking effect of the chemical treatments on the root development in terms of root weight which was determined at the end of the growing season.

Effect on Buds

Certain buds were noticeably damaged by the chemical treatments. Some became greatly enlarged and were also quite brittle (Fig. 4). Buds that were damaged were observed to eventually turn dark and become necrotic as time after treatment increased. The buds near the base of the shoots seemed to be more severely damaged than those with a higher location. This was indicated by a tendency for those further removed from the base to swell less than buds at more basal positions. Usually as the position of the buds progressed from the base toward the top of the shoots the effect of swelling would be lost and the buds or young branch tillers would appear normal. Branch tillers that had reached the point of emerging from the sheath of the subtending leaf of plants treated in October were not present on the mother shoots that were sampled in November. Shoots collected in November showed a rather striking retardation in the growth and development of branch tillers, while branch tillers taken from mother shoots at the October 15th date of sampling gave the appearance of

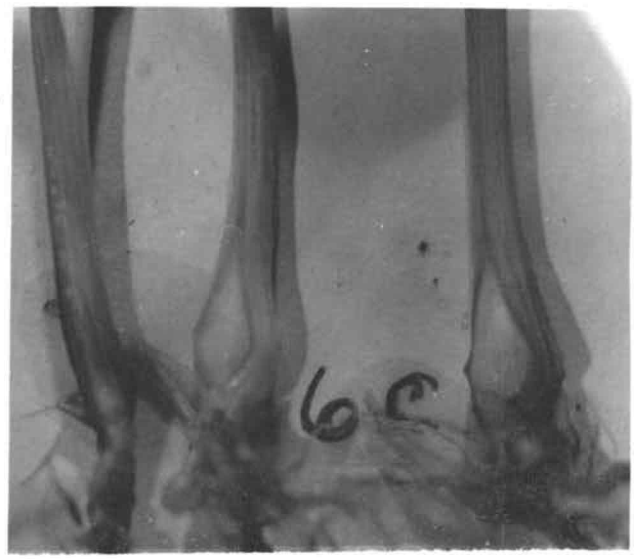

Figure 3. Bulb-like swelling at the base of leaves shown by shoots treated in October and sampled in November. Compare with control on the left.

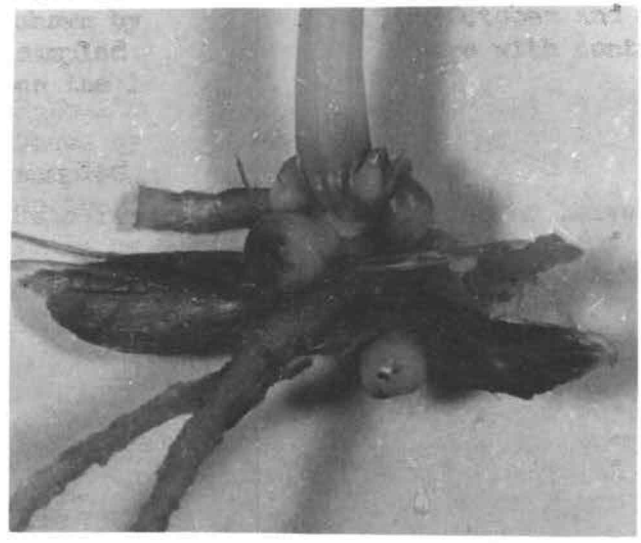

Figure 4. Typical 3 Chloro IPC injury to young buds and roots. Note the extensive swelling to these structures.

being relatively high in vigor.

The total accumulation of tillers present at the date of seed harvest depended on the time that 3 Chloro IPC was applied. Seed-producing plants were prone to stool less than non-seed producers. Of the plots producing no seed, those that had more time to recover from the application of 3 Chloro IPC produced the greatest number of shoots (Fig. 5).

CYTOHISTOLOGICAL STUDIES

Microscopic studies and examinations were made of internal tissues of sectioned materials. Structure and tissue of treated plants revealed that meristematic regions were quite noticeably more adversely affected by 3 Chloro IPC than tissues and structures made up of less active cells. Seasonal differences were also found to have a decided influence on the response of tall fescue to 3 Chloro IPC.

Effect on Leaf Tissue

The cytohistological effect of 3 Chloro IPC as influenced by maturity and activity of tissues is clearly indicated by studying its influence on various leaf tissues. Leaves which had only a part of their laminae exserted beyond the sheath of the next lowest leaf showed extensive cell enlargement in their growth regions, but were considerably less affected in other areas. The intercalary meristems at the base of the sheath and just above the ligule became greatly swollen (Fig. 8). Only the intercalary region of the sheaths

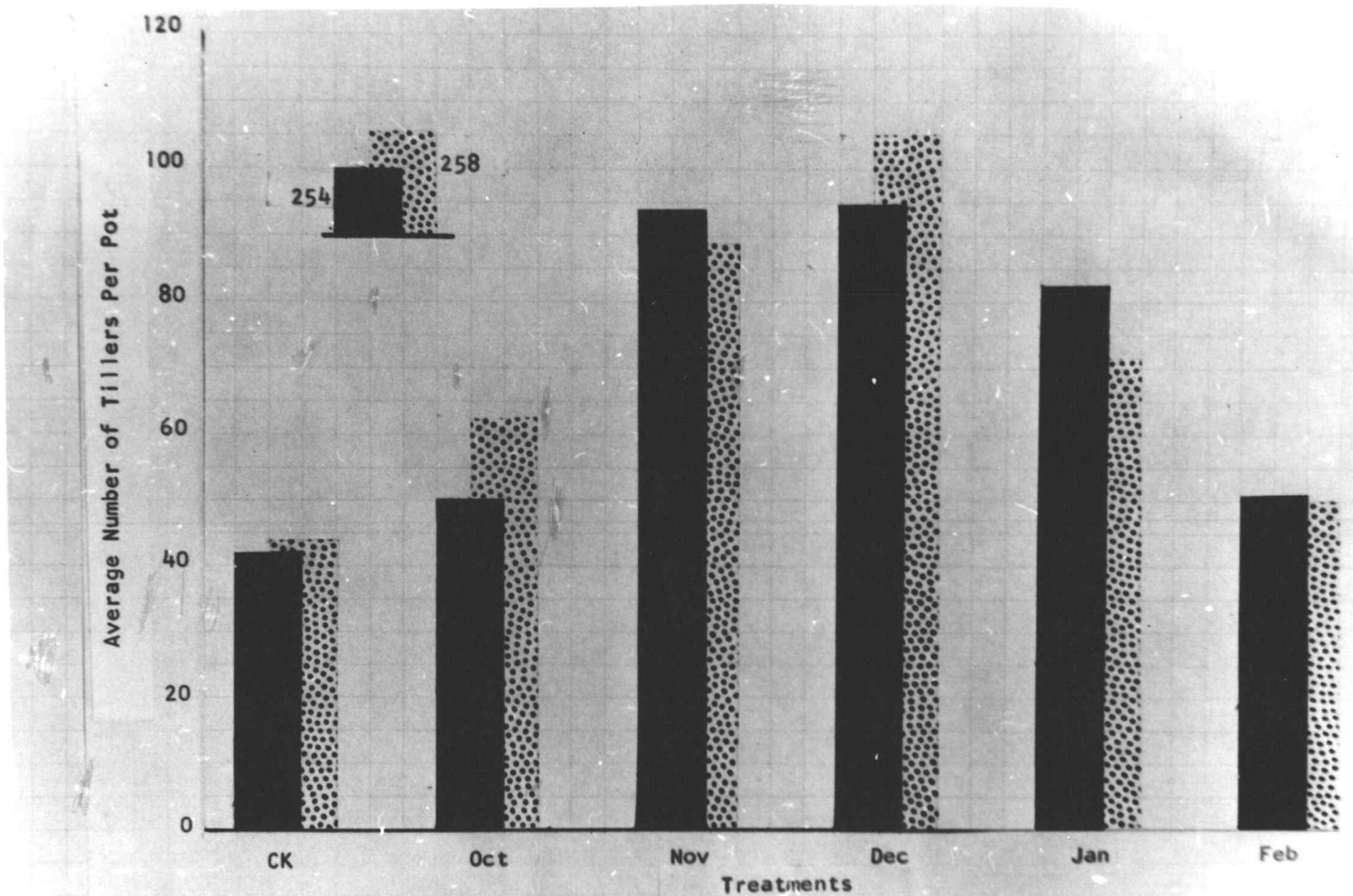

FIGURE 5: TILLERS COUNTED AT DATE OF HARVEST FOR GENOTYPES 254 AND 258.

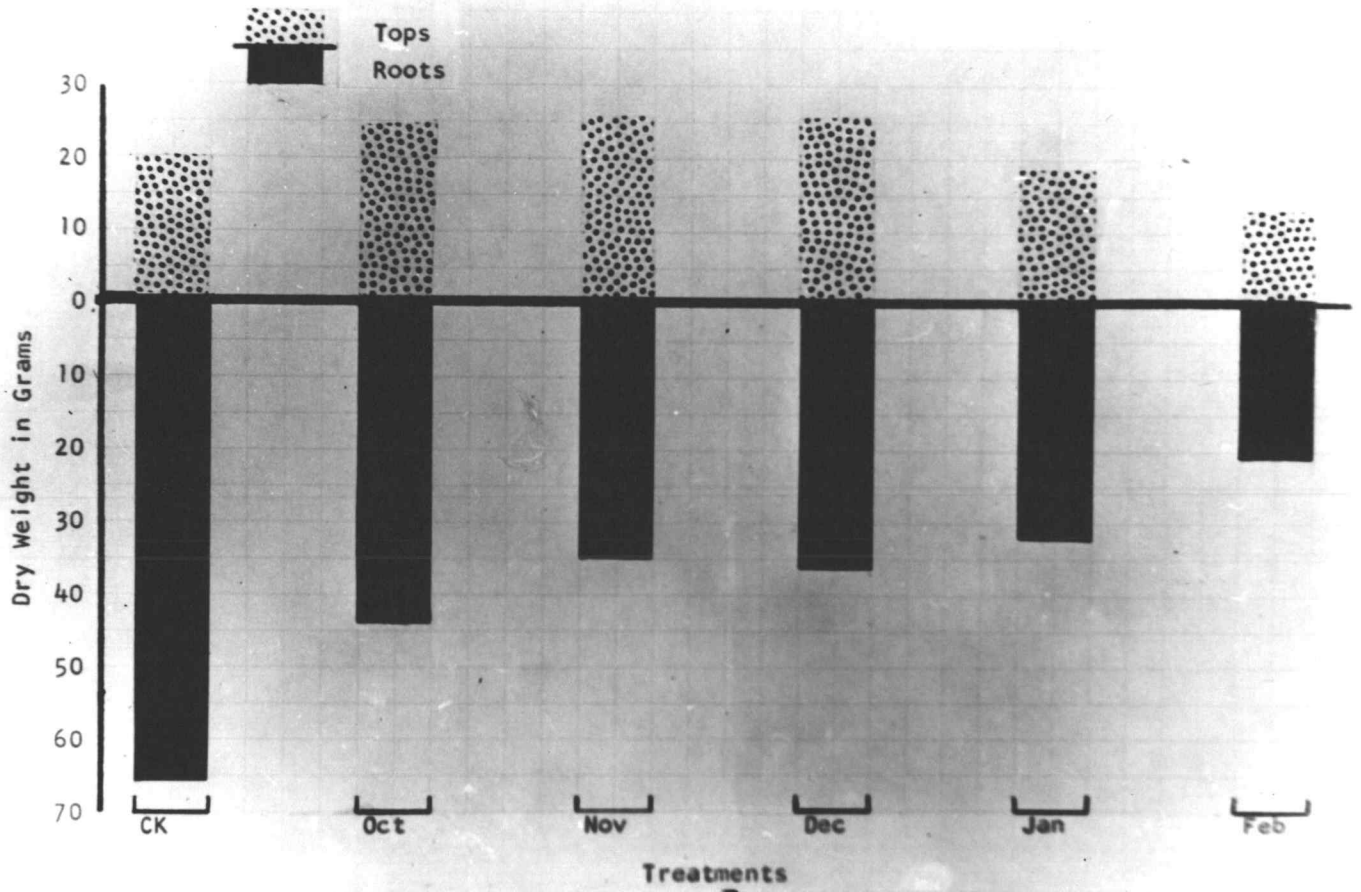

FIGURE 6: GENOTYPE 258. THE YIELD OF DRY MATTER IN GRAMS AS INFLUENCED BY THE VARIOUS TREATMENTS.

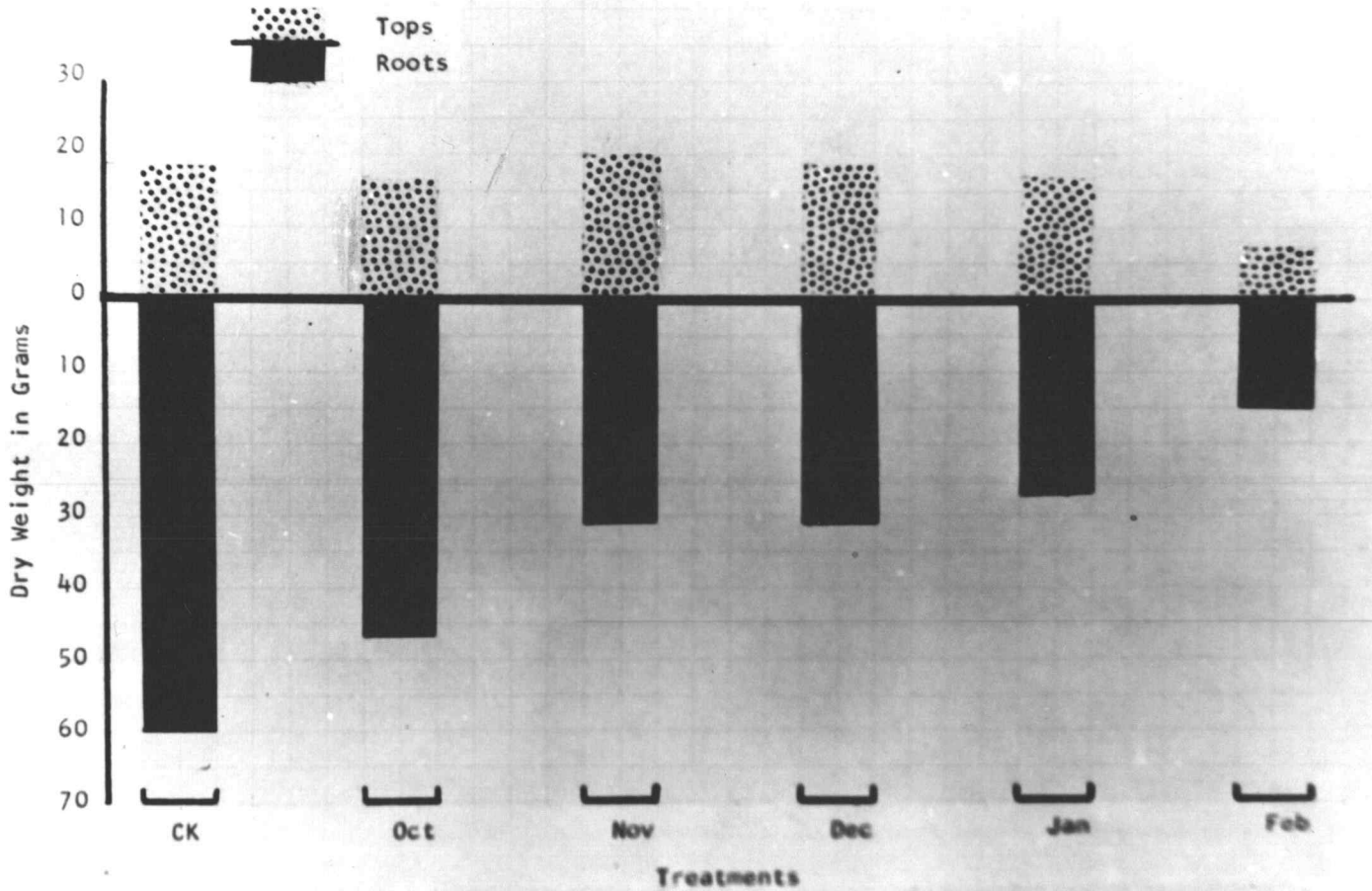

FIGURE 7: GENOTYPE 254. THE YIELD OF DRY MATTER IN GRAMS AS INFLUENCED BY THE VARIOUS TREATMENTS.

that were fully expanded possessed greatly enlarged cells. Young leaves not exserted but mature enough to extend beyond the shoot apex were generally swollen throughout their entire length (Fig. 9). Some showed a tendency to be more affected around the ligular region. Young leaves and leaf primordia still in the vicinity of the shoot apex were less affected and, at times, showed little or no effect of 3 Chloro IPC within the month immediately following application of the chemical. Fall and spring applications generally stimulated a quicker response of the various tissues to the chemical treatment.

Effect on Bud and Root Tissues

Buds at various stages of development often revealed no deleterious effect of 3 Chloro IPC, whereas the subtending leaves of the nodes below or leaves of the same phytometer were noticeably affected. On the other hand, young root tips showed the characteristic cellular damage that was common in meristematic tissue. These tips when examined whole with the unaided eye seemed to be enlarged over their entire length; however microscopic sections showed that this swelling was only apparent and that appreciable cell enlargement did not take place in the apical region of the root tip.

In comparing damage to buds and young root tips, the roots usually showed toxic effects of the chemical treatments before any toxicity was apparent to buds of the same relative location. When tips of adventitious roots and buds located at the same node were

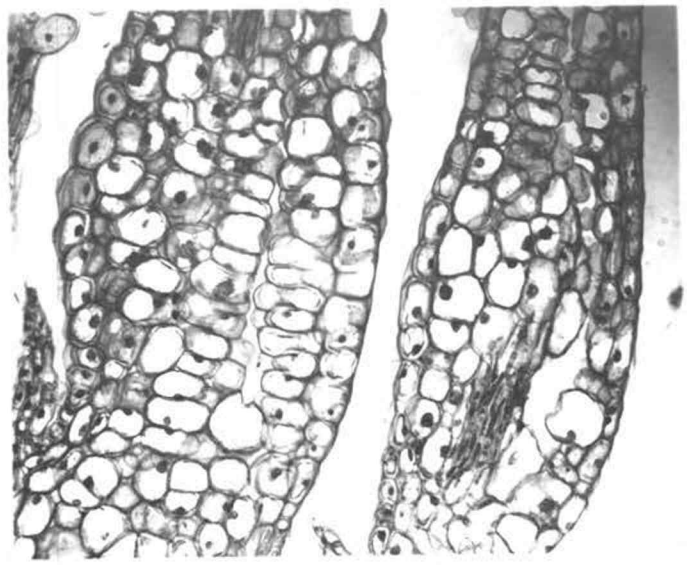

Figure 8. Example of sensitivity of meristematic tissue to 3 Chloro IPC. Figure shows enlarged cells of the intercalary meristem belonging to partially exserted blade.

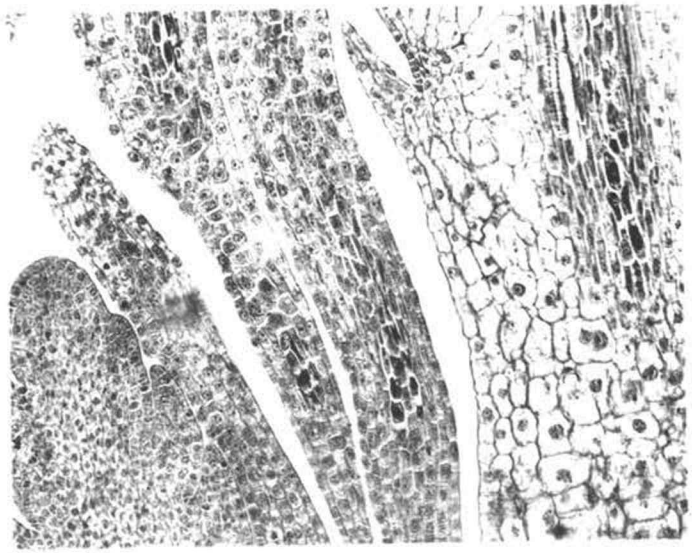

Figure 9. Next leaves inward from the leaf of figure 8. Entire leaf shows uniform response to 3 Chloro IPC. Younger leaves and shoot apex are little affected.

studied to ascertain the effect of 3 Chloro IPC on these structures, the root tips were often greatly enlarged while the buds appeared little, if at all, affected.

Seasonal Response to 3 Chloro IPC

The rate of progress and the extent of damage of 3 Chloro IPC to the various plant parts was noted to be greatly influenced by the time of application. The effect of 3 Chloro IPC on meristems and active tissues was greatly accelerated during the early fall months and the period of resumed activity in the spring. Plants that were treated in October and November generally proved to be extensively damaged one month after treatment. Applications in December and January stimulated little shoot response by the first collecting date the following month, and the bulb-like swelling usually present at the base of the leaves was entirely missing. Only the ocassional protruding tip of an adventitous root showed swelling that was characteristic of 3 Chloro IPC toxicity. These same conditions were also noted for plants treated in January. However, many of the shoots collected the month after the January application showed more visible exterior damage than was observed among the December treated plants a month after treatment. Sectioned material in some instances revealed minor damage to leaf tissue and swelling in the ligular region. A few specimens of the January-February period showed similar response to the chemical of that shown by fall-treated plants when both treatments were compared at an equal period of time.

Progress of Damage to Tissue

It was characteristic for plants treated with 3 Chloro IPC to show progressive deleterious effects of the toxicant. Tall fescue plants treated during October and November and collected for microscopic examination after three or four months appeared quite tattered. While the growing point itself appeared less damaged than the young leaves and surrounding tissue, it too appeared thin and empty of much of its contents (Figs. 10, 12 - A, C, D).

Treatments that produced little cytological damage during the December to January period became extensively damaged two months after treatment. Mother shoots maintained life for some time after being treated and were able to initiate floral primordia. Figure 16 shows the development of a nascent inflorescence as it appeared in March. This inflorescence was taken from a plant that was treated with 3 Chloro IPC during the previous month of February. Injury to the shoot apex during this period of accelerated activity was greater than for an equal period of time during mid-winter.

MORPHOLOGY OF THE SHOOT APEX

Organization

The shoot apex as it appeared in the fall of the year is pictured in figure 13. This is the usual angiosperm type that has been classified as type VII by Popham (51, pp. 249-270). Using the tunica corpis concept for describing the shoot apex of tall fescue, the normal vegetative apex consists of a relatively tall, well developed

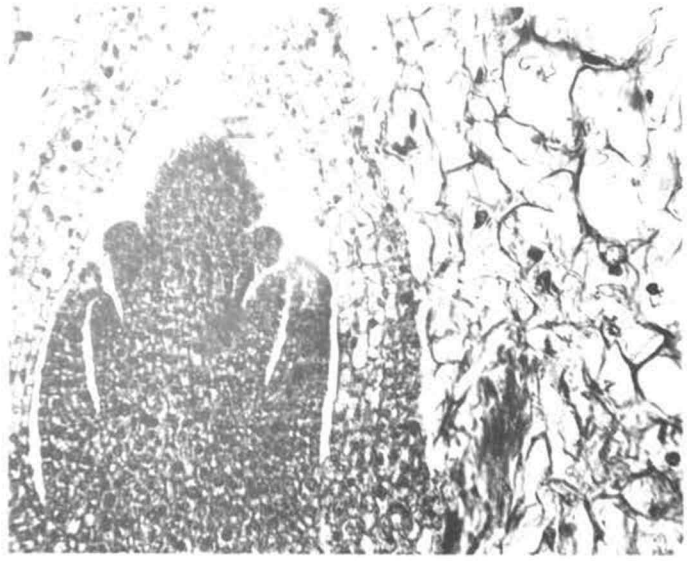

Figure 10. Disintegrated leaves and emaciated stem tip 4 months after October treatment. Although thin shoot apex is still intact.

Figure 11. Shoot apex showing rapid response to 3 Chloro IPC in spring. Young leaves and growing point show early effect of treatment. Shoot was treated in January and collected in March.

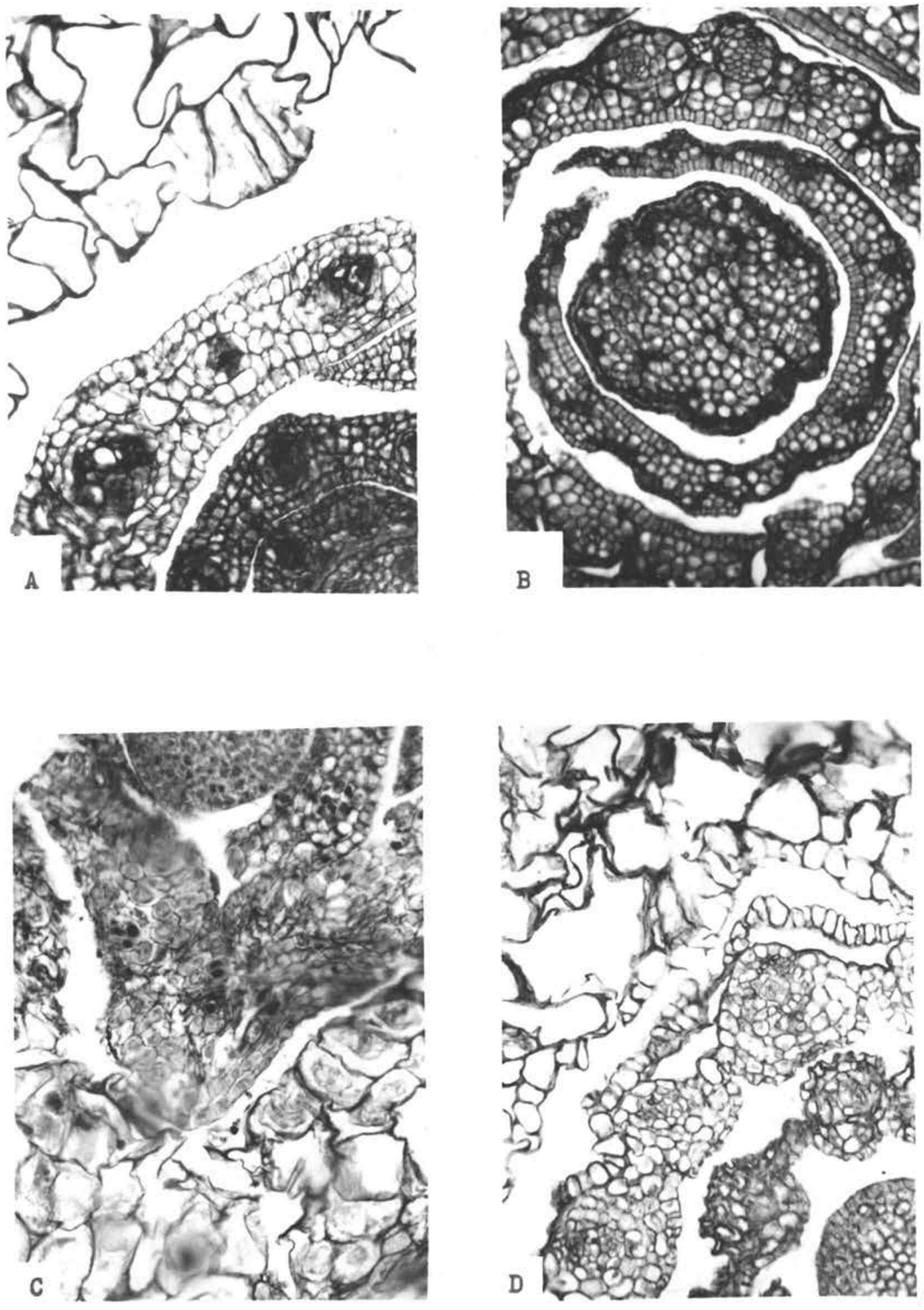

Figure 12. Cross section of shoot apex. A, C and D show effect of 3 Chloro IPC 3 months after application. Note less damage to inner leaves and stem tip. B shows winter injury to shoot apex.

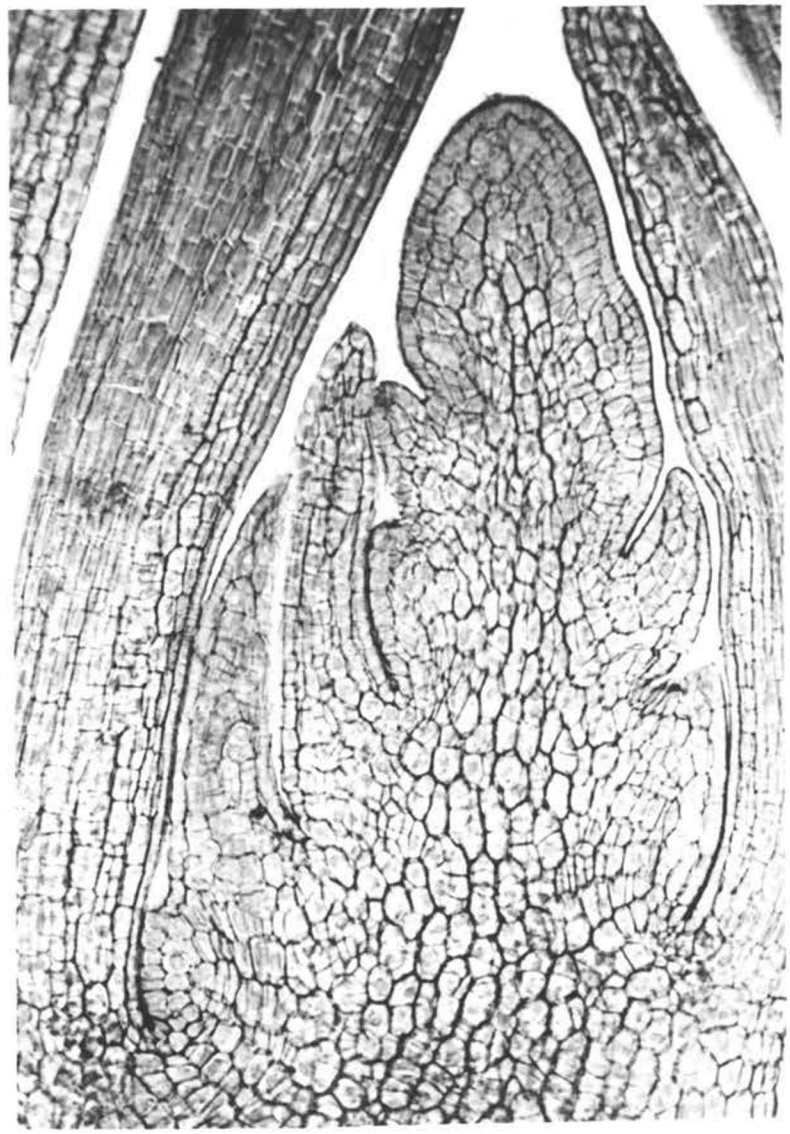

Figure 13. The appearance of shoot apex in October. Note high cone-shaped growing point, typical of grasses, and may be classified as Type VII according to Popham. There is a single layered tunica covering the corpus.

cone-shaped stem tip that is made up of a single layered tunica which perpetuates itself by anticlinal divisions and covers a central core or corpus in which cell divisions occur at random in all planes. No change was noted in this type of shoot apex until December, at which time there was a tendency toward a low, dome-shaped type. Some low, dome-shaped types were found to be quite marked and distinct in January. When shoots were collected on February 18th and examined microscopically it was found that a marked change had occurred in the shoot apexes of many tillers.

Initiation of the Inflorescence

Initiation of the inflorescence was marked by pronounced elongation of the apical meristem into an elongated slightly tapering cylinder. This signaled the transition of the shoot apex from the vegetative to the reproductive phase as shown in figure 14. At this stage of development, the leaf primordia continued to be laid down in rapid order toward the apex of the shoot. Branch primordia also started forming about this time in the axils of leaf primordia. This created a two-ridged structure which when reviewed in the distichous plane of the median longitudinal section gave a profile of a double-ridged lobe (Fig. 15). From this point onward the leaf primordia disappeared and floral branch primordia became the dominant feature of the shoot apex (Fig. 16).

There were wide variations in the stages of floral development of different shoots within the same clonal line and even within

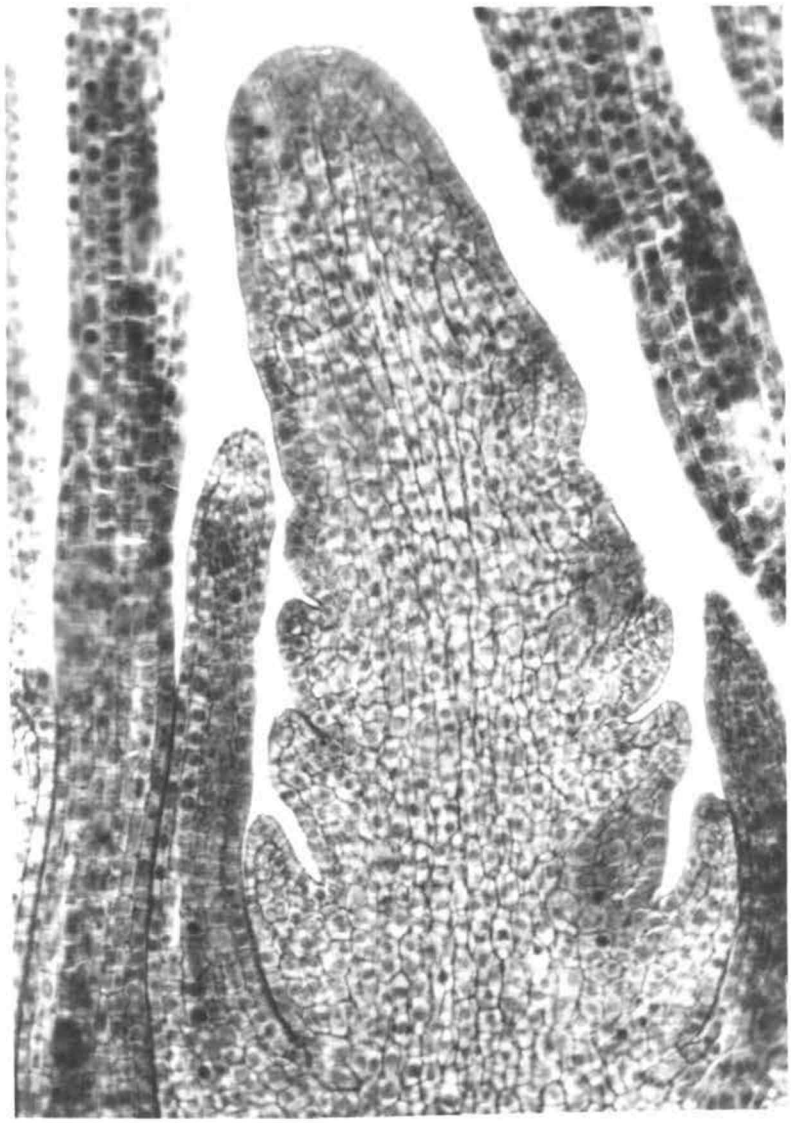

Figure 14. Transition of shoot apex from vegetative to reproductive phase. Shoot was collected from control treatment on February 18th and was the most advanced normal shoot apex found on that date.

Figure 15. The initiation of floral branch primordia in the axils of leaf primordia. This shoot apex is sectional in the longitudinal distichous plane and shows the profile, double ridged lobes of leaf and branch primordia in March.

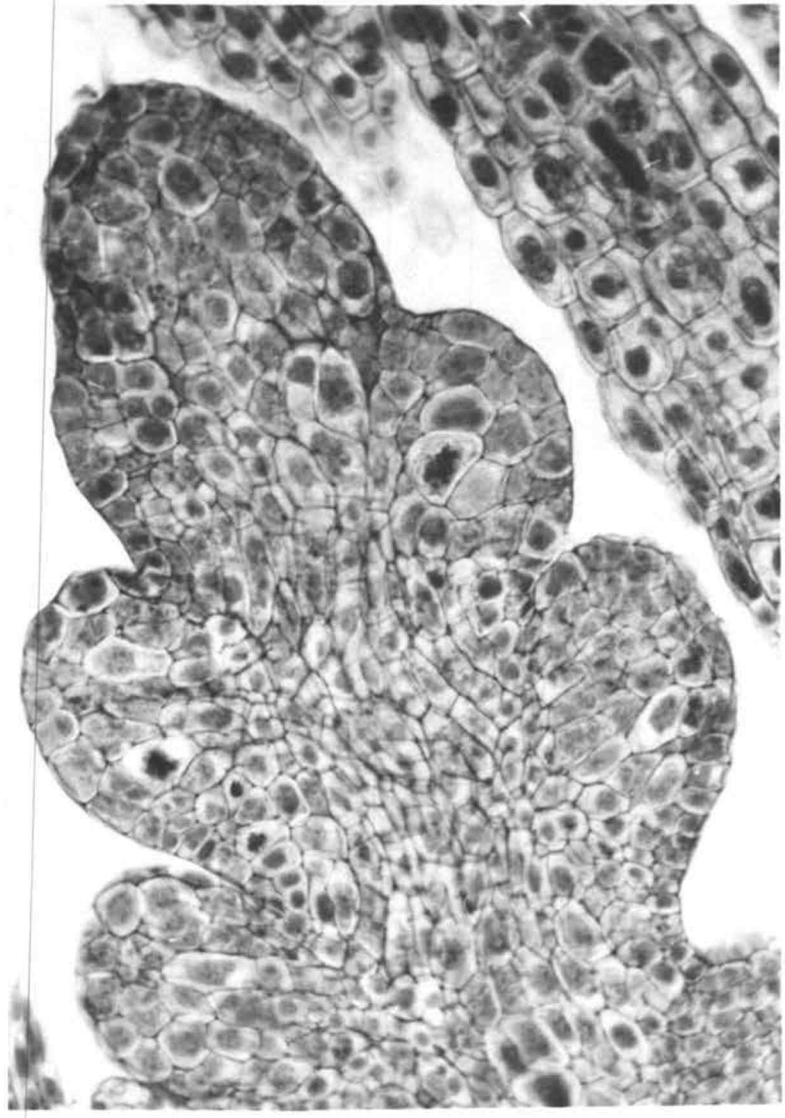

Figure 16. Most advanced stage of nascent inflorescence found up to March 17th. Leaf primordia have disappeared, floral branches are dominant features. At this stage, 3 Chloro IPC injury shows in apical region early. Enlarged cells with lobed nuclei show effect of chemical after one month.

the same plant. Figures 16 and 24 represent striking differences in the stages of development of shoots sampled from the same plant on March 17th. Figure 14 shows the most advanced stage of floral development of any shoot collected for study on February 18th. However, the majority of the shoots from untreated plots and those treated in January had begun to show signs of initiating an inflorescence. Plants treated in January were able to elongate even though these bore distinct signs of the harmful effects of 3 Chloro IPC. February treated plants were found to be even more active in initiating seed heads.

Shoot Types Sampled During Initiation Period

Five distinct types of shoot apexes were sampled during late winter and early spring when the plants were in the process of initiating seed heads. These may be listed as follows: (1) normal shoot apexes that were undergoing floral initiation (Figs. 14, 15); (2) shoot apexes showing signs of initiating an inflorescence but were injured by 3 Chloro IPC (Fig. 16); (3) shoot that had apparently succumbed to the effects of 3 Chloro IPC (Fig. 10); (4) shoot apexes with low smooth dome-shaped growing points that showed no signs of elongating or initiating an inflorescence (Fig. 17); and elongating shoots with necrotic tips (Figs. 18, 19).

Four types of these shoot apexes were found among the plants treated with 3 Chloro IPC in October. However, the majority of shoots sampled from the October treatment at this time as well as those treated in November and December were of the third type named. This type

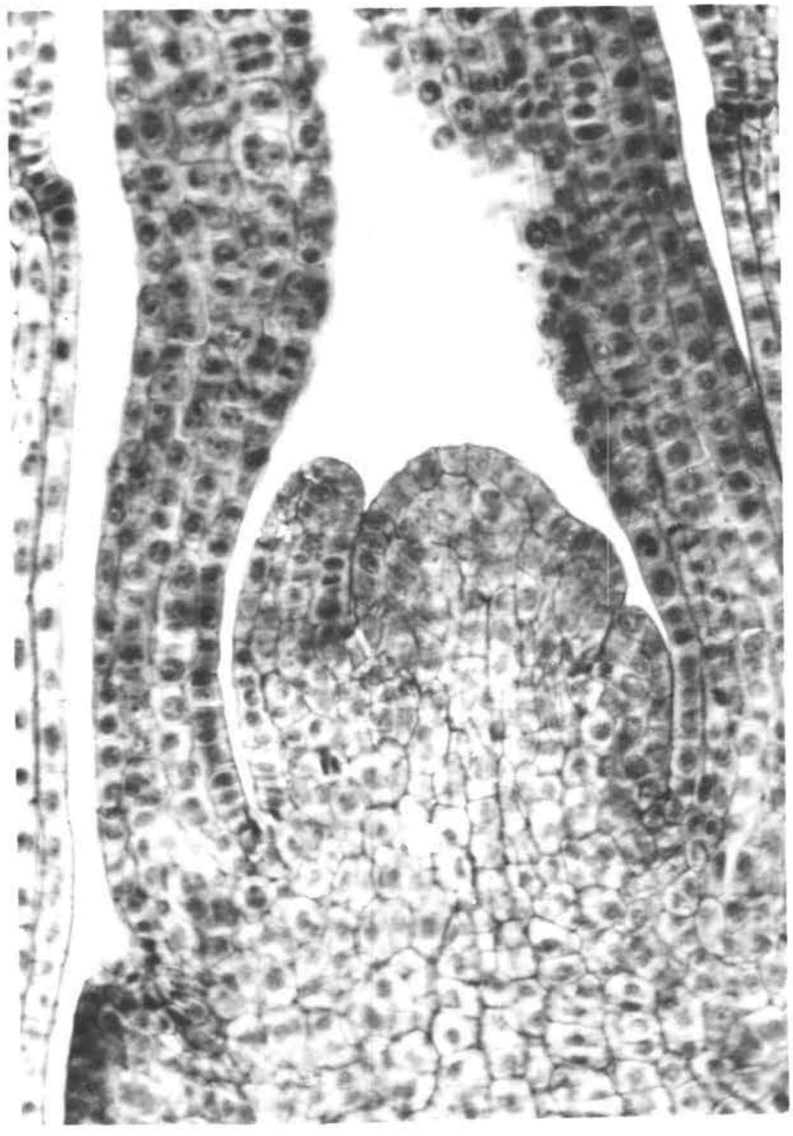

Figure 17. Typical sterile apex found on all treatments in late winter and spring. Low, dome-shaped apex indicates slow initiation of leaf primordia. This shoot was sampled in February from December-treated plants.

Figure 18. Winter injury to meristematic portion of Apex and leaves. Enlarged cell shows effect of 3 Chloro IPC applied one month previous to February 18th collecting date.

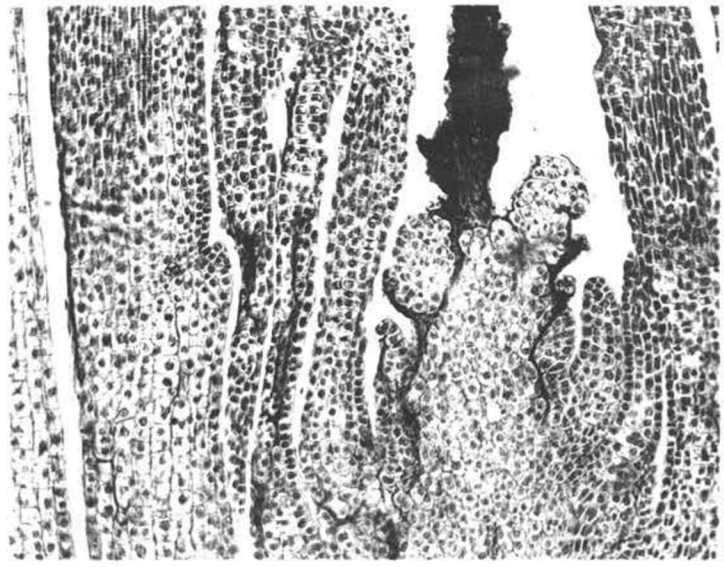

Figure 19. Necrotic tip of shoot from control plot on February 18th. Cells in leaves appear normal.

showed that damage by 3 Chloro IPC had progressed to the point that by spring no signs of life remained. No live shoots showing injury to the shoot apex by 3 Chloro IPC were found among plants treated in the fall and sampled during the period of floral initiation in the spring.

Non damaged shoots that initiated an inflorescence during the spring were confined to two treatments. These were the controls and the October date of chemical application. Only one shoot apex of this type was found among both genotypes of the October treated plants. The non-damaged shoot apex showing signs of forming a seed head was the most prevalent type among the check plots.

Shoots with necrotic tips and leaves suddenly appeared among samples collected in February and were also present in March. This is the fifth type described above. These necrotic types were commonly found during this time. They occurred among shoots taken from the controls and those plots treated with 3 Chloro IPC in January and February and once among December treated plants studied in February. The necrosis also appeared on young leaves in the vicinity of the shoot apex and in the shoot apex itself. Damage to the shoot apex usually started in the periphery of the apical meristem and would move inward toward the center and toward the base until most of the upper portion of the apical region became decayed or completely disintergrated. In spite of the missing tip, these shoots were elongating. Specimens showing signs of initiating an inflorescence, although damaged by 3 Chloro IPC, were found only among plots treated

Figure 20. Shoot with apex removed by necrosis. Precocious bud had developed in leaf axil. Stem shows extensive elongation. Shoot was harvested in February from plot treated in January with 3 Chloro IPC.

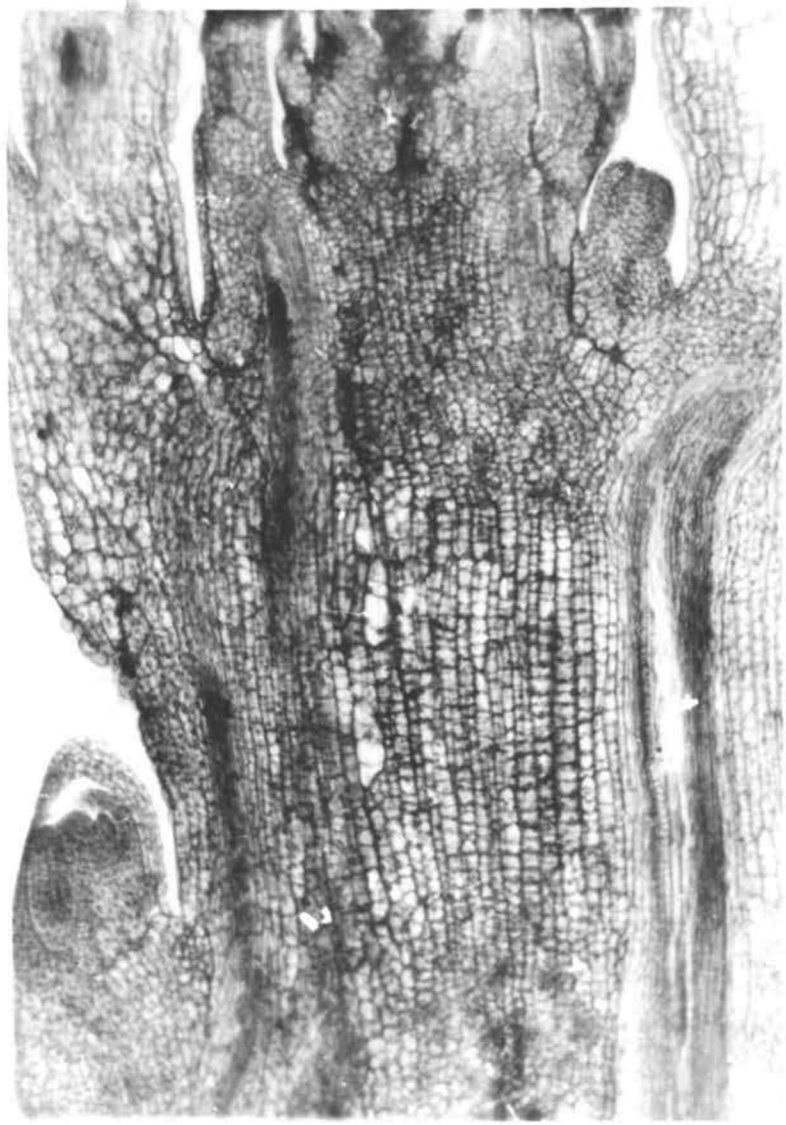

Figure 21. Winter injury to stem tip of shoot collected from a control plot in March. Shoot axis shows pronounced elongation and branch tillers in axils of upper leaves show early development.

in January and February. This is the second group described above.

There were also considerable numbers of vegetative shoots present among the control plots and also among plots of October treated plants. These are listed as type four above. Their shoot apexes were characterized by a low, dome-shaped apical meristem that remained vegetative and showed no signs of elongating or initiating an inflorescence. This type of shoot apex was observed among all treatments and was first noted among shoots collected in January.

In sharp contrast to this type of vegetative non-seed-head forming shoot apex found among the various treatments in late winter and early spring, only shoot apexes with high cone types were present during the fall months (Fig. 13). These types were also found in branch shoots sampled for examination in October just prior to their emergence from the leaf sheath as previously described, and shown in figures 22 and 23.

EFFECT ON SEED-HEAD FORMATION

Seed-head production was strikingly reduced by application of 3 Chloro IPC at the rate of 4 pounds per acre. Plants that were treated on October the 15th initiated relatively few seed-heads. The number of shoots that developed heads were far below those of the control plots. The results of these treatments are

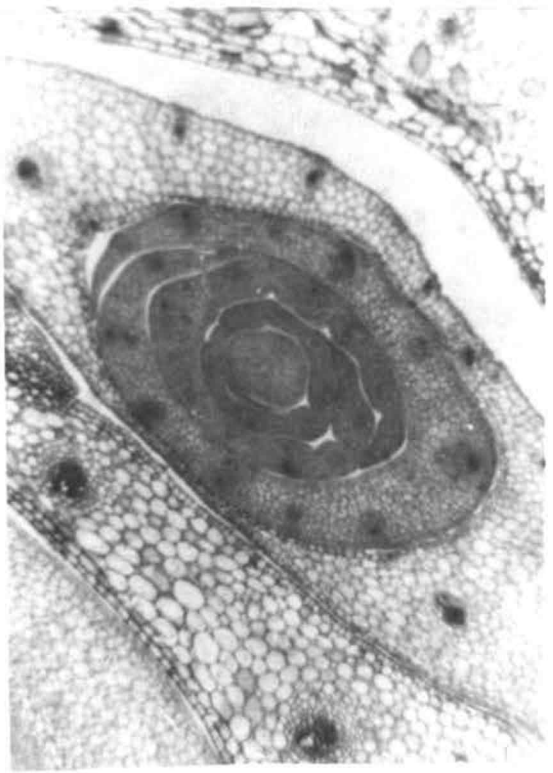

Figure 22. Cross section showing location of tiller in axil of leaf of mother shoot collected on October 15th.

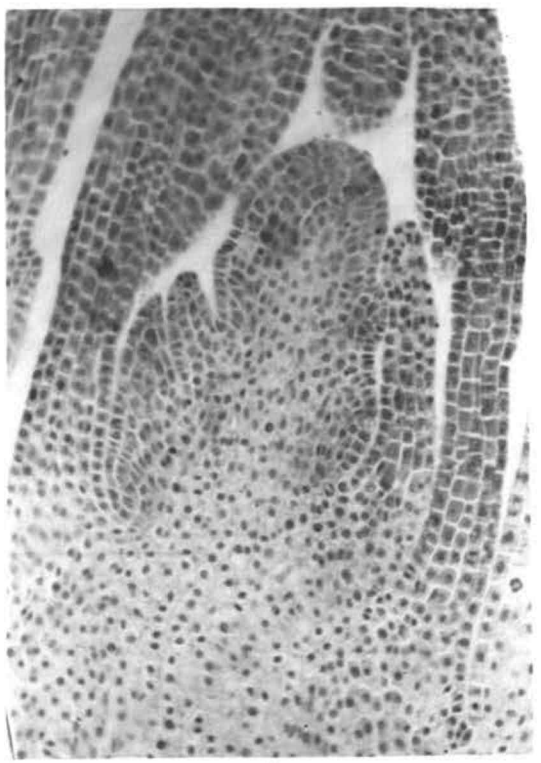

Figure 23. Longitudinal section of tiller in figure 20. Cone-shaped growing point typical of shoots collected in the fall.

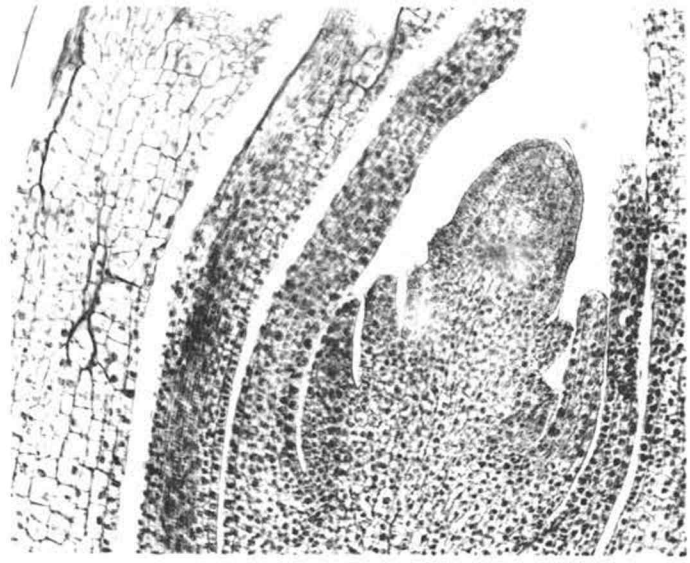

Figure 24. Effect of 3 Chloro IPC as influenced by plants state of growth. This shoot apex shows little effect of 3 Chloro IPC even though taken from same plant on date that young inflorescence in figure 16 was collected.

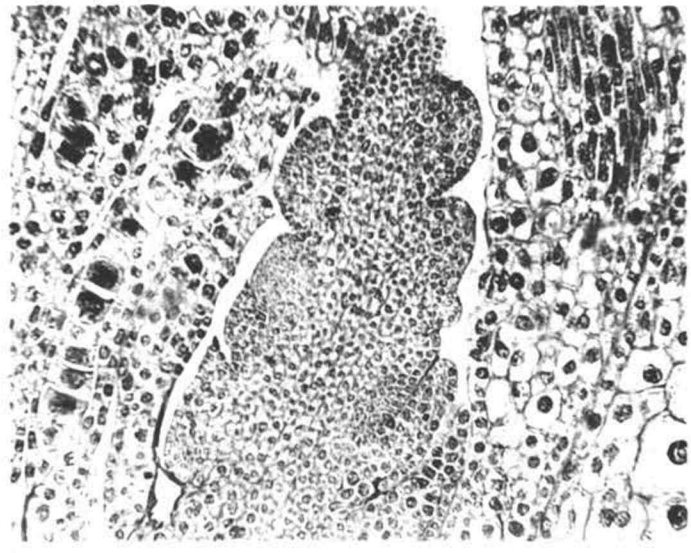

Figure 25. Shows wide difference in development of shoot apex and response to 3 Chloro IPC when compared with shoot apex above. The shoots are genetically alike and have the same treatment.

summarized in Tables I and II. Three heads per plot was the highest number initiated by plants treated in October. Some of the plots produced only a single head. This is considerably below the number of heads produced by the untreated plots which had an average of 25 and 21 for Genotypes 254 and 258 respectively.

Although there was a low number of heads produced by the plants treated with 3 Chloro IPC in October, it is significant that all plots initiated seed heads. This was not true for plants treated after October. In fact, only one pot produced seed when 3 Chloro IPC was applied after October. This was a plot of genotype 254. It produced 13 heads per plot which was considerably above any plot of the same genotype in the October treatment, but was also noticeably below the lowest number of heads in the control plots. No plants treated with 3 Chloro IPC after November produced seed.

There was a marked difference in yield per head between the two clonal lines. Genotype 258 showed a measured increase in seed yield per head over that produced by Genotype 254; however, both genotypes produced approximately the same total weight of seeds. This same relationship also existed between the genotypes for the October treatment. Yield per head obtained for the October treatment was found to be considerably above that of the control plots even though their total yield as pointed out above, was far less than the yield of the controls.

TABLE I

SUMMARY OF THE YIELD OF PLANT MATERIAL COLLECTED AT THE TIME OF SEED HARVEST FROM THE CONTROL PLOTS AND THOSE TREATED WITH 3 CHLORO IPC ON SUCCEEDING MONTHS FROM OCTOBER TO FEBRUARY.

GENOTYPE 258

Treatment	Replication	Seed Wt. (grams)	No. of Heads Per Pot	Heads Per Gram of Seed	Dry Wt. of Plant (grams)	No. of Tillers Per Pot	Top Wt. (grams)	Root Wt. (grams)
Control	1	6.45	36	5.60	93	41	20	73
	2	2.21	8	3.72	68	48	19	49
	3	2.63	15	5.60	84	34	17	67
	4	5.02	35	6.80	88	36	18	70
	5	2.59	10	4.86	97	61	26	71
Av.....		3.78	20.8	5.34	86	44	20	66
October	1	.05	1	.2	63	44	22	41
	2	----	---	----	---	--	--	--
	3	1.04	2	1.9	75	57	23	52
	4	0.65	1	0.9	80	84	29	51
	5	----	---	----	---	--	--	--
Av.....		0.58	1.3	1.0	72	63	25	44
November	1	----	---	----	50	64	21	29
	2	----	---	----	---	--	--	--
	3	----	---	----	72	88	25	47
	4	----	---	----	67	108	32	42
	5	----	---	----	75	101	33	42
Av.....		----	---	----	64	89	26	35

TABLE I CONTINUED

Treatment	Replication	Seed Wt. (grams)	No. of Heads Per Pot	Heads Per Gram of Seed	Dry Wt. of Plant (grams)	No. of Tillers Per Pot	Top Wt. (grams)	Root Wt. (grams)
December	1	----	----	----	55	102	26	29
	2	----	----	----	42	88	20	22
	3	----	----	----	73	92	29	44
	4	----	----	----	54	118	24	30
	5	----	----	----	77	127	32	45
Av.....		----	----	----	60	105	26	36
January	1	----	----	----	52	74	19	33
	2	----	----	----	50	65	15	35
	3	----	----	----	60	76	28	41
	4	----	----	----	40	64	12	28
	5	----	----	----	43	83	20	23
Av.....		----	----	----	51	72	19	32
February	1	----	----	----	38	71	15	23
	2	----	----	----	35	46	11	24
	3	----	----	----	49	62	19	30
	4	----	----	----	20	27	8	12
	5	----	----	----	27	44	10	17
Av.....		----	----	----	34	50	13	21

(---- missing value)

TABLE II

SUMMARY OF THE YIELD OF PLANT MATERIAL COLLECTED AT THE TIME OF SEED HARVEST FROM THE CONTROL PLOTS AND THOSE TREATED WITH 3 CHLORO IPC ON SUCCEEDING MONTHS FROM OCTOBER TO FEBRUARY.

GENOTYPE 254

Treatment	Replication	Seed Wt. (grams)	No. of Heads Per Pot	Heads Per Gram of Seed	Dry Wt. of Plant (grams)	No. of Tillers Per Pot	Top Wt. (grams)	Root Wt. (grams)
Control	1	4.73	26	5.50	69	31	15	54
	2	3.30	19	5.75	79	45	19	60
	3	3.64	23	6.30	84	52	19	65
	4	3.45	29	8.40	70	47	16	54
	5	4.08	30	7.35	87	40	20	67
Av.....		38.4	25	6.66	78	43	18	60
October	1	----	----	----	----	----	----	----
	2	0.96	3	3.12	65	78	18	47
	3	0.95	2	2.05	70	47	16	54
	4	0.30	1	3.34	75	47	17	58
	5	0.90	2	2.23	44	69	14	30
Av.....		0.62	2	2.66	64	50	16	47
November	1	----	----	----	54	93	19	35
	2	3.00	13	4.33	51	89	22	29
	3	----	----	----	64	104	27	37
	4	----	----	----	----	----	----	----
	5	----	----	----	46	87	15	31
Av.....		3.00	13	4.33	51	94	20	31

TABLE II CONTINUED

Treatment	Replication	Seed Wt. (grams)	No. of Heads Per Pot	Heads Per Gram of Seed	Dry Wt. of Plant (grams)	No. of Tillers Per Pot	Top Wt. (grams)	Root Wt. (grams)
December	1	----	----	----	54	86	21	33
	2	----	----	----	42	88	14	28
	3	----	----	----	47	79	20	27
	4	----	----	----	45	98	17	28
	5	----	----	----	60	93	23	37
Av.....		----	----	----	50	95	19	31
January	1	----	----	----	45	96	20	25
	2	----	----	----	43	86	20	23
	3	----	----	----	43	66	16	27
	4	----	----	----	36	76	13	23
	5	----	----	----	50	89	19	31
Av.....		----	----	----	43	83	18	26
February	1	----	----	----	28	43	9	19
	2	----	----	----	24	50	10	14
	3	----	----	----	23	58	6	17
	4	----	----	----	16	49	7	9
	5	----	----	----	23	55	9	14
Av.....		----	----	----	23	51	8	15

(---- missing value)

DISCUSSION

In this study 3 Chloro IPC was employed as an aid in observing the effect of various factors on the development of the seed head in tall fescue. The effect of 3 Chloro IPC on the growth processes of tall fescue found in this experiment was in some way typical of the effects of carbamates in general on grasses. However, in some respects, it differs in the degree of injury. This was partly due to the tolerance of tall fescue to the chemical and also to the rather low concentration applied.

Three Chloro IPC is essentially a mitotic poison and therefore, as expected, was especially injurous to meristematic tissue. This was shown to be true in that apical and intercalary meristems and provascular tissues were most adversely affected by 3 Chloro IPC treatments.

Effects of 3 Chloro IPC on Various Plant Parts

The effect of 3 Chloro IPC on the plant in general was typified by the effect on leaf tissue. The leaves themselves range from mature to the primordal stage, and in a single leaf the cells and tissues showed wide differences in stages of maturity. Starting with the outermost and therefore, most mature leaves, there was found comparatively little or no damage. However, an examination of these leaves showed that they could be grouped into three distinct tissue areas based on the maturity of the cells found in these respective areas. The separate regions of the mature leaf that were considered

here are the upper blade, and the intercalary regions of the blade and sheath. Since these areas showed an increasing sensitivity to 3 Chloro IPC in the direction from the top of the blade toward the base of the sheath and since this is also the order in which the leaf matures, this direction of development logically shows a significant relationship between the degree of injury and the maturity of the tissues involved.

In a like manner, the effect of the chemical on the various leaves in relation to their different stages of development which showed an intensification of 3 Chloro IPC toxicity in an inward direction, further indicates the relation between sensitivity to 3 Chloro IPC and the degree of maturation and activity of tissues. This was shown by comparing the next oldest leaf, which had only partly emerged from the "bud", with the fully expanded leaf that was described above. The same relationship exists between the various parts of the leaf, but the effects of the chemical on these areas were much more pronounced than it was in the same areas of the older leaf. Note the extensive swelling in the meristematic region of the blade shown in figure 8. Examination of the next leaf toward the interior showed that all the cells were relatively active and therefore, were generally enlarged uniformly throughout the length of the leaf. The slightly more noticeable swelling around the ligular region was due to the greater activity of the cells in this region of the intercalary meristem (Fig. 9).

Effect on Tissues as Influenced by Vascular Connection.

Observing the younger leaves in figure 9 previously referred to, it is seen that this leaf even though less mature and more meristematic than the next outward leaf shown, appears less damaged by chemical action. The only major damage seen is along the immature vascular tissue. The still younger leaf which had just "over-topped" the shoot apex showed even less damage and was relatively unaffected. At this point, the younger leaves indicated a reverse in sensitivity to the 3 Chloro IPC treatment in an inward direction. This condition does not result from any greater degree of tolerance by these younger structures. The younger, more meristematic parts, because of their immaturity and greater activity, would have shown increased response to 3 Chloro IPC if it had been possible for the chemical to have moved into these tissues. However, decreased absorption on the part of these younger structures of the shoot was the major reason for their relatively less response to the 3 Chloro IPC treatment. The young leaves, young branch tillers and the shoot apex were little affected by 3 Chloro IPC in the early stages of injury to the plant.

As pointed out by Freed (28, pp. 25-26), 3 Chloro IPC moves through the soil with great difficulty and this evidence points to the fact that it also moves through plant tissue with difficulty and needs fairly well developed vascular tissue to be translocated to tissue areas that are somewhat removed from the point of absorption

of the chemical. The difference in response of buds more distant from the base of the shoot as compared to the more serious damage sustained by buds near the base, indicated a difference in translocation of the chemical into the respective buds. No doubt, this was due to unlike maturity of their vascular tissues. It was also noted that in comparing the degree of toxicity of 3 Chloro IPC upon buds and roots, the relatively greater damage that occurred to young roots soon after 3 Chloro IPC was applied could be attributed to a difference in the development of their vascular tissues. In comparing the origin and vascularization of these two structures, it may be pointed out that the root is endogenous and is initiated in tissue near the periphery of the stem's vascular strands (18, p. 503). The vascular system of the root is found to be continuous and approaches to within a fraction of a millimeter of its apex (18, p. 489) and (18, p. 492). In contrast, the vascular system of the shoot differentiates largely or entirely in relation to the leaves (18, p. 511), with buds developing later in the superficial tissue of the more meristematic region at the base of the internode, with these branch shoots establishing vascular connections with the main axis much later than the leaves that subtend them. In view of this fact, and the knowledge that 3 Chloro IPC is easily fixed, one may explain the difference in the time of response of bud and root meristematic tissue to the toxicity of this chemical. 3 Chloro IPC is rather mobile under some conditions, because it was able to move relatively long distances through root tissue. Root tips as far as 6 inches from the soil's

surface showed marked effects of the chemical when they were examined the month following treatment. Again, this shows the apparent relation between the movement of 3 Chloro IPC within the plant and the extent of development of the vascular system.

The effect of 3 Chloro IPC on plants, as influenced by activity, was obviously not confined to separate tissue groups or organs of this plant, but to the entire plant as well. The promptness of response of the tall fescue to the 4 pound rate of 3 Chloro IPC was found to depend on the season of application. During a period of time in December and January, the plants decreased their activity and became relatively dormant, because shoots that were harvested for cytological examination on January the 15th showed none of the usual exterior damage to leaf tissue. Not only was the bulb-like swelling missing due to a lack of swelling in the intercalary areas of the outer leaves, but cell enlargement commonly found in younger leaves was significantly reduced. Time was also an important factor here because on February 18, two months after the December treatment, there was a marked increase in chemical injury and the plants showed damage that was typical for the more active periods, one month after 3 Chloro IPC was applied. Shoots of the January to February period were considerably more active than those of the December to January period, which indicates that the initiation of floral primordia during this period came at a time of greater activity by the entire plant.

The Shoot Apex and Seed-Head Development

A study of the various shoot apexes present in the plant population during late winter and early spring gives an over all picture of the various factors that have had a bearing on seed-head formation by the different treatments, and the conditions influencing seed-head development in tall fescue in general. Necrotic tips are the first of these to be considred (Figs. 17, 18, 19, 20). Here the damage to the shoot apex and to the leaves undoubtedly was due to winter injury. The suddeness with which this condition appeared among the shoots sampled in February indicated that it is associated with or related in some way with floral initiation and the increase in activity of the plants studied. It is significant to note that samples taken at this time for examination were the first to show definite morphological signs of floral initiation. Initiation is known to begin in the Alta variety of tall fescue in this area of the Willamette Valley around the first of February (77, p. 15). The necrosis appeared in the meristems and provascular tissues of the shoot apex and young leaves. Initiation of floral primordia by these necrotic tips took place considerably in advance of those on shoots that succeeded in producing seed heads. Shoot apexes in this advanced state of maturation along with the meristematic leaf tissues would be quite susceptible to winter injury; consequently, they would likely be killed by the occurrence of sudden cold periods during this time.

Shoots affected by this necrosis or winter injury were sampled from the February date to the end of the collecting period and made up approximately 40% of those taken from the check plots and the January and February treatments. A necrotic tip was also observed, on one occasion, among plants that were treated in December and collected in February. The fact that this type of necrosis was not observed among plants treated with 3 Chloro IPC during October and November, before or after February, and that it occurred among check plots with the same frequency as it did among the treated plants, indicated that 3 Chloro IPC was not responsible for its occurrence. There could possibly have been a secondary effect of 3 Chloro IPC on a necrotic shoot of this type, but even this is doubted, because no difference in the extent of necrosis could be distinquished for either treated or untreated shoots. However, treated and untreated shoots that were "winter damaged" could easily be distinquished from each other, because the non-necrotic tissues of treated plants still showed the typical symptoms of 3 Chloro IPC injury (Fig. 17).

Shoots with necrotic tips generally showed morphological signs of undergoing transition or having entered the reproductive phase of their cycles, and evidently, they were physiologically in a state of readiness for seed-head production. For the most part, these shoots appeared to be considerably more advanced in maturation than the normal shoots that were initiating an inflorescence at this time. As could be seen from the residual necrotic material

that remained, the shoot apexes of these tillers had, undoubtedly, already entered their reproductive phase. Sass also reported that flower primordia initiated prematurely by brome grass did not survive adverse climatic conditions (59, p. 517). Besides elongation of the shoot apex, there was marked elongation of the main axis of the shoot. According to Allard and Morgan, climatic conditions that affect flowering, affects stem elongation as well (3, p. 226-227). In a study of Avena, Purvis came to the conclusion that stem elongation cannot take place under conditions adverse to flowering (52, p. 928).

These shoots gave every indication of continuing their growth processes at the time they were harvested for cytological examination. It is probably safe to assume that their physiological condition was not without apical control. Even though the apex of the main axis seemed non functional, the next highest bud on such a shoot appeared distinctly precocious and no doubt, had taken over the duties of the necrotic apex (Figs 20, 21).

Floral Initiation by Treated Shoots

The mother shoots of tall fescue were found to be sufficiently tolerant to 4 pounds per acre 3 Chloro IPC to live for a month or possibly longer after the chemical was applied. Shoot apexes of plants treated in January appeared on a par in their state of maturation with those of the control when they were compared at the stage of the February harvest date. This was also found to be true for shoots treated in February and harvested in March. In fact, the

most advanced stage in the development of a seed-head found in cytologically examined material was a nascent inflorescence from plants treated in February and harvested in March (Fig. 16). There are indications that at certain seasons the originally treated mother shoot might have lived for as long as two months after the 3 Chloro IPC treatment. The December treatments showed evidence that some mother shoots lived until February and were able to show signs of initiating an inflorescence during this time. There was also a single case showing typical tip necrosis which was attributed to winter injury of shoots undergoing floral initiation. The fact that treated mother shoots were able to live from December to February is due to the relative inactivity of the plants during this period. 3 Chloro IPC applied to plants while they were in a more active state of growth were observed to cause as much injury in one month as was produced in two months when applied to tall fescue in December, and for an equal period of time, would be more lethal during the latter period of greater activity. January treated plants that were sampled in March showed no indication of having matured beyond the point at which they were observed in February. However, they exhibited considerably more injury than was noted at the end of the first month and were judged incapable of further maturation processes.

Normal Apexes

Although the control plots were the principal sources of normal

shoot apexes, these potential flowering apexes occurred on several occasions among the October treated plants. A study of the conditions under which normal shoot apexes were produced by plants treated in October furnishes one of the key factors in explaining how October treated plants produced seed heads. The first observance of a normal growing point among the treated shoots was taken in December from the October treatment. This shoot type appeared to be as free from damage by 3 Chloro IPC as the control shoots and looked to be normal in every way. The cells in the apical region were seen to be actually dividing with no apparent deviation from the natural pattern of activity. In contrast to this shoot, the other one harvested from the same pot possessed the typical 3 Chloro IPC injury that was characteristic of all the other treated shoots harvested up to this time. The difference in the toxicity of 3 Chloro IPC to these shoots cannot be explained on the basis of the application of unlike treatments, because they both came from the same pot to which the chemical was applied in sufficient solution to provide uniform chemical treatment to the entire surface of the soil. The difference in the effect of 3 Chloro IPC on the two shoots in all probability came from their unequal absorption capacity at the time of application. The decreased absorption of lethal quantities of 3 Chloro IPC by one shoot was evidently due to its less mature stage of development. As pointed out previously, the ease with which 3 Chloro IPC moves into tissues or organs depends on their vascular connection. Thus, it

was indicated that the shoot which showed no deleterious effects of the chemical had not developed to the point at which its vascular tissue was sufficiently matured to absorb harmful qualities.

Even the normal appearing shoots were not entirely free from the presence of 3 Chloro IPC. A root primordium was found in an apparently normal shoot which possessed irregular or lobed nuclei and increased numbers of nucleoli. This was suspected, since the root primordia are located deep in the interior of the stem next to the vascular system of the main axis. Because of location and the meristematic activity of root primordia, these structures would naturally be the most sensitive indicators of small quantities of 3 Chloro IPC.

As to when 3 Chloro IPC was taken into the normal shoots becomes a matter of concern. Most likely, it came from residual quantities present in the soil when the young shoots had developed sufficiently to absorb it. 3 Chloro IPC at the rate of 4 pounds has been found to remain in the soils of the Willamette Valley for as long as six weeks (28, pp. 25-26). Since the breakdown in chemical structure is responsible for the removal of 3 Chloro IPC from the soil (29, p. 2), it is hardly likely that this chemical could be held in plant tissues without being broken down or altered in form. At the time of absorption, the concentration of 3 Chloro IPC was obviously rather weak because no indication of its presence could be determined in tissues other than in root primordia. Even in root primordia, certain cells were able to undergo normal cell

division. Several early telophase divisions were seen in a root primordium in which the spindle substance was definitely organized, because there was distinct poleward orientation of fine fibrils.

Shoots from the October treatment that showed early signs of having the potential to form an inflorescence evidently continued to develop normally. 3 Chloro IPC also had no ill effects even at the formation stage of nascent inflorescences, and their young floral parts did not differ from those of the control in their cytological aspects. However, this does not mean that the shoots which are able to develop normally are free of 3 Chloro IPC. Tall fescue has tolerance to certain concentrations of this chemical that permits the shoot to continue its development without ill effect on the shoot apex even though low concentrations of the chemical may be taken into the tissues. Since the shoot apex is removed from the immediate area of absorption, it is unlikely that small residual concentrations will affect the normal activity of this structure to any degree. As pointed out in a previous example, the deleterious affect of 3 Chloro IPC on mitosis diminished even in the young root primordia when the concentration was low. This was shown by the ability of many of the cells in the root primordia to undergo normal mitosis, even though others had irregular shaped nuclei and increased numbers of nucleoli.

If shoots are able to survive the killing action of 3 Chloro IPC and form seed heads, the seed has been found to show no apparent ill effects of the treatment. Bayer found no maleffect of 3 Chloro

IPC on the seed heads produced on treated plots, and seed germination was unimpaired (8, p. 51). The relative infrequence of finding normal shoots among plants treated with 3 Chloro IPC in October is hardly accounted for by the size of the sample taken, but can most likely be attributed to the severe freezing weather that occurred after this treatment was applied. Damage to buds and tissues was unusually heavy. This unseasonably cold weather also came at a time when the plants had not become hardened and were quite active, because they had been supplied with high levels of nutrients and had been grown under greenhouse conditions until September 17. Under more normal conditions, the number of sampled shoots capable of forming seed heads probably would have been higher. Bayer reported no apparent effect of 3 Chloro IPC on seed production in tall fescue when it was applied in October (8, p. 23).

Besides the normal type of shoot apex as described above, those that remained vegetative were deemed to have had significant bearing on seed-head formation in tall fescue. Since this type was first observed in January and occurred with increasing frequency thereafter, the environmental conditions under which they developed were judged to have been responsible for their decided alteration from the fertile shoot apexes in morphological development.

It is evident that the rate at which a tiller initiated leaf primordia largely determined the morphology of its shoot apex. These reproductive sterile shoots were found to be initiating leaf primordia at a considerably slower rate than those present in October. The rate

of initiation was determined by counting from the youngest leaf primordium to the one just beneath the growing point. Leaf counts taken on fall plants ranged from 4-6 and from 5-6 for genotypes 258 and 254 and gave an average of 5.0 and 5.5, respectively, for these clonal lines. By comparison, dome shaped types that showed no inclination to produce seed heads usually had 2 or 3 and occasionally 4 leaf primordia beneath the shoot apex.

This strongly suggests that the season of the year in which a tiller is produced determines the morphological aspects of the shoot apex and hence its maturity and morphological capacity for floral initiation. Checking this point further it is noted that these apparently reproductive sterile shoots showed no visible effect of 3 Chloro IPC when the chemical was applied in October and November. This indicates that these shoots probably matured after the residual effect of the chemical had been dissipated. However, time in itself is not considered critical in the maturation of the shoot apex. The environment under which the tillers were initiated and developed seemed to have been the ultimate determining factor of their developmental potential (66, p. 25) and (53, p. 580). Purvis (52, p. 953) indicated that the differentiation of floral primordia in winter rye was subject to an interaction between day length and temperature during germination which determined the minimum number of leaves formed before floral primordia were initiated.

In this experiment, the young tillers of tall fescue examined in October, just prior to emerging from the sheath (Figs. 22, 23),

usually had four leaf primordia beneath the shoot apex. Even at this early stage of development, October tillers already possessed a high cone shaped apex similar to those of the mother shoots of the same period. This type of growing point was indicative of rapid leaf initiation. It thus appears that the reproductive potential of the tall fescue shoots was determined at an early stage in their development and that certain environmental conditions are necessary in order that they may reach the required state of readiness. In a like manner, Purvis (53, p. 580) reported that the minimum number of leaves necessary for "ripeness to flower" in winter rye was reached two weeks after germination and that most of these were present in the dormant embryo.

Up to this point in this discussion, the reproductive capacity of a shoot was considered in terms of sexual reproduction. However, the elimination of flowering by the application of 3 Chloro IPC did not eliminate future sexual reproduction in these plants. Even though the treatments after October were incapable of flowering, they were quite prolific vegetatively, and when given sufficient time to recover from the killing effect of 3 Chloro IPC, their vegetative activity was stimulated beyond the treatments that produced seed-heads (Fig. 5). This increased vegetative activity accounts for the high seed-yielding capacity by this crop the year following 3 Chloro IPC applications (56, p. 51). Even though in the spring of the year in which the treatments were applied, the individual shoots were sterile from the standpoint of sexual reproduction, the tillers produced

subsequently by these shoots over the summer and fall would have had the same potential for seed-head formation as those propagated from plants that were fertile. It is quite likely that the original shoots present in the spring would have died or become non-functional during the late summer or early fall; however, their tillers should have developed the same capacity to reproduce sexually because all plants possessed the same inherent capacity for sexual reproduction and any deviation from this potential would largely be determined by the environmental conditions under which the shoots themselves developed. The environment under which their parents developed would have no effect on the capacity for flowering of the daughter shoots.

From the considerations presented in this experiment it appears that in tall fescue the shoot apex must reach a certain state of readiness or "ripeness to flower" before it has the potential or capability for producing a seed head. This state of potential can be ascertained by the rate of leaf initiation, and hence, by the morphological aspects of the shoot apex. Because this state of "readiness to flower" is influenced by environmental conditions, it appears that the terminal date in any locality could be altered by manipulating certain environmental factors. This does not preclude any of the phases of flowering studied by Loomis (31, pp. 202-212), but seems to be a necessary phase in the developmental cycle of the shoot before it attains the capacity for subsequent induction, initiation, and development of an inflorescence.

SUMMARY AND CONCLUSION

Three Chloro IPC was used in this experiment to study the effect of this chemical on seed-head development in tall fescue. It was possible to practically eliminate seed-head formation in this species by applying 3 Chloro IPC after October. Cytohistological and morphological observations made on the treated and untreated plant material collected at monthly intervals during the fall, winter, and early spring are summarized according to the following findings:

1. The toxicity of 3 Chloro IPC was mainly due to its deleterious effect on the mitotic activity of the cells; therefore, its effect was most pronounced on meristematic tissue.

2. The severity of the damage produced by 3 Chloro IPC was found to be influenced by the activity, maturity, position, and vascular connections of the tissues and tillers involved. Length of time after treatment was also an important factor.

3. Cells in the intercalary regions of plants treated with 3 Chloro IPC became greatly enlarged, and with an increase in time, necrosis usually occurred in these regions.

4. Apical meristems of the shoot were little affected during the initial stages of damage to the shoots. However, root tips were affected relatively soon after treatment. This unequal response to 3 Chloro IPC of tissues in the apical regions of the roots and shoots indicates a difference in the movement of the

chemical into these structures due to a difference in the development of their vascular systems.

5. The injurous effect of 3 Chloro IPC was progressive and the tissues of treated plants usually showed signs of disintergrating after the shoots had been treated for several months.

6. Tall fescue plants were found to be less active during December and January and were significantly less affected by 3 Chloro IPC during this period of the experiment.

7. Mother shoots treated with 3 Chloro IPC were able to live as long as a month or more before they eventually died. However, the lives of the plants were continued by the production of tillers.

8. The shoot apexes of tillers produced during October were strikingly different from those produced during the late winter and spring. Branch tillers as well as mother shoots present in October were characterized by high, cone-shaped apexes which indicated rapid leaf initiation and the capacity for seed-head production.

9. Tillers that were produced during the late winter and spring were marked by a low dome-shaped apex which initiated leaves very slowly. This type of shoot remained vegetative and showed no signs of initiating an inflorescence; therefore, indicating that it was reproductive sterile.

10. The morphology of the shoot apex was determined largely by the rate of leaf initiation; hence, by the environmental conditions under which it developed.

From the evidence of this study, it is apparent that the shoot apex must reach a certain state of maturity before the shoot is capable of forming a seed head, and that this maturation takes place because of specific environmental conditions under which the shoot develops. In this experiment, evidence indicates that tillers produced in October developed under climatic conditions that enabled them to attain the capacity for subsequent floral induction and initiation that ultimately resulted in seed-head production. On the other hand, tillers developing after the October to November period generally did not reach the potential state of maturity necessary for floral initiation and seed-head formation.

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