A STUDY OF SEED PRODUCTION

IN

'GRASSLANDS RUANUI' PERENNIAL RYEGRASS (LOLIUM PERENNE L.)

'GRASSLANDS KAHU' TIMOTHY (PHLEUM PRATENSE L.)

AND PRAIRIE GRASS (BROMUS UNIOLOIDES H.B.K.)

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by

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CONTENTS

LIST OF TABLES

LIST OF PLATES

LIST OF FIGURES

LIST OF APPENDICES (presented in separate volume)

21. Seed yield - perennial ryegrass, timothy and prairie grass (1966).

22. Seed yield - perennial ryegrass, timothy and prairie grass (1967).

23. Relationship between seed yield and germination capacity at different harvest periods following anthesis depending on harvesting method (1966).

24. Relationship between seed yield and germination capacity at different harvest periods following anthesis depending on harvesting method (1967).

25. Daily anthesis data - perennial ryegrass (days 1 to 12).

26. Correlation matrix - perennial ryegrass.

27. Daily anthesis data - prairie grass (days 1 to 6).

28. Correlation matrix - prairie grass.

29. Average length of time individual florets remained open - prairie grass.

30. Percentage of seeds developed from florets open on different days and harvested at intervals up to 30 days after anthesis.

31. Percentage germination of seed developed from florets open on different days and harvested at intervals up to 30 days after anthesis.

INTRODUCTION

The place of grasslands in the economy of New Zealand is paramount. Consequently grassland seeds must and do play a vital role in the agricultural industry.

Increasing land values and soaring costs make it imperative that our farms are sown with seed of the highest quality.

On many farms seed production is only considered as secondary to the production of meat and milk. It is only in seasons when stock feed is abundant that many areas are closed for the production of seed. It would be to the advantage of the seed industry if grass seed production was viewed more as a primary consideration with stock grazing being employed to assist in the management of the seed crop rather than the present 'catch' crop system employed on many farms. This system would also help to reduce the large annual fluctuation in national seed production.

Herbage seed production in this country amounts to about 18,000 tons annually although fluctuations in this figure do occur (1967 20,370 tons, 1968 17,430 tons, 1969 18,770 tons, 1970 14,880 tons). In 1970 seed exports represented a total value of over $7 million, of which approximately $0.7 million was obtained from the export of perennial ryegrass seed.

In recent years a number of grassland workers have carried out studies on various aspects of seed development and production. Despite this, however, much work still remains to be done before the physiological processes underlying seed production are fully understood. Some of these workers have found it necessary to study the position and contribution of individual tillers to seed production. In comparison, studies of the factors influencing anthesis, fertilisation and seed maturation have been somewhat neglected. The production of a large number of head-producing

tillers, each bearing large numbers of florets is obviously not enough. A high percentage of these florets must undergo anthesis, be effectively fertilised and ultimately develop to maximum seed weight and germination capacity if the potential yield of the crop is to be fully realised. This suggests that seed yield might be considerably increased if the conditions required at each of these stages were more fully understood. During the late summer, autumn and winter tillers grow vegetatively and it is not until the spring that those tillers destined to produce heads actually begin reproductive development. It is at this time that the first contribution to total seed yield occurs, viz. the number of reproductive tillers per unit area. Ear development continues until shortly before ear emergence at which point the number of florets per head is fixed. Subsequently, anthesis, pollination and fertilisation follow to determine the seed-set component of total yield. Finally the seeds develop and mature to determine the final yield component-seed weight.

In view of the considerable economic value of the New Zealand grass-seed crop, the fact that national yields fluctuate widely from season to season, and the paucity of New Zealand investigational work on the factors affecting seed yield, a study was carried out over a three year period, commencing 1st April, 1966, at Massey University, the main objectives of which were to:

1. Relate seasonal variations in tiller production to head development and seed yield at harvest.
2. Describe the morphological changes occurring during floral initiation and development.
3. Study the influence of selected environmental variables on anthesis, seed set and seed development.

4. Study the response of selected grass species to various treatment combinations of grazing and nitrogen application.

The grass species included in this study were 'Grasslands Ruanui' perennial ryegrass (Lolium perenne L.), 'Grasslands Kahu' timothy (Phleum pratense L.) and a local strain of prairie grass (Bromus unioloides H.B.K).

STUDY OUTLINE

The overall study was divided into two sections.

1. A field study of seed development in prairie grass, perennial ryegrass and timothy.
2. A study of the effect of five selected environmental variables on anthesis, seed set and seed development in prairie grass and perennial ryegrass.

The object of the initial work was to study the sequence of seed development in the field, taking into account the time of individual tiller formation and following this through the sequence of floral development, ear emergence, anthesis and subsequent seed development. In each species individual tillers were marked at the 2-leaf stage of development at monthly intervals from sowing through to full seed development and harvest. The role of these tillers of known month of origin and their relative contribution to final seed yield was observed. Records were obtained of the time of floral initiation of marked tillers and of their progressive development through seed head production, ear emergence and anthesis to seed maturity. Successive harvests were made at weekly intervals commencing 7 days after peak anthesis and continuing for 6 weeks. This allowed samples of seed at varying stages of development to be obtained for seed moisture, purity, germination, 1000-seed weight and seed colour assessments and for total seed yield measurements.

The object of the second part was to study in greater detail the effects of prevailing environmental conditions on daily anthesis, and subsequent seed set and seed development. It was hoped that analysis of daily anthesis records would give information on the environmental variable(s) which influence the onset of daily anthesis, time of peak anthesis, duration of daily flowering, total number of florets open each day, and the duration of time individual florets remained open on a particular day. At intervals following anthesis seed samples were harvested for assessment of seed 'set' (effective fertilisation) and to determine whether or not the number and rate at which individual seeds develop was affected by the environmental conditions prevailing following fertilisation. Individual seeds of known age from anthesis were also dissected from individual seed heads and subjected to a germination test to obtain a picture of the stage in seed development at which the onset of seed viability occurred.

Because of the large amount of published literature on seed production only that with particular reference to the species studied viz. perennial ryegrass, prairie grass and timothy will be reviewed in each section. In cases where work pertaining to other crops is quoted this will only be made where the article concerned is of particular relevance to the subject being reviewed.

GENERAL DESCRIPTION OF THE GRASSES STUDIED

The three species considered in this study; Lolium perenne, Bromus unioloides and Phleum pratense are respectively classified into the tribes Hordeae, Festuceae and Agrostidiae.

1. Lolium perenne L.

This species is known under various common names. These include Perennial Ryegrass, English Ryegrass, Eavers Ryegrass, Ryegrass and Raygrass. The name 'Perennial Ryegrass', because of its more common usage will be used to describe Lolium perenne in this study.

Descriptions of the morphological features of L. perenne have been made by Armstrong (1937), Hubbard (1959), Mosher (1918), Lewis (1967), Hitchcock (1935) and Terrell (1968).

Perennial ryegrass is the most widely sown grass in New Zealand. Its useful habitat range is extremely wide, being limited at one extreme by excessive moisture, and at the other by low fertility and excessive dryness. Between these two extremes there is a wide range of country on which perennial ryegrass can be profitably grown.

It is an excellent seed producer, thus making its distribution easy and profitable. It is also one of the easiest and quickest of the grasses to establish from seed, thus competing with quick growing weeds and can be grazed much sooner after sowing than many other grasses. Perennial ryegrass is highly productive under close grazing and high fertility, producing its maximum herbage yield in the spring when feed is at a premium.

In the process of selection and breeding the characters of high tiller production, rapid tiller development and high annual production of both herbage and seed have been retained. Since it is a strongly tillering perennial species it is widely used to provide all-purpose grazing and is the main component sown in New Zealand pastures. Because of this it is grown widely as a specialist crop or cash crop for seed production. Perennial ryegrass responds well to nitrogen, the timing of application of this nutrient having a strong influence on the production

of both herbage and seed. However, with all of these advantages perennial ryegrass has the disadvantage of being dormant in the hottest part of the summer, especially when fertility is low or when clovers are absent.

Seed crops yielding 50-60 bushels of M.D. seed per acre are not uncommon although an average yield is about 20 bushels per acre (Smith 1957, Palmer 1937).

2. Bromus unioloides H B K

Grasses of this genus are widely distributed. Some important forage species belong to this genus (e.g. B. inermis, B. unioloides) and also some troublesome weeds (e.g. B. tectorum, B. commutatus, B. sterilis, B. mollis).

Assessment trials on both the tiller and seed production of a wide range of New Zealand and overseas Bromus species have been carried out by Rumball (1968), who has observed both inter and intra-species variation is high, particularly with regard to tiller number, growth habit, heading behaviour and resistance to head smut.

Descriptions of the morphological features of prairie grass (B. unioloides H B K) have been published by Hitchcock (1935), Mosher (1918), Hoover et al (1948), Wheeler and Hill (1957), Barnard (1964), Whyte et al (1959) and Allan (1936).

The common name of the species varies from one locality to another. In Australia and New Zealand it is called prairie grass and in the U.S.A. rescuegrass or more rarely Schrader's bromegrass. Karim (1961) notes that the Spanish name for it is Cebadilla.

Although it is generally recognised as belonging to the genus Bromus, some controversy exists regarding the specific name for prairie grass - whether the specific name catharticus be accepted in preference to the older unioloides.

Three 'specific' names have been used in the literature, carthariticus by Wheeler (1950), Hitchcock (1935), Pantall (1961), Whyte et al (1959) and Karim (1961); unioloides by Beddows (1931), Langer and Wilson (1965), Barnard (1957) and Rumball (1968); and willdenowii by Raven (1960). In view of the general confusion regarding the specific name of this grass, the name Bromus unioloides HBK, as listed in the Standard Common Names for Weeds in New Zealand (1969) will be used throughout this thesis.

Bromus unioloides is a native of South America. It is best adapted to humid conditions with mild winters and behaves as a winter annual in regions where it is most valuable. It is a rich-land grass, growing vigorously in good soil but only meagerly on poor land (Wheeler 1950).

Prairie grass is an erect, tall-growing plant, heavy seeding, and though perennial in character, is often short-lived if subjected to indifferent management such as overgrazing, inadequate fertility, or if grown in unsuitable soil conditions (Pantall 1961).

Very little experimental work has been carried out on prairie grass in New Zealand, no certified seed is available, and apparently no official identification of various local strains has been made. These factors must therefore be taken into account when criticising the weakness of prairie grass and comparing it with other grasses of pedigree strain which have been improved and specially selected for particular characteristics over a long period.

Prairie grass has been recognised as a valuable species for special purpose pastures, its main feature being its excellent growth during the late autumn, winter and spring, and for its high palatability to all classes of stock (Pantall 1961).

Donald (1939) attributed the poor performance of some stands of prairie grass in Australia to the indiscriminate use of poor quality seed (genetically), susceptibility to head smut and unsuitable management. He suggested that the use of controlled grazing techniques might improve the production of the species under general farming conditions.

For seed production, Saxby (1956), suggests that prairie grass should be sown alone, at rates of up to 70 lb per acre in order to secure a sufficiently thick stand to warrant it being maintained as a special pasture. Provided it is dominant and is not grazed too closely, prairie grass will remain in a pasture for many years because of its vigorous growth. This is particularly the case when seedcrops are harvested, as the stand is strengthened by the establishment of shed seed.

Compared with most herbage grasses prairie grass is a slow tillering species. However, the application of nitrogen is important in influencing the number of tillers which become reproductive (Karim 1961).

Wheeler and Hill (1957) state average yields of M.D. seed of 600-800 lb per acre with a maximum of up to 2000 lb per acre. They also state that seedcrops which have been carefully harvested and dressed should have a purity of at least 95%, and a germination of 90% or over.

One of the interesting points about prairie grass is that it behaves as a facultatively cleistogamous species, chasmogamous flowering occurring at photoperiods of between 10.5 and 12.5 hours, while the cleistogamous condition occurs when plants are exposed to longer photoperiods of up to 16 hours per day (Ragonese and Marco (1941), Karim (1961), Langer and Wilson (1965)).

3. Phleum pratense L.

Of the 10 known species in the genus Phleum, Timothy (Phleum pratense L.) is the only one under general cultivation, and all except P. alpinum are indigenous to Northern Europe (Gorman 1950a), Wheeler (1950), Hoover et al (1948)).

Descriptions of the botanical features of timothy have been given by Wheeler (1950), Hitchcock (1935), Mosher (1918), Hubbard (1959) and Armstrong (1937).

Phleum pratense is a late maturing perennial grass which thrives in damp situations, but also grows on a wide variety of soils. It is a highly palatable grass, requiring a relatively fertile soil (Gorman 1950a).

It is well adapted to cool, humid conditions and to a considerable range of soil reactions, but is adversely affected by high acidity and is rather sensitive to deficient moisture conditions during the summer period when it is heading (Wheeler 1950). Weather conditions often determine whether a timothy pasture is harvested for hay or seed. Sometimes excess or frequent rainfall delays harvesting a crop intended for hay until the seed has become nearly mature, and for this reason it is harvested for seed.

Timothy is generally regarded as a non-persistant species under intensive grazing but with judicious management it can be retained in pastures for many years providing a heavy bulk of feed for cattle or sheep. The results of nitrogen application to timothy seedcrops have been somewhat contradictory. The seed is often slow to germinate and establish and particular care with land preparation is considered to be one of the most important factors in the establishment of a successful stand, whether this be intended for grazing or seed production.

Timothy readily produces large quantities of seed, an average M.D. yield being about 160 lb. per acre. A small quantity of hulled seed is an indication that the crop is completely ripe when harvested, the proportion of hulled seed in a seedline usually being higher in dry summers. (Armstrong 1937).

Certification of timothy using seed grown from imported seed of the S48 strain was introduced in New Zealand in 1945, and since that time a pedigree strain, bred and selected for New Zealand conditions has been released as 'Grasslands Kahu' timothy (Gorman 1950b).

Probably the most outstanding and unusual morphological feature of the timothy plant is the enlargement of the basal internode to form a bulbous haplocorm which functions as an area of food reserve storage. (Sheard (1968)).

MATERIALS AND METHODS

1. LAND PREPARATION AND SOWING OF SEED FOR FIELD TRIAL

The seed lines used in the field study were Certified Breeders 'Grasslands Ruanui' Perennial Ryegrass, Certified Basic 'Grasslands Kahu' Timothy, and a commercial line of M.D. Prairie Grass.

The trial area was cultivated out of pasture and sown to perennial ryegrass and timothy plots (21.4.1966) in 18 inch rows. Each treatment included 10 rows of 15 or 21 feet in length. Potassic superphosphate was drilled with the seed at a rate of 2 cwt per acre.

Seeding rates for perennial ryegrass of 8 lb per acre, 2 lb per acre for timothy and 28 lb per acre for prairie grass, were used.

Owing to difficulties in obtaining an even flow of prairie grass seed through the coulters of the drill, prairie grass plots were hand sown in 18 inch rows, the seed being placed into the grooves made by the ring-roller used in the final stages of cultivation.

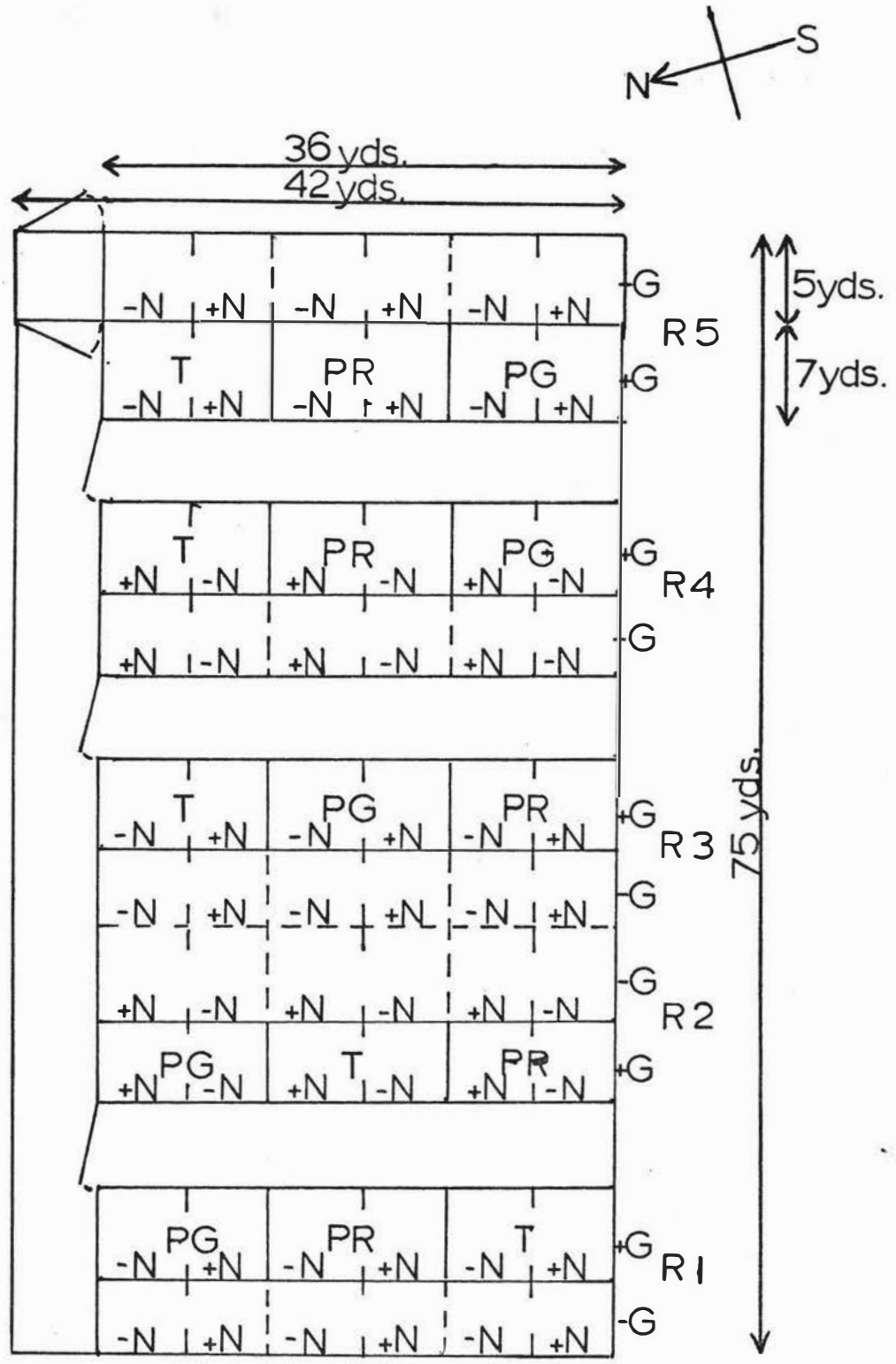
The trial consisted of 5 replicates, the position of each species within a replicate being chosen at random.

The race area between replicates, was sown broadcast with white clover at 3 lb per acre.

As soon as seedlings were sufficiently developed to allow identification of the position of individual rows in each treatment the entire area was fenced.

The experimental layout of the area is shown in Figure 1, and Plate 1.

FIGURE 1. FIELD TRIAL LAYOUT.



PR PERENNIAL RYEGRASS
PG PRAIRIE GRASS
T TIMOTHY
+G GRAZED PLOTS
+N NITROGEN APPLIED
R REPLICATE

total area
0·65 acre.

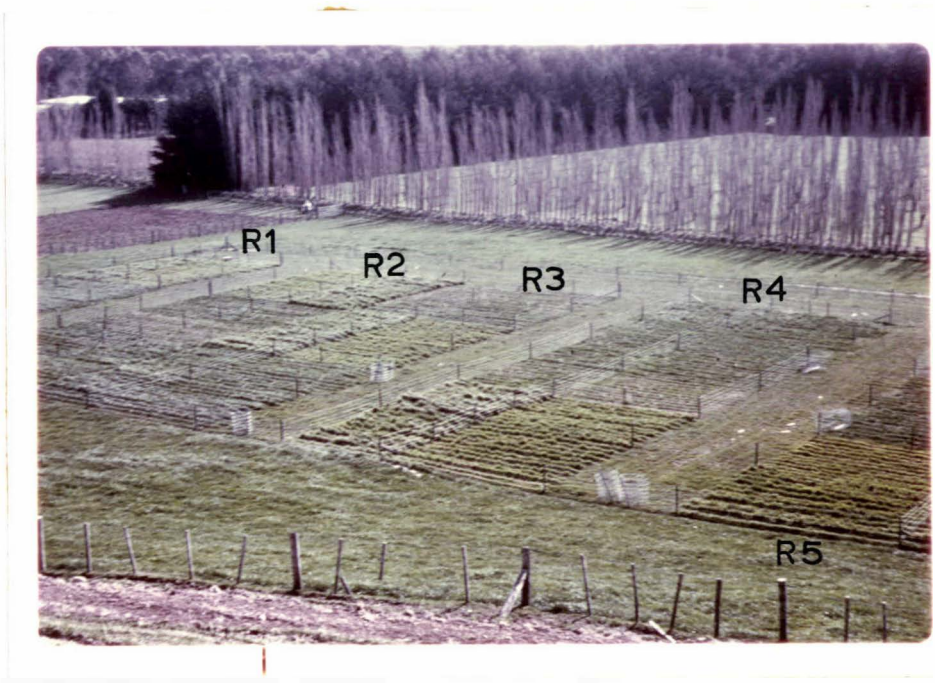


Plate 1 Elevated view of field trial area (September 1966)

2. TRIAL MANAGEMENT

The major aspects of management of the field trial area involved the application of nitrogen, the management of sheep to graze the plots, inter-row cultivation, the spraying of the area to control weed growth, and the application of insecticide to control aphids. (Appendix 1).

Apart from an annual application of P & K (2 cwt of potassic superphosphate) over the entire area of the field trial, the only additional nutrient applied was N. The nitrogen-treated plots (designated +N) received a side dressing of urea granules along each row, at a rate equivalent to $1\frac{1}{2}$ cwt per acre at approximately monthly intervals for 5 months following sowing. N application recommenced following seed harvest in 1967. Wherever possible urea was applied immediately after a grazing period. Frequent nitrogen application was thought desirable to provide plants with a relatively continuous supply of this nutrient.

Grazed plots were stocked with approximately 10 sheep per treatment, the objective being to obtain even grazing of the plots (designated +G). Grazing was allowed to continue until the foliage was approximately 1" in height at which time all stock were removed, and the ungrazed foliage above 1" in height removed with a reciprocating mower.

It was only possible to graze each species twice in the first season before grazing was discontinued due to the onset of floral initiation. A table of operations is presented in Appendix 1.

Because the test species had all been sown in spaced rows it was necessary to carry out inter-row cultivation of the trial area to control weed growth, particularly in the early stages of crop establishment using a 'Bantam' rotary hoe. Despite the use of inter-row cultivation a number of weed species (predominantly Holcus lanatus, Ranunculus repens, Rumex spp

and Glyceria fluitans) established among the crop plants within the rows. Although the weed grass species were not completely controlled despite some hand-weeding, two spray applications of 'Embutox'* (2 fl. oz. per gallon) at monthly intervals in the spring were found to give effective control of broad-leaved weed species.

A single application of 'Disyston'* granules was also necessary to control aphids in the late spring and gave apparently complete control. The granules were applied as a side dressing along the row at the rate of 60 lb per acre. This operation necessitated a temporary halt in the use of animals and for the defoliation following the application grazing was replaced by mowing. The bulk of plant material involved required the cut material to be removed.

3. TILLER MARKING

Numerous workers have suggested methods for identifying individual tillers of plants as they are formed. The marking materials employed include coloured cloth (Wells 1959, Miravelle 1965), coloured plastic wire with label attached (Wilson 1959), string (Grabe 1956) and plastic rings or labels (Anslow 1963, Lambert 1963b, 1967a, Langer 1956, 1959b, Langer and Lambert 1963, Langer and Ryle 1959). Any technique which is used must be relatively permanent and enable easy identification of marked tillers at a later date. Although different labelling materials

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* Embutox = Sodium salt of 4-(2,4 - dichlorophenoxy) butyric acid.

* Disyston = a.i. 5% W/W Disulfoton (o.o - diethyl -S-2 (ethylthio) ethyl phosphorodithioate).

have been used with success by various workers, none of the trials in which they were used apparently incorporated grazing treatments. Lambert (1967a) however, did undertake monthly tiller labelling, using expansible plastic rings, under cutting treatments.

Because grazing treatments were included in the present work an initial small trial was conducted to determine the effectiveness and ease of application of different labelling materials to tillers in grazed plots. From this trial it was found that coloured plastic wire and plastic tubing rings were least affected by the grazing animal and were the best materials for use when large numbers of tillers were to be marked. These materials also remained relatively permanent compared with coloured wool, coloured cloth and coloured string, all of which tended to rot or fade, or be pushed into the soil by stock. For this reason tillers were marked with rings of plastic covered wire (prairie grass) and rings of coloured plastic tubing (perennial ryegrass and timothy).

For marking tillers of prairie grass, plastic covered wire was formed into a loop approximately $\frac{1}{2}$" in diameter and the ends twisted. This provided a ring of suitable size for marking prairie grass tillers, at the same time allowing for radial growth of the leaf sheath without apparent constriction. A ring was applied by gently sliding it over the top of the tiller so that it finally rested at the base of the shoot at, or slightly above, ground level.

In the case of perennial ryegrass and timothy, $\frac{1}{4}$" lengths of 4 m.m. diameter plastic tubing were slit longitudinally and applied to the base of the tiller from the side. The slitting of the tubing enabled expansion of the ring with increase in tiller diameter.

A colour code was devised so that tillers marked at different dates could be identified.

Previous work by Langer and Lambert (1959) and Lambert (1963b) also showed that expandible rings did not restrict normal tiller development.

Sufficient tillers per month were marked in each plot to allow a minimum of 200 tillers to be identified at seed harvest. Nevertheless a greater number of rings were 'lost' in the grazed than the non-grazed treatments.

It is of interest to note that during crop establishment many markers, especially those coloured red and yellow, could be found lying alongside tillers which had been marked as recently as the previous day. This detachment of coloured markers was attributed to removal by birds. Once the crop developed sufficient top growth the number of markers detached from tillers decreased to a very low level, the major sources of loss being the uprooting of marked tillers by grazing stock and tiller death during the spring and summer months.

4. SHOOT APEX DISSECTION AND PHOTOGRAPHY

Tillers for dissection were removed approximately 1" below ground level. The leaves of a tiller were then removed, using a pointed scalpel and binocular microscope as required.

When an apex was to be photographed it was placed in a dish of clean tap water for about 15 minutes. This allowed it to become fully turgid and better able to withstand the intensive lighting which had to be used. At first considerable difficulty was experienced because intense illumination damaged the apices. This difficulty was mainly overcome by dimming the lamp during focussing, full intensity light only being used during the exposure itself.

5. MOISTURE CONTENT DETERMINATION

In each of the three test species moisture determinations were carried out using the air-oven method with samples being held at 130°C for 60 minutes as prescribed in the I.S.T.A. Rules (1966). Each determination was made in duplicate. In cases where results differed by more than 0.2% the determination was repeated in duplicate.

In the case of determinations carried out on seeds of high moisture content (over 25%) the two-stage drying method was used as prescribed in the I.S.T.A. Rules (1966). The initial stage was carried out by drying a weighed seed sample in an air-oven at 130° for 15-20 minutes, the objective being to reduce the moisture content to 12-15%. After removal from the oven, the seed was air dried at room temperature for two hours and weighed. The sample was then ground and the second stage drying carried out by the air-oven method at 130° for 60 minutes. If S1 is the moisture lost in stage 1, and S2 that lost in stage 2, each expressed as a percentage, the original moisture content was calculated on a wet weight basis according to the formula.

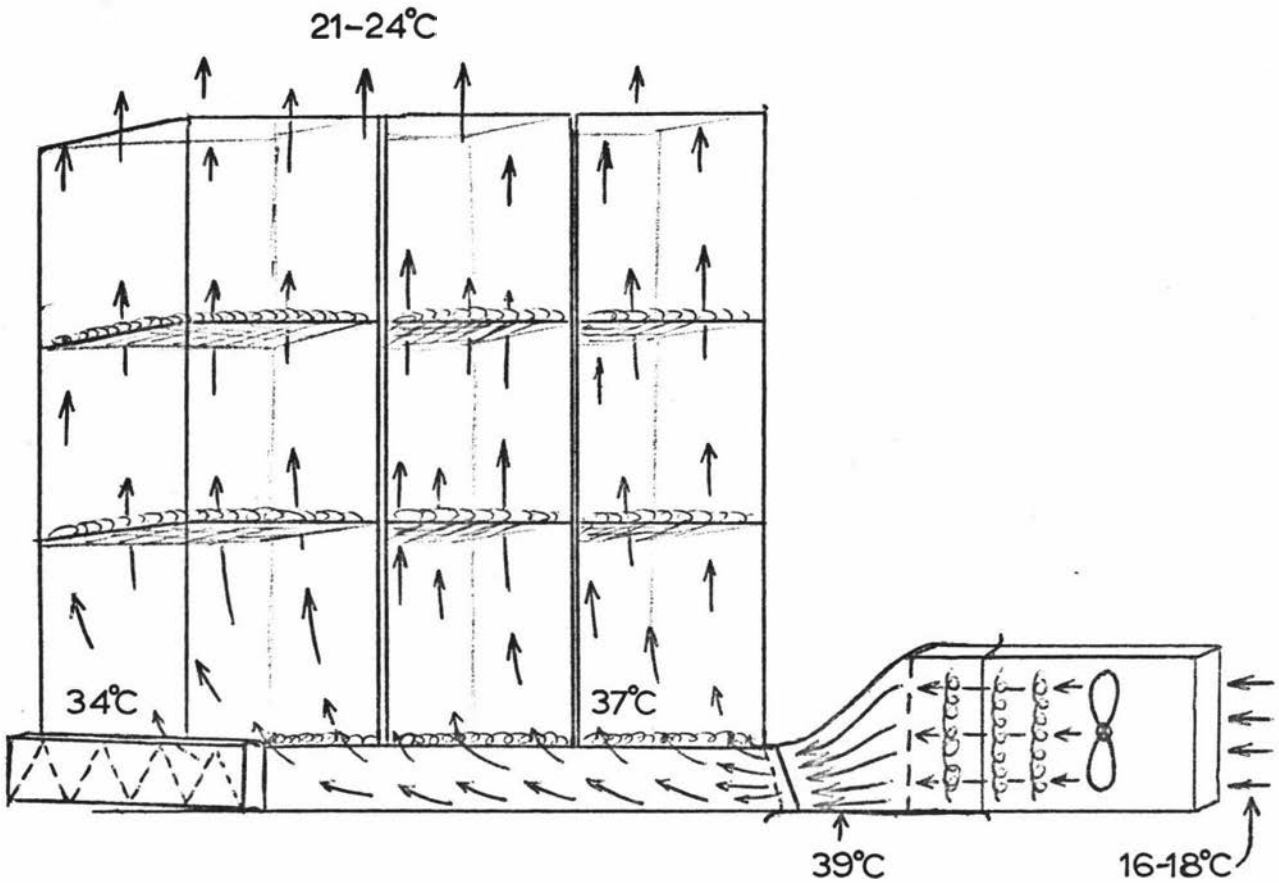
$$S1 + S2 - \frac{S1 \times S2}{100}$$

Determinations were carried out in duplicate.

6. SEED DRYING

Because of the problems associated with the storage of immature and high moisture content seed, it was found necessary to artifically dry seed harvested at over 20% seed moisture content to prevent damage to the seed in storage by heating and mould development. Artificial drying was accomplished by the use of a commercial fan heater, heated air (between 34°C and 39°C) being blown through the seed samples which had been spread in thin layers in gauze-bottomed trays for 24 hours. A diagrammatic representation of the apparatus is shown in Figure 2.

FIGURE 2. APPARATUS FOR ARTIFICIALLY DRYING SEED.



7. PURITY ANALYSIS

A modified purity analysis technique was used in the present study which nevertheless followed the principles prescribed in the International Seed Testing Association (I.S.T.A.) Rules (1966). The main object of the analysis was to determine the number and weight of pure seed harvested. In addition the purity analysis was employed to determine the pure seed: empty glume ratio and to provide a sample of pure seed for duplicate germination tests. Because seed was hand-harvested complications in the purity determination caused by the presence of 'other crop seeds' and 'weed seeds' were avoided. The 'inert matter' fraction included pieces of broken or damaged seeds, empty glumes, lemmas, paleas and unattached sterile florets, attached sterile florets which were removed from fertile florets during the analysis and a small proportion of chaffy matter and straw. In addition, seeds in which the caryopsis was considered to be less than one quarter the length of the palea (measured from the base of the rachilla) were classified as inert matter.

The minimum weights of purity samples for each species were used as prescribed in the I.S.T.A. Rules (1966).

A standard procedure was used to obtain sufficient seed for the purity analysis. Seedheads were removed from a sample of harvested material, air-dried at room temperature, and the seed gently rubbed out of the heads on a stippled rubber surface and weighed. The empty glume fraction was roughly separated from the pure seed on a Leggat blower set at a standard predetermined air blast for each seed species. The two separations were examined over a diaphanoscope and precise separation of the pure seed and empty glume fractions carried out. The number of pure seeds in the sample was determined and the fraction weighed. The number of empty florets present in the inert matter fraction was recorded.

The results obtained allowed the percentage of florets which contained seed to be calculated.

8. GERMINATION TESTING

For each of the test species duplicate germination tests were carried out with seeds from the pure seed separation and germinated T.P. (top of paper) in 2 replicates of 100 for perennial ryegrass and timothy and 4 replicates of 50 for prairie grass. The respective alternating germination temperatures were 20-25°C 15-25°C and 20-30°C with daily counts and removal of normal germinated seedlings. The duration of the germination test was determined by the time prescribed for the final count for each species in the I.S.T.A. Rules (1966), but the 3 day chilling pretreatment of the seed at 5°C which was required to break dormancy, was not included in the test period. The test was therefore terminated after 12 days for perennial ryegrass, 10 days for timothy and 28 days for prairie grass. In the event of variability exceeding the maximum tolerance ranges in percent germination specified in the I.S.T.A. Rules (1966) a further duplicate germination test was conducted. Samples of seed of both prairie grass and timothy in addition to being prechilled at 5°C for 3 days prior to the commencement of the germination test period, were placed on blotters which had been soaked in a 0.2% solution of potassium nitrate. This procedure was used to prevent germination results being confounded by problems of seed dormancy.

9. FIXATION, EMBEDDING AND SECTIONING OF SEED AND PLANT MATERIAL

The fixing and killing solution used for preserving plant tissue and seeds consisted of a mixture of formalin, glacial acetic acid and 70% ethyl alcohol in proportions 2:1:17. Despite some possible loss of

colouration of preserved specimens, this fixative proved to be very convenient as samples could be left in the fixative until required. However, one difficulty arising from the use of this fixative was that any material preserved for periods of more than a few weeks became very brittle and problems in wax penetration during embedding for sectioning occurred.

The preparation of specimens for embedding followed a standard procedure as outlined by Johansen (1940), with some modifications. Following washing in 70% alcohol to remove fixative, preserved specimens were dehydrated by sequential immersion for 10 minutes in tertiary-butyl-alcohol (TBA) solutions of each of the following concentrations - 70%, 85%, 90%, 95% and 100%. Infiltration was accomplished by a gradual transfer from the TBA to paraffin by allowing the specimens to remain in a 50% TBA/paraffin mixture for at least 1 hour at room temperature. The tissue was placed on the surface of solidified paraffin wax, covered with TBA/paraffin mixture and the beaker placed in an air-oven at 60°C overnight. The tissue sank slowly through the melting wax until it came to rest on the bottom of the container. The entire mixture of wax, oil and traces of alcohol was decanted and replaced with pure melted paraffin wax. The latter process was repeated twice during the next 6 hours the last change being made into paraffin wax: sudan III mixture. The tissue was embedded by placing the specimens in a paper embedding tray containing liquid wax, and quickly cooling the entire mass in a refrigerator. Rapid cooling was necessary to prevent wax crystallisation. The blocks were removed from the paper mould, excess wax trimmed off and stored in dust proof containers pending sectioning.

Microtoming was carried out on a rotary microtome set to cut sections 5μ in thickness.

Haupt's adhesive was used to affix the ribbon of sections to microscope slides using the procedure described by Johansen (1940). The slides were allowed to dry overnight and stored in dust proof boxes if staining could not be carried out immediately.

Before the sections could be stained the paraffin was removed by immersion of the slide in xylol for at least 5 minutes. The slide was then placed for 5 minutes in each of the following solutions, 50/50 xylol-absolute alcohol, absolute alcohol and alcohol solutions 95%, 85%, 70%.

The sections were then stained in safranin for 5 minutes and excess stain washed off with water. Differentiation was carried out in 50% alcohol slightly acidulated with hydrochloric acid (2 drops HC1 in 100 ml water). The slides were then thoroughly washed in water for 5 minutes, transferred into Delafield's Haematoxylin for 15 minutes, washed in tap water and briefly destained in acidulated water. Following washing for 20 minutes to remove traces of acid, the sections were dehydrated by immersion for 5 minutes in each of a series of alcohol solutions (50%, 70%, 85%, 95% and absolute alcohol). Following 5 minutes immersion in solutions of both 50/50 xylol: absolute alcohol and pure xylol the sections were permanently mounted in balsam.

In a few cases where wax penetration was unsatisfactory, infiltration was carried out under vacuum.

A series of different stains were examined to assess their relative merits in providing structural definition and contrast for black and white microphotography. Delafield's Haemotoxylin and Safranin or Bismark Brown appeared most satisfactory for this purpose.

FIELD STUDY
TILLER PRODUCTION

INTRODUCTION

A grass crop comprises a population of individual tillers, each capable of growth and vegetative reproduction and with a finite life. As such it is subjected to the normal dynamics of any population in which individual tillers adjust to varying environmental conditions and to inter-relationships with other tillers in the same habitat.

The amount of growth from a tiller and its rate of vegetative reproduction, are determined not only by the availability of nutrients, light and moisture, but also by competition from other tillers.

Whether the life span of an individual tiller can be measured in weeks, months, or years, is dependent on the genetic makeup of the species concerned and by general environmental conditions, including crop management.

The objective of this aspect of the study was to follow quantitative changes occurring in tiller numbers from sowing until the autumn of the second year.

LITERATURE REVIEW

In the Gramineae the seedling emerges as a single shoot with an extremely short stem bearing leaves in opposite ranks. In the axil of each leaf, buds are produced. From these, axillary shoots or tillers are formed. (Langer 1963).

For the production of its first tiller a shoot appears to require a certain minimum number of leaves. Langer (1963) states that in timothy about 5 leaves are normally visible before the first tiller appears, but in ryegrass tillering can occur as soon as there are 3-4 expanded leaves on the main shoot. (Whyte et al 1959).

In grasses, the coleoptile or primary tiller may produce lateral branches and these in turn other tillers. Under favourable conditions, therefore, several dozen tillers may be formed from a single seed. As the internodes are much shortened, the branches appear to come out at one point (Robbins 1924).

Tillers grow either upwards within the sheath of the subtending leaf (intra-vaginal) as in prairie grass or may burst out through the base of the leaf sheath (extra-vaginal) as in ryegrass and timothy.

Langer (1963) states that, following its appearance a tiller normally produces its own adventitious root system, although it may remain in vascular connection with the parent plant. The question of whether tillers function as independent units or whether they are physiologically interdependent has not been conclusively answered. However Barnard (1964) has shown that eventually they become independent, and in turn supply carbohydrates to tillers developing in the axils of their lower leaves. However, Barnard does not specify even approximate times following formation when tillers may continue their morphological development as independent units.

Langer (1963) has presented a review of factors affecting tillering in herbage grasses including both genetic and environmental effects.

Most studies on tillering in grasses have been made under controlled conditions, many workers having undertaken studies with single plants. Few workers have studied tillering in the field.

Results on the effect of cutting and grazing on tillering are sometimes difficult to interpret, since a number of factors may conflict with or assist tiller production. These include removal of elongated stems (Langer 1956, 1963, de Booysen et al 1963), temperature (Mitchell 1953a), light intensity (Alberda 1965 , Brougham 1959), grazing severity (Mitchell & Glenday 1958, Donald 1939, Lambert 1962, Langer 1963) and mineral supply (notably nitrogen) (Vose 1960, Langer 1959b). As Langer (1959b) suggests, increased tiller production may also be attended by a high death rate, indicating severe competition effects.

Under controlled conditions several workers have shown that unless flowering stems are removed, defoliation is unlikely to increase tillering in single plants (Mitchell 1953a, Mitchell & Coles 1955, and Langer 1963).

Perennial herbage grasses produce many more tillers than are capable of reaching the flowering stage. Langer & Ryle (1959) have shown the ability of tillers to produce ears declines the later they appear, irrespective of the time of sowing. The position of a tiller also plays a part, tillers inserted on the main stem tending to have a higher chance of flowering than other tillers on the same plant which have appeared at the same time (Langer & Ryle (1959), Langer (1956),

Lamp (1952)).

In timothy, Langer (1956) found that although tiller buds were initiated, their subsequent development or dormancy was determined by environmental factors. The onset of reproductive growth in the apical meristem imposes a further inhibitory influence on the growth of lateral buds; although those commencing development before floral differentiation in the apical meristem may continue to grow. During the later stages of reproductive development i.e. at ear emergence, the inhibitory influence apparently disappears in some grasses. Langer found this to coincide with the production of large numbers of new tillers in timothy.

Because each new tiller arises as a bud in the axil of a leaf on the parent tiller, the potential rate of tillering depends on the rate of leaf production which, in turn, varies with the species and is influenced by environmental factors. Consequently during early seedling growth, until competition for light, water or nutrients occur, the total number of leaves and the total number of tillers increases geometrically (Whyte et al 1959).

Summer formed tillers tend to remain vegetative possibly because they require vernalisation, have an obligatory juvenile development phase, or because flowering is inhibited by high summer temperatures (Cooper & Calder 1964).

Mitchell (1953a) showed that the daily rate of increase in tiller numbers on ryegrass plants depended on the rate of appearance of successive leaves on the main stem which determines the rate of formation of the axillary buds, and the proportion of these buds which grow into visible tillers.

Mitchell (1953b) noted that in ryegrass, unfavourable conditions for tillering delay the time of appearance of tillers. He has also observed (1953a) that high temperatures, low light intensity and partial defoliation can all induce bud inhibition.

In timothy, Cooper (1958) found an inhibitory effect of high temperature on inflorescence development, even though photoperiod was adequate. He observed that high temperature did not prevent internodal elongation and that under long-day conditions or continuous light most tillers become elongated, whether heads were initiated or not.

It has been noted by Ryle (1961) in timothy and Forde (1966) in perennial ryegrass that reduced light intensity appreciably affected vegetative and reproductive growth. Ryle suggested that low light intensity near ground level during the spring may account for the elongated sterile tillers frequently observed in timothy seedcrops. These sterile tillers may have received insufficient light for inflorescence initiation.

The rate of tiller formation in perennial grasses normally declines or ceases during stem elongation and flowering, although it may be resumed after ear emergence. This periodicity, which depends on the number of reproductive tillers present, has been observed in several species. (Rethman & Booysen (1968), Lambert 1967b, 1967c).

Several workers have commented on the seasonal variation in tiller numbers of perennial herbage grasses. This variation has been observed in ryegrass (Cooper & Saeed 1949, Wilson 1959, Ryle 1964, Schwass & Jacques 1956) in timothy (Langer 1956, 1958, Wilson 1959, Evans 1927, Saxby 1956) and in Bromus spp. (Lamp 1952, Saxby 1956).

In a general discussion on seasonal growth in swards of perennial grasses Barnard (1964) outlines a general pattern as follows: In the winter leaf growth is slow but some tillering and strong root growth may occur. In the early spring acceleration of leaf growth and stem elongation follow floral initiation with a decline in both tiller and root initiation, although there may be a depth increase in established roots. After flowering in the summer there is often a decrease in leaf growth and some renewal of both tillering and root growth. In autumn there is generally an increase in tillering and the initiation and growth of roots.

As a result of these cycles of growth of the various organs of a plant, the number of leaves, and the number of tillers and roots in established perennial swards are extremely dynamic.

Lambert (1964), in studies on timothy, showed that high rates of nitrogen (122 lb N/ac/yr) had only a small positive effect on tiller numbers. The response was not as great as that found by other workers (Langer 1959b, Wilson 1959). Later results (Lambert 1966) showed that increased levels of nitrogen decreased

(or did not increase) seed yield. At high levels of nitrogen, plants had smaller root systems than at lower levels of nitrogen and sometimes fewer roots than plants to which no nitrogen had been applied. These findings supported Lambert's earlier suggestion (1963a) that plants grown at high levels of nitrogen were susceptible to moisture shortage and explained some of the plant mortality observed under field conditions in dry seasons.

Langer (1956) suggested that, as plant weight increased, rate of tillering was adversely affected through competition for light. The time at which this occurred could vary with environmental conditions, in particular water, temperature, incidence of reproductive tillers, and interplant competition. However, within any one season the proportion of tillers produced could also be modified by nutrition and grazing. In an established sward the number of tillers is strongly influenced by soil nitrogen status. Where the nitrogen level in the early spring is low, there may be little production of new tillers. Most tillers will have received adequate exposure to winter conditions and will form heads in the spring, with a high proportion of fertile to vegetative tillers. An increase in available nitrogen will encourage the production of new tillers in the mid - to late-spring. Most of these remain vegetative until the following year, thus increasing the leaf : stem ratio in the current season. Similarly, close grazing by removing young inflorescences as they elongate, will end the inhibition of the lower axillary buds by the main growing points and encourage the production of new tillers (Whyte et al 1959).

Cooper (1951) suggested the limiting factor in spring growth of grass in the field may not be the effect of temperature on leaf and tiller production, but nitrogen deficiency due to winter leaching. While the limiting temperature for tillering in perennial ryegrass is 39-40°F nitrifying bacteria are not active until a higher temperature (unspecified!), and hence the effect of nitrogenous fertilisers on early spring growth.

Studies on the effects of nutrients on seed yield and tiller production have generally shown that the master factor in manuring grasses is nitrogen, with

phosphate and potash being required to a much lesser extent (Evans 1937b, Langer 1959b, Lambert 1966).

According to Brown (1968) herbage yields of perennial ryegrass and timothy are not reduced by stock treading. He found seed yields were increased under treading rates up to 12 sheep equivalents - an effect he attributed to increased fertile tiller formation. The application of urea (56 lb/ac) every four weeks in all seasons except winter may have influenced Brown's results.

Brougham (1959), in studies on the grazing of a grass/clover sward suggested that low tiller counts in response to frequent close grazing were due to plant mortality, while in tall-growing pasture low light conditions were unfavourable for tillering.

The grazing management of prairie grass has been discussed by Saxby (1956) Langer (1962), and Karim (1961). Donald (1939) attributed the susceptibility of this species to over-frequent grazing to the depletion of root reserves during rapid shoot elongation following grazing, the fact that prairie grass has a poorly developed crown which is readily injured by stock and because, being highly palatable, prairie grass is liable to be selectively grazed. In addition, Langer (1962) noted that the tendency for prairie grass to produce flowerheads through the year has a bearing on its recovery from grazing. The best management of prairie grass pastures appears to be one of short periods of grazing interrupted by a rest period (Crawford 1960, Pantall 1961). To some extent overgrazing effects can be corrected by allowing natural reseeding to occur. (Langer 1962).

In Bromus inermis new tiller formation was observed by Lamp (1952) to be pronounced at or about the time of anthesis, whether or not flowering stems were harvested. New shoot production continued into the autumn. Tillers emerging in late summer and autumn showed no internodal elongation but continued to initiate and exsert leaves until low winter temperatures stopped further growth. These tillers remained dormant through the winter. In the spring many emerging tillers represented shoots previously arrested in growth by low winter temperatures.

Inflorescence primordia appeared first on shoots which emerged during the previous autumn and later on shoots formed in the spring. Thus Lamp (1952) recognised two periods of active tiller formation in Bromus inermis. The first began in the autumn and the second, and more active period, started after peak anthesis. At the time of harvest tillering was still continuing. Between these two main periods few tillers emerged.

Langer (1956) recorded the pattern of variation in tiller numbers in S48 timothy. Under United Kingdom conditions he found that tillering started some 5 weeks after germination. Through the winter, tiller production continued slowly until the end of February. From then onwards the rate increased, reaching a first peak in April. After a decline in May, which coincided with the beginning of rapid stem elongation, tiller formation increased again to a second maximum at the end of July. After that a downward trend continued until the end of November.

The seasonal growth pattern of perennial ryegrass has been described by Armstrong (1937) and Davies & Calder (1969). The main features of tiller production in this species are the rapid increase in tiller numbers during the autumn, winter and early spring, and the decrease in tiller numbers coincident with the onset of reproductive development. In this latter respect perennial ryegrass follows the same sequence as described above for Bromus inermis and timothy. The tillering capacity of ryegrass is high, its rapid establishment from seed and intensity of tiller formation being pronounced features of vegetative development. After mid-summer there is a reduction in new tiller production and a drop in tiller numbers due to tiller mortality. This latter effect can be hastened by dry soil conditions (Wheeler & Hill 1957).

MATERIALS AND METHODS

Tiller counts were carried out on 6 inch lengths of row, at least five counts being made per treatment of each species at each sampling date. Initially tiller counts were made 'in situ', but as tiller numbers increased it was necessary to remove a marked length of row (Plate 2) and separate individual tillers for counting. One of the problems inherent in removing unit row lengths was the 'end' error. To help minimise variability because of this factor 6 inch lengths of row were chosen at random in each treatment and deliminated by permanent pegs.

PLATE 2 Prairie grass sample removed for tiller density counts

RESULTS

The effects of grazing and nitrogen on tiller numbers in each species are presented in Figures 3, 4 and 5 for perennial ryegrass, timothy and prairie grass respectively. (Data recorded in Appendix 2).

Analyses of variance was carried out on a representative number of sampling dates spanning the experimental period and at those dates where treatment differences showed particular interest or trends.

1. Perennial Ryegrass

In this species (Figure 3) there was no significant treatment difference in the first 4 months after sowing. Tiller numbers rose steadily to a peak in late October, when many heads were in the boot stage of development (B). At this stage nitrogen application resulted in significantly increased tiller numbers, the response being much greater in the absence than in the presence of grazing. Grazing per se also increased tiller numbers significantly but to a lesser extent.

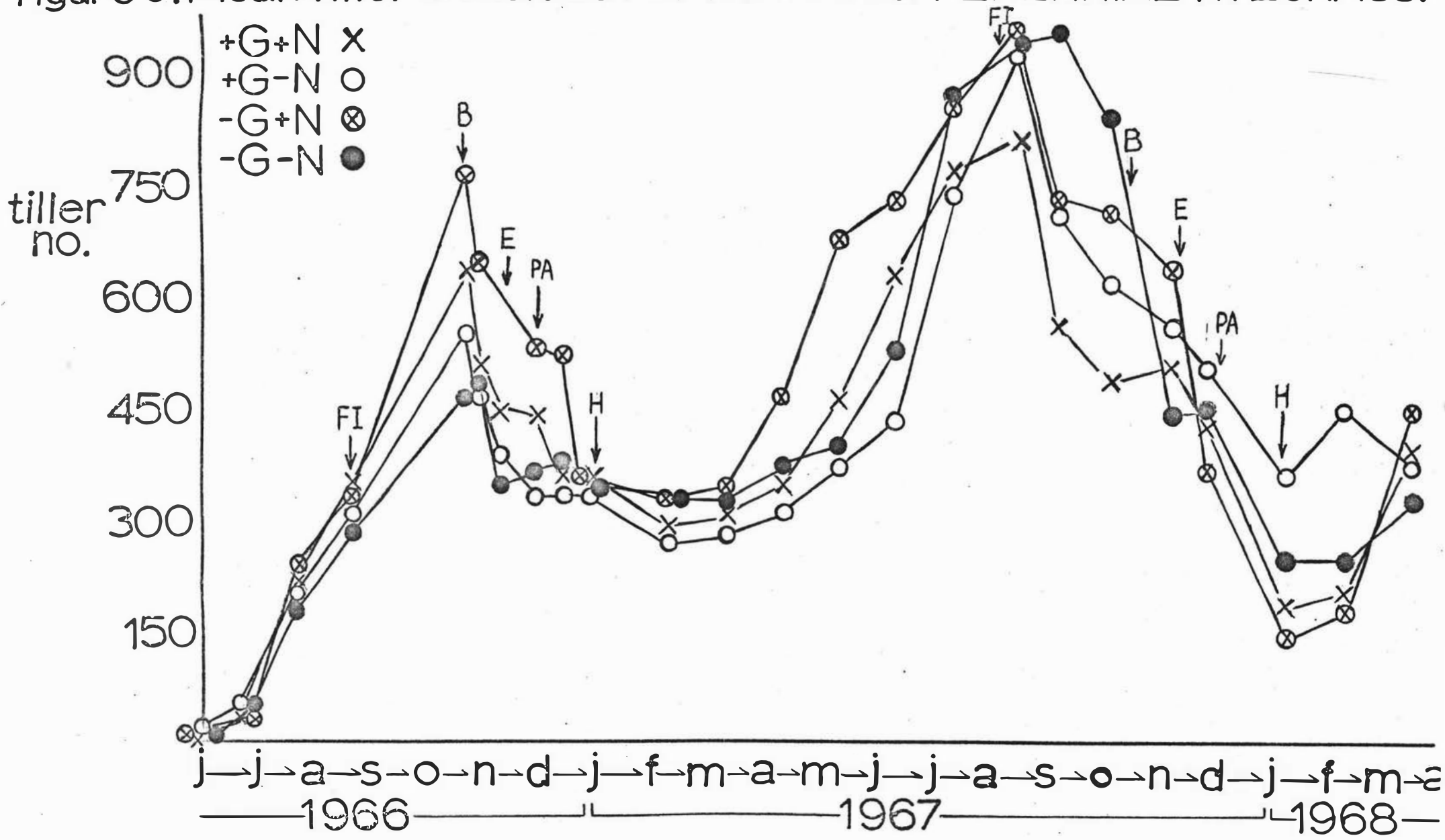
During the summer, a decline in tiller numbers occurred. Treatments receiving nitrogen contained more tillers than those not receiving nitrogen. This general trend continued through until harvest (1966) by which time treatment differences largely disappeared.

Throughout the following autumn and winter tiller numbers progressively increased to a peak in late August (1967), with nitrogen application resulting in significantly more tillers being present. Following floral initiation tiller numbers fell sharply, particularly during the months September to January. Following harvest in January 1968, a flush of new tillers occurred, extending into the autumn.

It is interesting to note the contrasting effect of grazing on tiller numbers following the 1966 harvest through to floral initiation in August 1967. Throughout this period grazing tended to depress tiller numbers particularly in the presence of nitrogen.

Because the seasonal variation in tiller numbers did not occur at the same point on the calendar scale in 1966 , and 1967 their interpretation is more difficult. Differences in seasonal conditions may have contributed to this effect. In addition the corresponding drop in tiller numbers following the boot stage of development (October) in 1966 occurred at an earlier stage coincident with floral initiation (August) in 1967. Possibly competition between plants in the first 6 months after sowing was not sufficient to cause a tiller number reduction through stresses imposed on the plants by floral initiation.

Figure 3. Mean Tiller Densities Per Row Foot. PERENNIAL RYEGRASS.



It is of interest that tiller numbers fluctuated between treatments during the spring and early summer - particularly in the second year. By harvest time in the second year treatment order was completely reversed compared with the previous autumn, with nitrogen tending to decrease, and grazing to increase tiller numbers. The complete reversal of treatment order at the time of peak anthesis (P.A.) between years was also an interesting feature.

2. Timothy

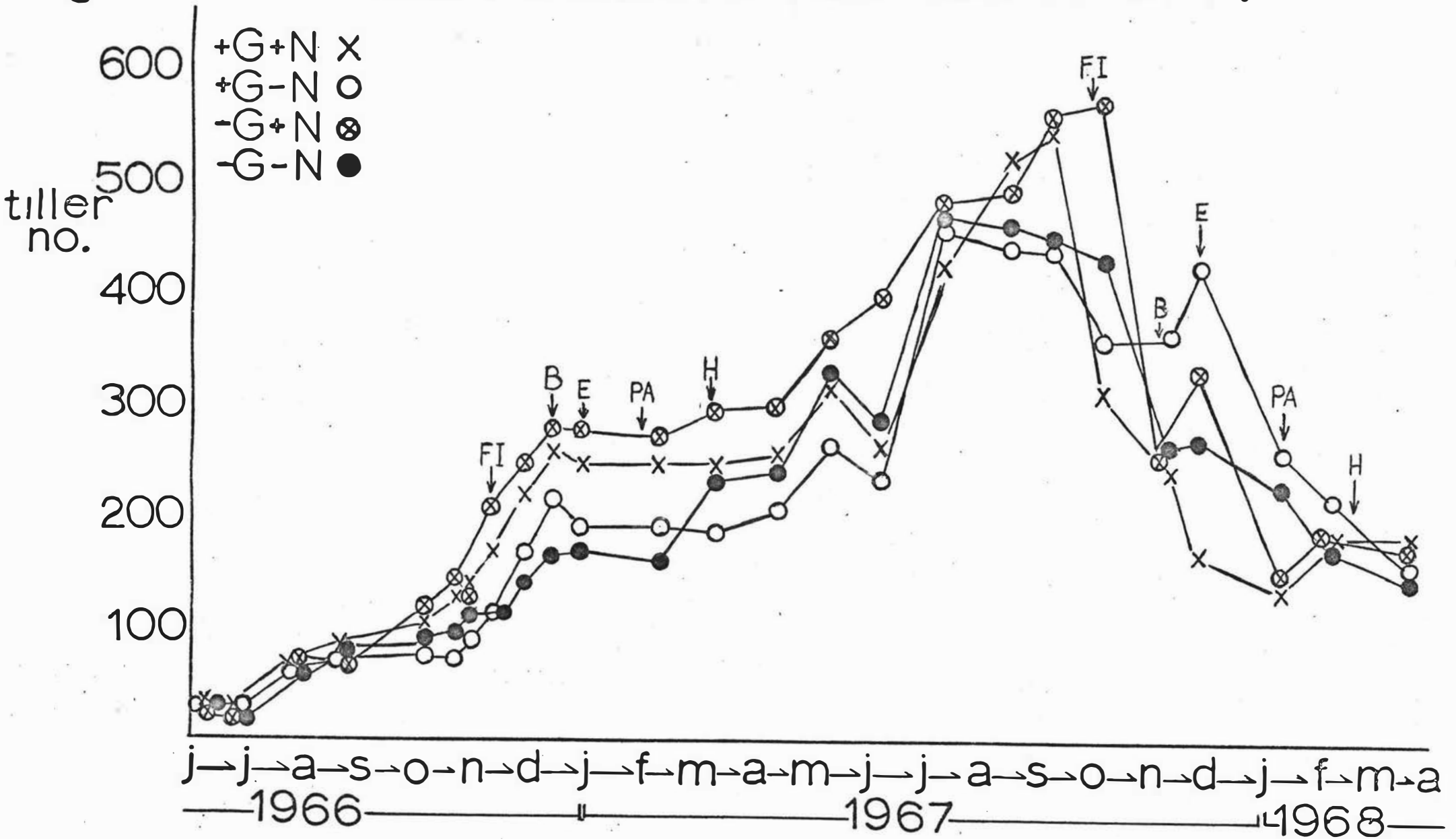
In timothy (Figure 4) the initial increase in tiller numbers following sowing was more prolonged than in the other two species studied (possibly as a result of slow seedling establishment), extending for up to 6 months after sowing (April to October). Prior to the onset of floral initiation (F.I.) in the first year management caused no significant variation in tiller numbers between treatments, which continued to rise until the boot stage of development (B). At floral initiation applied nitrogen significantly increased total tiller numbers irrespective of whether plots had been grazed or not. In contrast grazing depressed tiller numbers but only in the presence of nitrogen.

Total tiller numbers in each treatment remained relatively constant over the summer following sowing, with a gradual rise in tiller populations over the following autumn and winter to a peak in mid-winter for no-nitrogen treatments and continuing into the early spring for plots receiving nitrogen.

Following floral initiation tiller numbers fell, this downward trend continuing to the time of harvest (H) in February 1968. At ear emergence in the second year significantly higher tiller numbers were present in the grazed treatment without nitrogen than in all other treatments. The treatment incorporating both grazing and nitrogen was the poorest in terms of tiller numbers.

As with ryegrass, nitrogen appeared to increase tiller numbers while grazing, apart from a period in the summer of 1967, tended to decrease

Figure 4. Mean Tiller Densities Per Row Foot. TIMOTHY.



tiller numbers. Similarly, towards harvest (1968) the order of treatments was reversed compared with that pertaining in the previous autumn and winter.

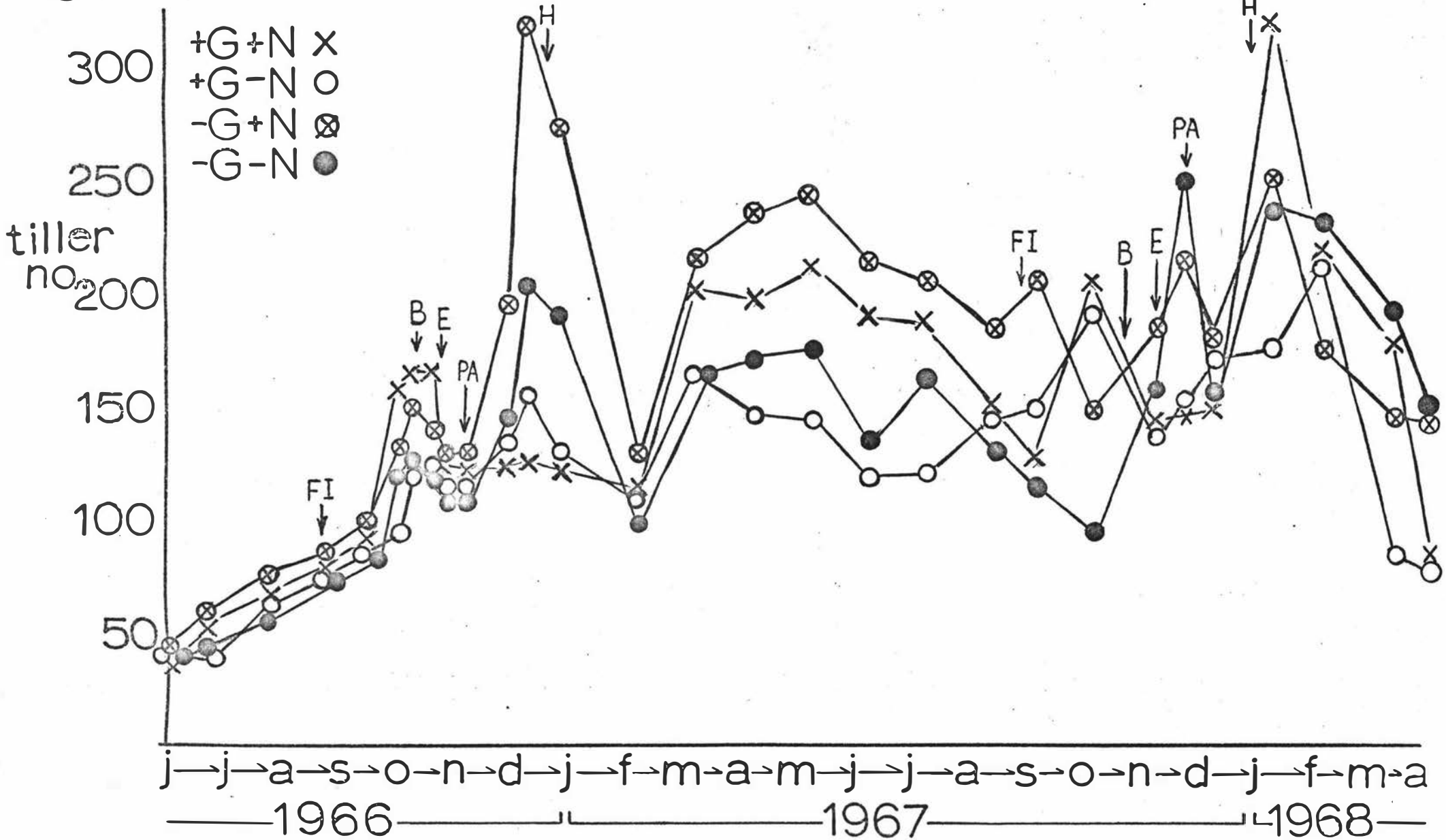
3. Prairie Grass

In prairie grass (Figure 5) there was a slow increase in tiller numbers from sowing through to the boot stage (B) in mid-October 1966. During this time management did not influence tiller numbers significantly between treatments. At the boot stage nitrogen significantly increased tiller numbers compared with no nitrogen whether plots had been grazed or not. After mid-October tiller numbers fell for approximately one month, followed by a sharp and steady increase in most treatments until immediately prior to harvest in December.

Grazed plots showed fewer tillers present over this period than ungrazed plots. After harvest tiller numbers again declined to a minimum level in the late summer (February), followed by a sharp rise to a relatively constant or slowly declining level during the autumn and winter, to floral initiation (F.I.) in late August. During the autumn and winter, nitrogen application significantly increased while grazing significantly decreased tiller numbers.

Following floral initiation (1967) treatment effects became more variable, fluctuating tiller measurements being obtained between treatments. By October in 1967 grazed plots contained significantly more tillers than ungrazed plots irrespective of presence or absence of nitrogen. Approximately one month later, however, ungrazed plots showed higher tiller densities. Immediately prior to seed harvest (H), tiller numbers increased to a sharp peak in January with applied nitrogen treatments being superior to no nitrogen treatments. Significantly higher tiller numbers were recorded in grazed plots receiving nitrogen compared with all other treatments. Subsequently tiller numbers fell until the beginning of the autumn (1968), with grazed plots showing a significant inferiority in terms of tiller numbers compared with ungrazed plots irrespective of nitrogen application or not.

Figure 5. Mean Tiller Densities Per Row Foot. PRAIRIE GRASS.



As shown in Figure 5 tiller numbers fluctuated widely and at times unexplainably between treatments, particularly over the spring and early summer of 1967.

DISCUSSION

In the first year of the experiment tiller numbers increased substantially in all three species from sowing through to the boot stage. By this time management effects were also becoming evident, particularly in ryegrass, where nitrogen appeared to increase tiller numbers. This increase in tiller numbers following applied nitrogen has been previously reported in ryegrass (Cooper 1958) and in prairie grass (Karim 1961). The effect of grazing however was more variable, sometimes causing an increase, sometimes a decrease in tiller numbers.

In all species tiller numbers remained relatively static or increased over the autumn with nitrogen application resulting in higher tiller numbers by the end of the autumn, particularly in ryegrass and prairie grass, than no nitrogen treatments irrespective of whether grazing had taken place or not. Grazing on the other hand generally depressed tiller numbers.

In each species there was one main period of increased tiller numbers each year. In the sowing year highest tiller populations were recorded at the boot stage in ryegrass and timothy followed by a sharp fall in tiller numbers in ryegrass and a relatively constant level in timothy over the summer and autumn with both tiller production and death apparently balancing each other. In prairie grass highest tiller numbers occurred during the period of seed maturation, particularly in December.

In the second year highest tiller numbers of ryegrass and timothy occurred at the time of floral initiation in August and October respectively. Subsequently tiller numbers fell sharply to low levels at harvest. In prairie grass a similar annual pattern of maximum tiller numbers occurred compared with the sowing year, with an increase during seed maturation to a peak at seed harvest. However during the early autumn tiller numbers rose to a fairly constant level in each treatment in March, April and May.

During the vegative growth stage, tillering was the dominant process, but when reproductive development became advanced, tillering virtually ceased causing a significant reduction in tiller formation.

In all three species (in the second year in particular) the main feature of the pattern of tillering, was the decrease in tiller numbers recorded in the late spring and continuing through the summer. This reduction occurred first in prairie grass, and later in ryegrass and timothy. Such behaviour seems to be entirely concomitant with the depressing effects of flowering on tiller production reported by other workers (Lamp 1952, Langer 1958). The apparent high rate of mortality of tillers (probably the relatively large number of very small tillers observed) in the spring, (September to November) may be interpreted in the light of Langer's (1963) observation that imposition of a stress factor on a plant (in this case a possible combination of morphological and environmental stresses) causes death of most recently formed tillers first. This mortality possibly occurs through competition for environmental factors which are in short supply. In addition this effect may be due to emphasis on the growth of established tillers rather than on the production of the new tillers. It is also possible that increased growth of the sward at this time will reduce the amount of light penetrating to the base of the plant. Such basal shading would reduce tiller production as shown by Mitchell and Coles (1955).

In all species the replacement of both fertile and other tillers that died between spring and mid-summer gave rise to a second increase in production of new tillers commencing approximately two months after seed harvest in the summer and through the autumn. The annual cycle of tiller production is similar to that described by Barnard (1964), Lamp (1952) in Bromus inermis and Langer (1956) in timothy.

It is also possible that many of the new tillers produced in the summer, particularly under dry soil conditions, must rely on the established roots of the parent tiller for water and nutrients until soil conditions become

more suitable for root growth and development. Seasonal conditions over the spring and summer period were abnormally wet in 1966 whereas in 1967 very dry conditions prevailed over the same period. Timothy in particular is generally acknowledged as thriving best under moist soil conditions. Under dry conditions the effect of defoliation by stock and the inability of the plant to absorb soil nitrogen may provide sufficient stress to be reflected in high mortality of young tillers. This is partly reinforced by the suggestion by Lambert (1966) that nitrogen effects may be modified by availability of soil moisture. Timothy, being a late maturing species is likely to be more adversely affected by dry summer conditions than the other two earlier-maturing species.

Throughout the second year significant treatment differences were more in evidence in all species. As mentioned earlier nitrogen fertiliser generally appeared to increase, while grazing appeared to decrease, tiller numbers. However, at, or just prior to, harvest in the second year (1968) a reverse effect appeared in ryegrass and timothy, with nitrogen tending to depress and grazing stimulate tiller numbers. No such trend was observed in prairie grass. One possible explanation would be to interpret this treatment order reversal in terms of fertile tiller production. Those treatments producing the highest tiller numbers in the autumn and winter prior to floral initiation would be likely to show the lowest number of vegetative tillers at harvest because of the higher population of seedheads being produced. Nitrogen application would tend to emphasise this effect by stimulating more reproductive tillers at the expense of vegetative tillers. Grazing would tend to have the reverse effect. This emphasises the importance of management in altering the balance between vegetative and reproductive tiller numbers at different times of the year.

CONCLUSION

Within each of the three species studied total tiller numbers exhibited a distinct annual cycle. This indicates that environmental effects and plant physiological processes regulate the rate at which new tillers are produced. Two phases of tiller production occurred. An initial phase in the first six months after sowing during which tiller numbers rose significantly irrespective of nitrogen and grazing management. Thereafter, following floral initiation, treatment effects became evident about the time of the 'boot' stage of reproductive development. The number of tillers formed either remained static or fell sharply. High tiller mortality occurred in ryegrass and timothy during the spring. Following harvest tiller production generally occurred over the late summer, autumn and winter periods. Following floral initiation in the spring total tiller numbers again fell sharply. In prairie grass there were two periods of tiller production, the first in the autumn and a second more pronounced peak during seed maturation. Between these two periods fewer new tillers were produced. In ryegrass and timothy the majority of new tillers were formed over the autumn and winter periods, a marked reduction in tiller numbers occurring at, or slightly prior to floral initiation in the second year. Management influenced tiller numbers in each species. Nitrogen application increased tiller numbers in all three species, particularly over the autumn and winter. Grazing generally depressed total tiller numbers, although this depression was partly overcome by nitrogen application.

TILLER LONGEVITY AND SURVIVAL

INTRODUCTION

Perenniality in grasses is expressed by the fact that in a plant bearing several hundred tillers only a small proportion produce seedheads. Most of the remaining tillers die before the maturity of seed in fertile tillers is complete, or following harvest, but some survive. In addition, new tillers are formed at the base of the plant following harvest and extending into the autumn and winter. With this general growth pattern the plant is perpetuated. In seed production it is important to know what proportion of tillers become reproductive, the tiller numbers originating at different times of the year, and which tillers contribute most to the final crop of seedheads and hence to total seed yield.

In any attempt to analyse seed yield components of perennial grasses, it is necessary to consider the longevity and survival of individual tillers and their development in relation to the seasonal environment. During the late summer, autumn and winter, tillers grow vegetatively and it is not until the spring that those destined to bear ears actually become reproductive.

The longevity of individual tillers in a grass sward can be extremely variable depending on genotype and environment.

In the present study, attempts were made to follow the life histories of individual tillers to determine what proportion became reproductive and the contribution of tillers produced in particular months to total seedhead production.

LITERATURE REVIEW

The life history and longevity of tillers may vary with time of origin and environment. Langer (1963) distinguishes 3 different types, one or more of which can be represented on the same plant.

(1) Tillers which flower and consequently die in the year of formation, describing an annual life cycle.

(2) Tillers which flower and die in the year after formation in the manner of a biennial plant.

(3) Tillers which fail to flower and whose length of life may vary from a few weeks to a year or more.

Langer notes (1963) that under conditions of environmental stress, recently formed tillers tend to die first, their life being terminated after only a short time. Once established however they can remain alive for longer periods provided they remain vegetative. The proportion of the above 3 types of tillers determines the habit of the plant.

The length of life of individual tillers is an important factor in the survival of the whole plant. Langer (1956) examined the perennial habit of timothy in terms of tiller production and survival. He showed that tillers were relatively short-lived, and only a proportion of those formed each year produced inflorescences. He also suggested (Langer 1957a) that many vegetative tillers on timothy plants in his experiments would probably have flowered in the following year, describing a biennial life cycle. The remainder would have eventually died in the vegetative condition. He observed that tillers formed in the spring, even if they failed to form seedheads, tended to die predominantly during the following autumn, winter and spring while tillers formed in late summer appeared to suffer fewer casualties. Origin in late autumn was attended by a high mortality rate during the following summer. Tillers formed during the late summer apparently make the major contribution to the vegetative growth of the plant the following year.

Ryle (1965b) similarly observed that tillers formed in the late summer and early autumn provided the bulk of the ear-bearing tillers the following spring. Also, tillers arising at successively later dates had a proportionately smaller chance of developing an ear (Langer & Lambert 1959). At all times, however, there was a large and changing population of tillers which remained vegetative. Ryle (1965b) has noted that in single plants over half the tillers fell into this category. In the sward, the situation was much the same in early spring, but many vegetative tillers died as inflorescence development proceeded. Ryle suggests this partition within the plant between fertile and vegetative tillers is inherent in the genotype of the variety.

The contribution of tillers of different ages to the final number of seedheads produced in meadow fescue and cocksfoot has been shown by Langer &

Lambert (1959) to be unaffected by increased nitrogen. Although their studies stress the influence of the autumn tillering period on subsequent fertile tiller production, seed stands need continued good management in the spring at floral initiation. Langer & Lambert (1959) suggest that seed yield at harvest depends largely on the number of tillers formed before the winter, possibly quite soon after the previous harvest.

In studies on plant density and seed production in timothy Lambert (1964) observed that although late-formed tillers may produce ears, percentage fertility based on spring tiller numbers is the best index of reproductive capacity. Most tillers which do not become fertile die prior to harvest and new tillers may be formed at the base of the plant as the ears mature. Ratios of ear numbers to vegetative tillers at harvest are therefore, Lambert suggests, of limited value as expressions of fertility.

Langer & Ryle (1959) have shown in timothy that tillers continued to be produced until ear emergence when the rate of tiller production declined, with only occasional new tillers being recorded. This decline in tiller production for 2-3 weeks following ear emergence has been also noted in timothy by Evans (1927). Similar results were obtained by Silsbury (1966) in perennial ryegrass, Lamp (1952) in Bromus inermis, and by Laude et al (1967) in barley. The latter workers found that tiller senescence and mortality was similar in both sterile and fertile plants of barley up until 10 days after awn emergence. After awn emergence, new tillers were produced. They concluded that mobilisation of reserves in the developing grains was not a factor determining tiller mortality. In addition, shoot mortality prior to awn emergence was not related to nutrient deficiency, reduced light intensity, or seed development but Laude et al (1967) could offer no conclusions on the cause of tiller senescence or death at this stage of development.

In plants bearing many tillers, it appears that larger tillers are more likely to become fertile than smaller ones. This is presumably why the majority of ears at harvest have been found to be produced by tillers initiated

in the previous late summer and autumn periods in a number of different grass species (Griffiths et al (1967)).

Lambert (1963b) found in cocksfoot that as tiller populations per plant increased with age of stand, fertility fell. The efficiency of tillers in producing ears was low. Wastage of tillers was high and as many tillers did not extend more than 2 inches and had limited life-spans, Lambert suggested they could be regarded as parasites. Therefore, means of controlling tiller production at certain times of the year might be thought advantageous. In addition, higher fertility in tillers produced is obviously desirable. In this respect judicious control of grazing and nitrogen application might well be important to control tillering and increase the number of fertile tillers.

MATERIALS AND METHODS

In order to follow the life history and longevity of individual tillers from their month of formation through until seed harvest a method for identifying individual tillers was devised as described earlier. (Materials and Methods page 13).

In prairie grass new tillers were labelled at approximately monthly intervals at the 2-leaf stage, by which time it was possible to see them arising from the leaf sheath. In timothy and ryegrass, however, basal tillers could often be identified at an earlier stage and were marked when approximately 1" in length.

In the present study the coleoptile tiller was designated 'primary' and tillers developing from the base of the plant 'secondary'. These correspond to the tillers designated by Mitchell (1953b) as the 'coleoptile tiller' and the 'first-order tiller'.

At seed harvest, examination allowed the classification of marked tillers into 'reproductive', 'vegetative' and 'dead' categories according to their month of tiller origin.

Time of seed harvest in each year was January (for ryegrass and prairie grass) and March (for timothy).

RESULTS AND DISCUSSION

The results for 1966 and 1967 which are presented in Tables 1 and 2 respectively, show that many labelled tillers that did not produce ears died before seed harvest. Also, the proportion of reproductive tillers was generally highest amongst the oldest tillers in all three species in both years. The majority of tillers originating during the earlier months either became reproductive or died in the vegetative condition before seed harvest, describing an annual life cycle. However, from July 1966 and from October or November 1967 onwards, an increasing number of tillers remained vegetative through to seed harvest. It is suggested that the great majority, if not all, of these tillers died without producing seedheads before the following autumn as no tillers marked in 1966 could be found in April 1967. These tillers in fact behaved as biennials. It was particularly noticeable that a larger number of spring-formed tillers had died at seed harvest in all species in 1966. In the following year tillers formed in September in ryegrass, October and November in timothy and August and September in prairie grass generally showed highest losses through tiller death as determined at the following harvest.

In all three species tillers formed during the immediate post-harvest period and through the autumn produced a high percentage of the total seedheads at the following harvest and had a lower mortality rate than tillers produced in the spring and early summer. This indicates that efforts should be made to encourage the production of high tiller numbers during this period. The present results support the findings of other workers with cocksfoot (Langer & Lambert 1959, Lambert 1963b, 1967a, 1967c); timothy (Lambert 1967b, Langer 1956, 1957a, Langer & Ryle 1959, Ryle 1963, 1964, 1967, Wilson 1959); Bromus inermis (Lamp 1952); Prairie grass (Saxby 1956) and perennial ryegrass (Roberts 1958a, Wilson 1959, Ryle 1964, Schwass & Jacques 1956, and Cooper & Saeed 1949).

Probably the main reason for the high proportion of tillers producing seedheads in the year of sowing (in all species) was that the primary tiller

TABLE I FATE OF TILLERS FORMED EACH MONTH AS DETERMINED AT TIME OF SEED HARVEST (FIRST YEAR 1966)

		Month of tiller origin (April sowing)								
PERENNIAL RYEGRASS %		May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
+G+N	Reproductive	97	94	75	56	3	-	-	-	325
	Vegetative	-	3	16	31	71	93	96	93	403
	Dead	3	3	9	13	26	7	4	7	72
+G-N	Reproductive	96	90	63	56	2	1	-	-	308
	Vegetative	1	3	22	28	66	93	97	96	406
	Dead	3	7	15	16	32	6	3	4	86
-G+N	Reproductive	97	95	84	60	1	2	-	-	339
	Vegetative	-	4	10	28	62	91	94	96	385
	Dead	3	1	6	12	37	7	6	4	76
-G-N	Reproductive	94	92	64	46	3	-	-	-	299
	Vegetative	2	2	19	34	67	90	93	98	405
	Dead	4	6	17	20	30	10	7	2	96
TIMOTHY %										
+G+N	Reproductive	95	85	89	72	59	23	10	-	433
	Vegetative	-	3	1	7	14	38	86	97	246
	Dead	5	12	10	21	27	39	4	3	121
+G-N	Reproductive	95	91	82	68	31	23	3	-	393
	Vegetative	4	2	11	23	28	54	86	91	200
	Dead	1	7	7	9	41	23	11	9	108
-G+N	Reproductive	97	89	81	75	58	33	15	1	449
	Vegetative	-	4	7	9	11	41	78	95	245
	Dead	3	7	12	16	31	26	7	4	106
-G-N	Reproductive	92	89	72	57	33	23	7	-	373
	Vegetative	5	4	11	24	47	56	91	95	333
	Dead	3	7	17	19	20	21	2	5	94
PRAIRIE GRASS %										
+G+N	Reproductive	94	96	78	67	12	-	-	-	347
	Vegetative	1	-	11	17	69	95	93	99	385
	Dead	5	4	11	16	19	5	7	1	68
+G-N	Reproductive	97	91	82	54	2	-	-	-	326
	Vegetative	-	2	7	26	67	93	95	97	387
	Dead	3	7	11	20	31	7	5	3	87
-G+N	Reproductive	95	97	77	55	9	-	-	-	333
	Vegetative	1	-	9	23	68	94	94	97	386
	Dead	4	3	14	22	23	6	6	3	81
-G-N	Reproductive	97	90	72	41	4	-	-	-	304
	Vegetative	-	6	12	31	63	89	91	98	390
	Dead	3	4	16	28	33	11	9	2	106

TABLE 2 FATE OF TILLERS FORMED EACH MONTH AS DETERMINED AT TIME OF SEED HARVEST (SECOND YEAR 1967)

		Month of Tiller Origin												
		Jan.	Feb.	Mar.	Apl.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
PERENNIAL RYEGRASS (%)														
+G+N	Reproductive	63	62	71	62	38	16	12	1	-	-	-	-	385
	Vegetative	10	12	17	16	13	34	35	31	28	78	91	97	462
	Dead	27	26	2	22	9	50	53	68	72	22	9	3	413
+G-N	Reproductive	52	47	42	36	31	2	-	-	-	-	-	-	210
	Vegetative	18	29	37	37	31	52	33	46	19	83	96	96	577
	Dead	30	24	21	27	38	46	67	54	81	17	4	4	413
-G+N	Reproductive	69	61	60	68	33	9	13	2	-	-	-	-	315
	Vegetative	12	18	13	9	29	39	29	40	27	86	89	97	578
	Dead	19	21	27	23	38	52	58	58	73	11	11	3	396
-G-N	Reproductive	56	62	53	47	40	6	8	-	-	-	-	-	272
	Vegetative	16	21	27	23	32	45	30	38	19	81	92	91	515
	Dead	28	17	20	30	28	49	62	62	81	19	8	9	413
TIMOTHY (%)														
+G+N	Reproductive	71	63	68	57	61	50	41	47	32	21	18	2	531
	Vegetative	12	26	11	15	28	23	32	37	51	16	31	91	373
	Dead	17	11	21	28	11	27	27	16	17	63	51	7	296
+G-N	Reproductive	68	61	64	58	52	41	47	38	31	24	12	3	479
	Vegetative	12	13	13	19	22	38	33	43	42	19	22	89	365
	Dead	20	26	23	23	26	21	20	19	27	57	56	8	336
-G+N	Reproductive	57	53	61	52	46	49	33	36	20	11	8	1	427
	Vegetative	29	28	18	27	36	25	29	27	59	17	29	82	406
	Dead	14	19	21	21	18	26	38	37	21	72	63	17	367
-G-N	Reproductive	77	71	76	68	67	53	56	37	33	26	7	3	574
	Vegetative	11	13	16	14	21	26	23	47	51	17	26	92	357
	Dead	12	16	8	18	12	21	21	16	16	57	67	5	269
PRAIRIE GRASS (%)														
+G+N	Reproductive	82	67	50	30	38	7	10	-	-	-	-	-	284
	Vegetative	-	-	25	35	19	33	11	13	6	68	87	92	389
	Dead	18	33	25	35	43	60	79	87	94	32	13	8	527
+G-N	Reproductive	83	65	32	30	50	5	-	-	-	-	-	-	265
	Vegetative	10	31	17	38	39	13	21	2	14	89	88	93	455
	Dead	7	4	51	32	11	82	79	98	86	11	12	7	480
-G+N	Reproductive	85	59	28	62	39	8	20	3	-	-	-	-	304
	Vegetative	1	8	11	17	6	14	24	23	29	97	88	90	408
	Dead	14	33	61	21	55	78	56	74	71	3	12	10	488
-G-N	Reproductive	98	57	60	48	31	5	14	-	-	-	-	-	313
	Vegetative	-	12	10	25	17	28	47	28	40	95	92	94	488
	Dead	2	31	30	27	52	67	39	72	60	5	8	6	399

produced from each seed was more likely to persist until it was induced to flower under appropriate environmental conditions. This was shown by the fact that in all species, tillers formed in May and June 1966 (in the first 5-10 weeks after sowing) were highly persistent. Generally, 90% or more of these tillers produced seedheads. Those tillers which did not initiate seedheads either died or in rare cases remained vegetative. Similar observations have been made by Langer (1956). In S48 timothy he found that more than twice the number of secondary tillers produced fewer total inflorescences than primary tillers on the same plant. The same effect has been reported by Lamp (1952) in Bromus inermis.

Seedheads of prairie grass produced by tillers formed in the first few weeks after sowing are of particular interest. In the majority of heads subsidiary panicle branches were formed, their stems arising from the base of the first node below the seedhead on the main culm. This emphasises the high development potential and intensity of floral initiation and seedhead development of primary tillers of this species. The high proportion of early tillers producing seedheads is probably responsible for the increased monthly percentage of seedheads produced in the first year, compared with those formed in the second year.

One factor which appeared to influence tiller survival in some treatments was severe weed competition - particularly from Holcus lanatus and Glyceria fluitans growing within the rows. Weed growth was particularly severe in ungrazed plots to which nitrogen had been applied in timothy and to a lesser extent in ryegrass. Prairie grass effectively smothered the ingress of weeds. It is possible that this weed growth could have accounted for the apparent change in the contribution of tillers of different ages to the final number of seedheads produced, particularly in timothy, in the ungrazed treatment in the second year. Apart from this effect there was no consistent evidence of either grazing or nitrogen influencing the contribution of these different aged tillers, as also found by Langer & Lambert (1959).

CONCLUSION

Tiller identification according to month of origin allowed the fate of individual tillers to be determined at harvest. Many vegetative tillers died before harvest, behaving as annual tillers.

Spring formed tillers made a major contribution to the vegetative growth of the plant over the summer and early autumn. These tillers generally died before the following winter, and were therefore biennial. Winter and early spring tillers in prairie grass and ryegrass showed a high mortality, particularly in the second year. In timothy, mortality was highest amongst tillers formed in the late spring. In all species tillers formed in the immediate post-harvest period and through the autumn made a major contribution to the number of seedheads at harvest. These tillers had a lower mortality rate than those formed in the spring. Primary tillers formed after sowing were highly persistant and became almost exclusively reproductive.

FLORAL INITIATION AND DEVELOPMENT

INTRODUCTION

The morphological changes occurring during floral initiation and development have been described in a number of grass species.

These descriptions have explained many aspects of reproductive developmental morphology but few attempts have been made to apply such studies to field situations. The present study describes the visible changes occurring during reproductive development and follows the sequence and rate of inflorescence development in tillers formed some months previously in the sowing year.

LITERATURE REVIEW

An understanding of reproductive development is fundamental in any consideration of seed production capacity of a plant, (Thomas 1961).

The initiation and development of grass inflorescences is usually controlled by temperature and photoperiod, the course of such development being broadly divided into three stages (Cooper 1960).

1. Floral induction, during which apical meristems become capable of responding to flowering stimuli (Lambert (1967c) quotes Kleb's 1910 use of the term 'ripeness to flower'.)
2. Floral initiation, in which visible changes in the inflorescence occur in response to environmental conditions.
3. Floral development, of the meristem tissue with accompanying elongation of the stem internodes.

1. Floral Induction

As floral induction was not studied no review on this aspect will be made. However, it is relevant to mention, in view of later discussion, that many temperate perennial grasses also possess a 'winter' requirement for low temperatures and short days before floral initiation is possible, (Peterson et al 1958). This requirement is obligatory for Lolium perenne (Breese 1966), but not for Phleum pratense (Cooper 1960) or Bromus unioloides (Karim 1961).

2. Floral Initiation and Development

The morphology of the grass apex, the course of its development and visible changes occurring during reproductive development have been described by Cooper (1950), Williams (1965), Sharman (1947), Purvis (1934) and Olugbemi (1968). Detailed studies on the development of shoot apices in specific species have been carried out by Sharman (1947) in Agropyron repens, Evans & Grover (1940) in perennial ryegrass, timothy and cocksfoot; Johnston & MacDonald (1967) in Festuca scabrella Torr; Evans and Allard (1934) and Griffiths et al (1967) in cocksfoot; Barnard (1955a) in Triticum aestivum L; Sharman (1960) in Anthoxanthum odoratum L; Jeater (1956) in perennial ryegrass, cocksfoot, timothy and meadow fescue; Evans (1960) in Cynosurus cristatus; Anderson (1954) in cereals; and Cooper (1950) in a range of ryegrasses. The floral histogenesis of a number of species, including Bromus unioloides and Lolium multiflorum Lam has been described by Barnard (1957) and in the Gramineae generally by Williams (1965).

Workers generally agree that shoot apices of temperate grasses remain vegetative through the autumn and winter, initiating floral primordia in the following spring in response to increasing daylength and temperature. The production of mature flowers and seeds is likewise favoured by long days (Evans and Allard (1953), Gardner and Loomis (1953).

According to Evans and Grover (1940) the timing of floral initiation is variable in grasses according to species, tiller order, tiller age and leaf number, nutrition, seasonal conditions, daylength, latitude and probably other factors as well.

In many herbage grasses, internodal elongation does not occur until the late spikelet bud stage, when the apical meristem is transformed into the apical spikelet. (Cooper 1956). He suggests also (Cooper 1952) that once ear initiation has occurred, the rate of inflorescence elongation is influenced mainly by temperature.

A number of workers have attempted to measure onset of floral development by recording the number of leaves on tillers at floral initiation. Cooper

and Saeed (1949) recorded this leaf number in S24 perennial ryegrass as over 20 under continuous light, whereas only 10-11 expanded leaves were required before floral development occurred in the field (Cooper 1951). Sharman (1947) recorded that in Agropyron repens 10-11 leaves must be produced on the main axis before that tiller could become reproductive and Lamp (1952) noted in Bromus inermis that the number of leaves on tillers at floral initiation varied from 5 to 14, with 80% of tillers producing leaf numbers in the 7 to 10 range. Lamp suggests that no one leaf number can serve as an accurate measure of the onset of reproductive development.

Purvis (1934), working on rye, found that in short days apparently non-flowering tillers had in some cases actually formed an inflorescence which did not elongate and decayed within the leaf sheath. Similar effects have been noted by Cooper (1951, 1952) in perennial ryegrass, and Langer (1956), Cocks (1958a) and Cooper (1959a) in timothy. They also suggest there appears to be an inhibitory effect of high temperatures on inflorescence development. Such conditions however do not appear to prevent internodal elongation. In timothy plants grown in continuous light or long day conditions, many shoots elongate, whether heads have been initiated or not. Similarly, Wilson (1959) noted the almost complete absence of floral initiation in a range of grasses after late December, even though daylength at this time was approximately 2 hours longer than that prevailing during the main period of floral initiation.

MATERIALS AND METHODS

At intervals commencing the first week of August for prairie grass and ryegrass, and mid-October for timothy, samples of tillers of known month of formation were removed for examination. At each sampling twenty dissections were carried out on tillers of different months of origin in each treatment. The percentage of reproductive apices was recorded. This allowed comparison of the rate of onset and extent of floral development between treatments and also between tillers formed in successive months during the year. Selected apices were photographed to show the sequence of floral development of each species. (See materials and methods, page 15).

RESULTS AND DISCUSSION

Development stages are shown in Figures 6, 7 and 8 for ryegrass, timothy and prairie grass respectively. A short series of additional photographs taken on a scanning electron microscope (see acknowledgements) are presented in Appendix 3.

Because of similar development in these species a series of common developmental stages were used to describe the sequence of reproductive development. These stages were based on those used by Jeater (1956). However, it was felt that difficulties of interpretation would arise if too many different stages were included. This agrees with the findings of Jeater (1956) who suggests that it is better to have a small number of stages with large morphological differences between each.

The code in Figures 6, 7 and 8 refers to the following stages of development.

(a) Vegetative, apex short. (Vegetative primordia ryegrass 5-7, timothy 6-10, prairie grass 3-4).

(b) Vegetative - apex elongated (minimum vegetative primordia ryegrass 8, timothy 11, prairie grass 5).

(c) 'Double ridge' Stage (internodal elongation in timothy).

(d) Spikelet primordia visible ryegrass, secondary primordia visible in timothy and prairie grass.

(e) Glume ridges visible in ryegrass, tertiary and/or quarternary primordia visible in timothy and prairie grass.

(f) Floret buds developing and glumes elongating in ryegrass, glume ridges visible in timothy and prairie grass.

(g) Florets developed, glumes elongated, lemmas elongating, internodal elongation in ryegrass. Elongation of inflorescence glumes visible on most of apex, lemmas elongating, floret buds visible in timothy and prairie grass.

(h) Lemmas and glumes covering some or all florets.

(i) Ear emergence in ryegrass and timothy (not shown) secondary branch elongation in prairie grass.

FIGURE 6 STAGES OF REPRODUCTIVE DEVELOPMENT
PERENNIAL RYEGRASS

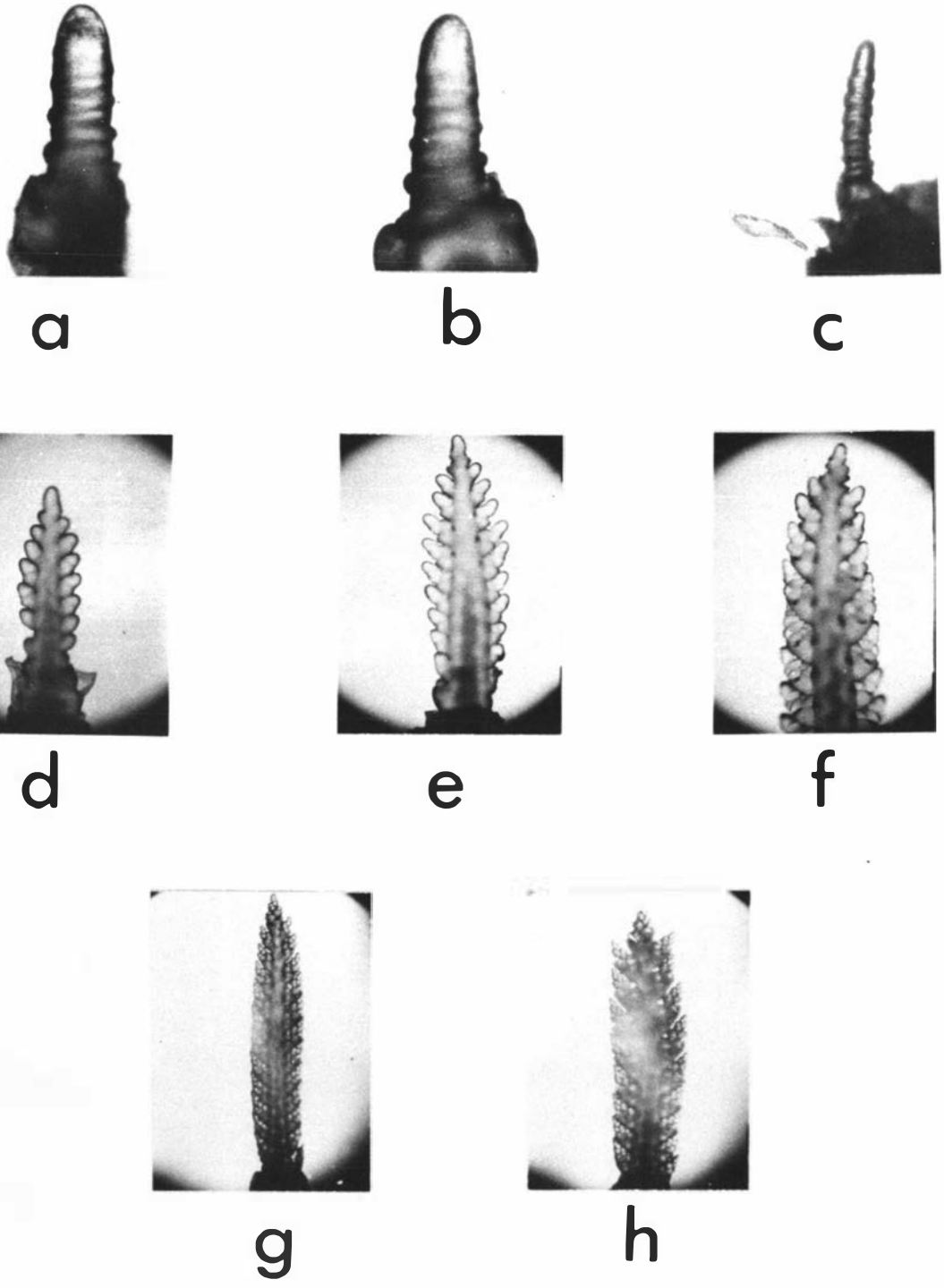
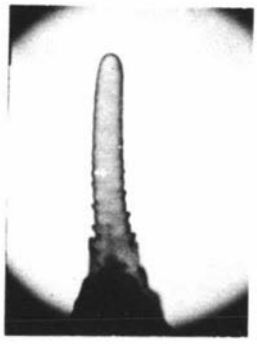


FIGURE 7 STAGES OF REPRODUCTIVE DEVELOPMENT
TIMOTHY

a



b

c

d

e

f

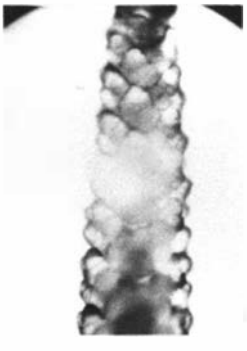


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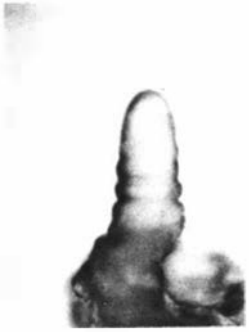
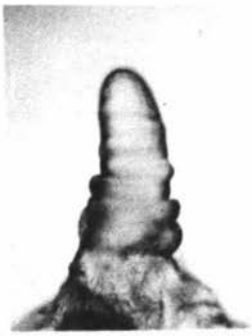
FIGURE 8 STAGES OF REPRODUCTIVE DEVELOPMENT
PRAIRIE GRASS

a



b



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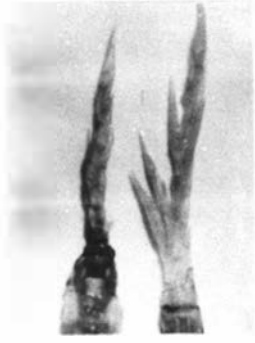


j

(j) Boot stage through to ear emergence in prairie grass.

Apex Morphology

(a) Vegetative

On the vegetative apex primordia are visible as transverse ridges across the apex in the same plane as the leaves. (Plate 3).

Prior to initiation the apex elongates and there is an increase in the number of vegetative primordia, these appearing as small collars.

(b) Reproductive

The change-over from a vegetative apex to a young inflorescence is a rapid process. Buds in the axils of some of the leaf primordia develop forming the transitional 'double-ridge' stage (Plate 4). This change occupies only a short period of time. Double ridges are visible as alternate rows of double 'bumps'; the lower ridges representing the leaf primordia (Figure 6c, 7c, 8c) and the upper ones representing the buds in the leaf axils.

Further development proceeds in both acropetal and basipetal directions, the most advanced stage being in the central region of the developing inflorescence. (Figure 6d, 7d, 8d).

Spikelet primordia develop rapidly, showing as rounded protuberances arranged opposite and alternately on the apex. Their development soon makes it difficult to detect the subtending leaf primordia.

To this stage reproductive development in all three species was similar. Further development differed according to the type of inflorescence. In ryegrass, the spike has an unbranched axis with the spikelets sessile. In both timothy and prairie grass, the inflorescence takes the form of a panicle, the main axis being branched and rebranched, and the spikelets pediceled. In the case of timothy the panicle branches are short and hidden by the spikelets, the inflorescence appearing to be in the form of a spike. The spreading panicle is regarded by Barnard (1964) as the most primitive form of inflorescence. The ultimate form of the inflorescence is mainly due to the number of times branching is repeated before spikelet differentiation and the relative length of the internodes of the various branch orders. In all three species, once spikelet

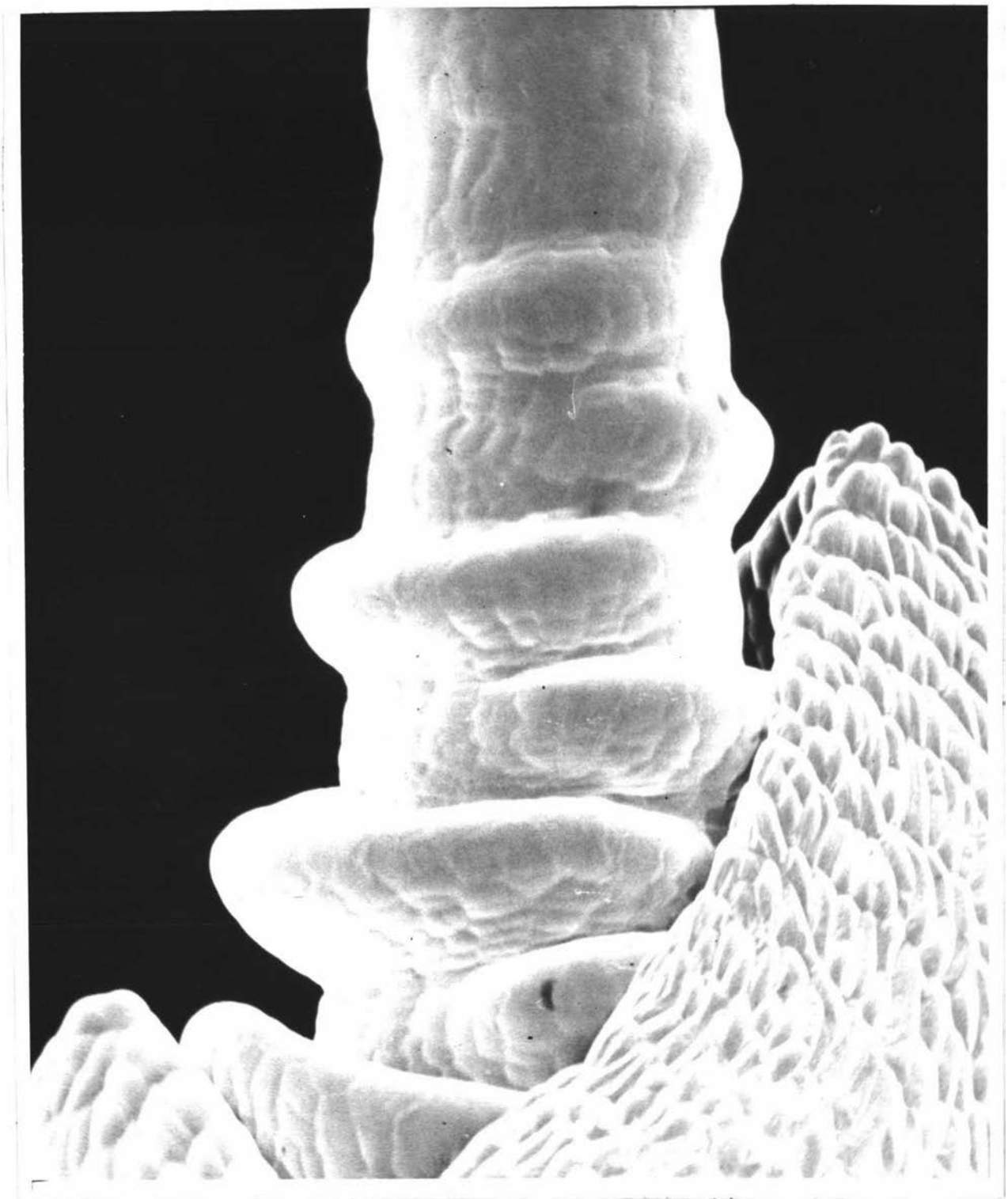


Plate 3 - Vegetative apex showing leaf primordia - perennial ryegrass x343

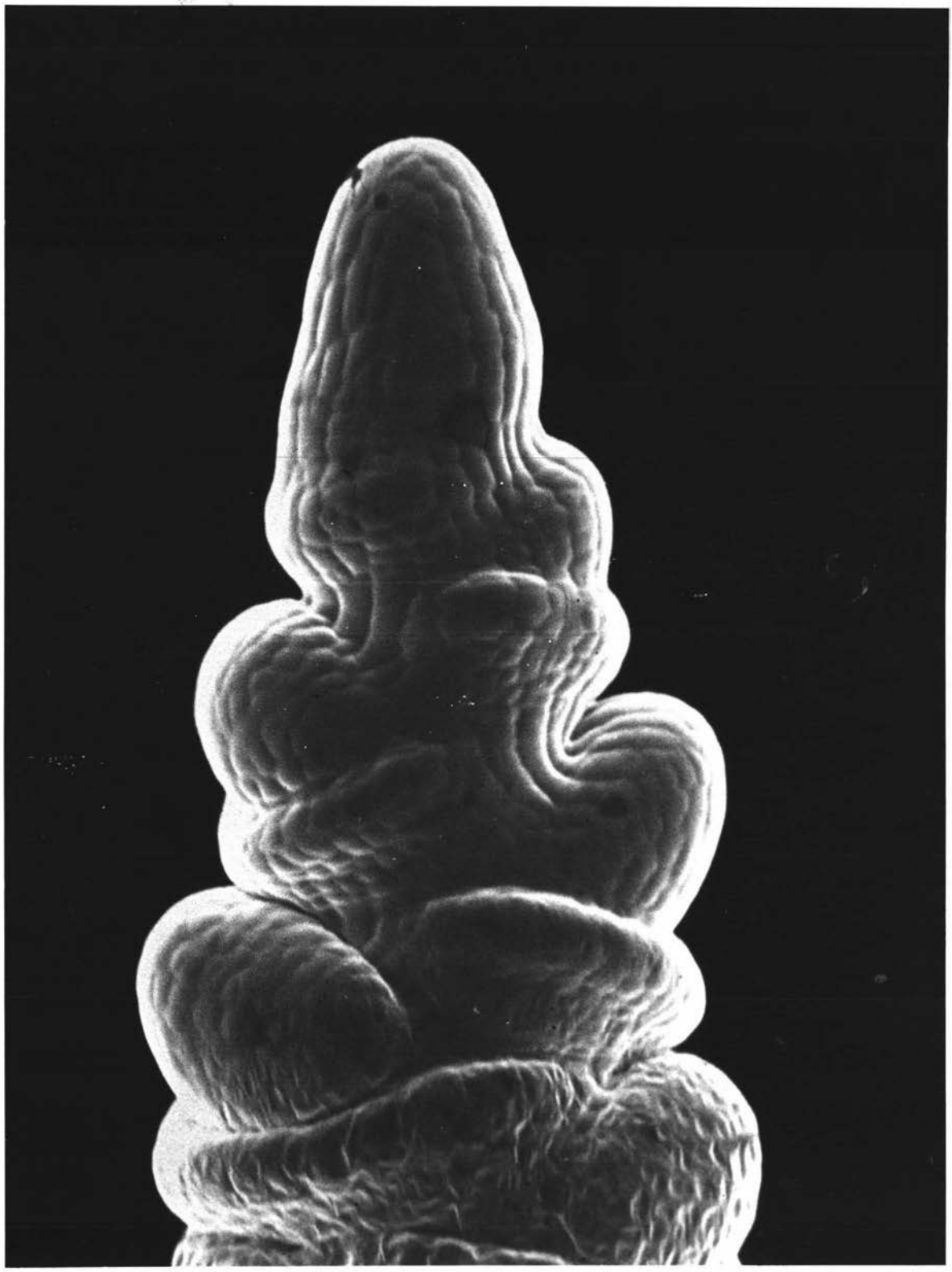


Plate 4 - Reproductive apex, double ridge stage - perennial ryegrass x196

initials have been produced subsequent development of florets, carpels and stamens is similar in all three species. Firstly the glume ridges appear closely followed by those of the lemma and palea. These elongate and eventually envelope the developing stamens. At ear emergence both the male and female parts are completely enclosed within the glumes, lemmas and paleae.

Secondary protuberance production and subsequent spikelet and floret formation might be expected to progress in the same order as phytomer organisation on the apex. This does not occur however. Secondary protuberances are generally formed initially in the central region of the apex, further development occurring distally and basally. Generally, however, further development of spikelets and florets takes place more rapidly in distal regions than in central and basal regions of the developing head. In both timothy and prairie grass those secondary protuberances near the apex produce relatively few branches of higher orders while those at the base continue to produce higher order branches and spikelets for some time. This helps to explain, in these species at least, the fact that anthesis and seed formation progress from the apex down the inflorescence in the reverse order to phytomer formation.

In ryegrass the explanation is more difficult. Corresponding with the more rapid specialisation and development of distal florets, anthesis and seed maturation also commence in this region of the head. That the last florets to bloom or the last seeds to mature in a ryegrass head are those in the basal spikelets has been partly explained by Evans and Grover (1940), who suggested that florets at the base of the head in fact originated from phytomers which were the last to produce secondary protuberances. In addition, however, any explanation has to show how the last florets to form eventually develop to the stage where they undergo anthesis before florets produced by protuberances which had their genesis earlier than corresponding protuberances formed distally on the head. Possibly the explanation lies in the relative concentration and distribution of growth-promoting substances within the apex itself. It is possible that the terminal region of the apex, being meristematic, retains or

contains growth substances, say auxin, capable of increasing the rate of development of apical primordia compared with spikelets in basal positions on the apex. It is postulated, therefore, that a concentration gradient of growth substance(s) may occur from the terminal to the basal regions of the developing apex. This idea perhaps explains why terminal primordia, actually complete their development more quickly, and begin anthesis prior to florets formed centrally on the seedhead.

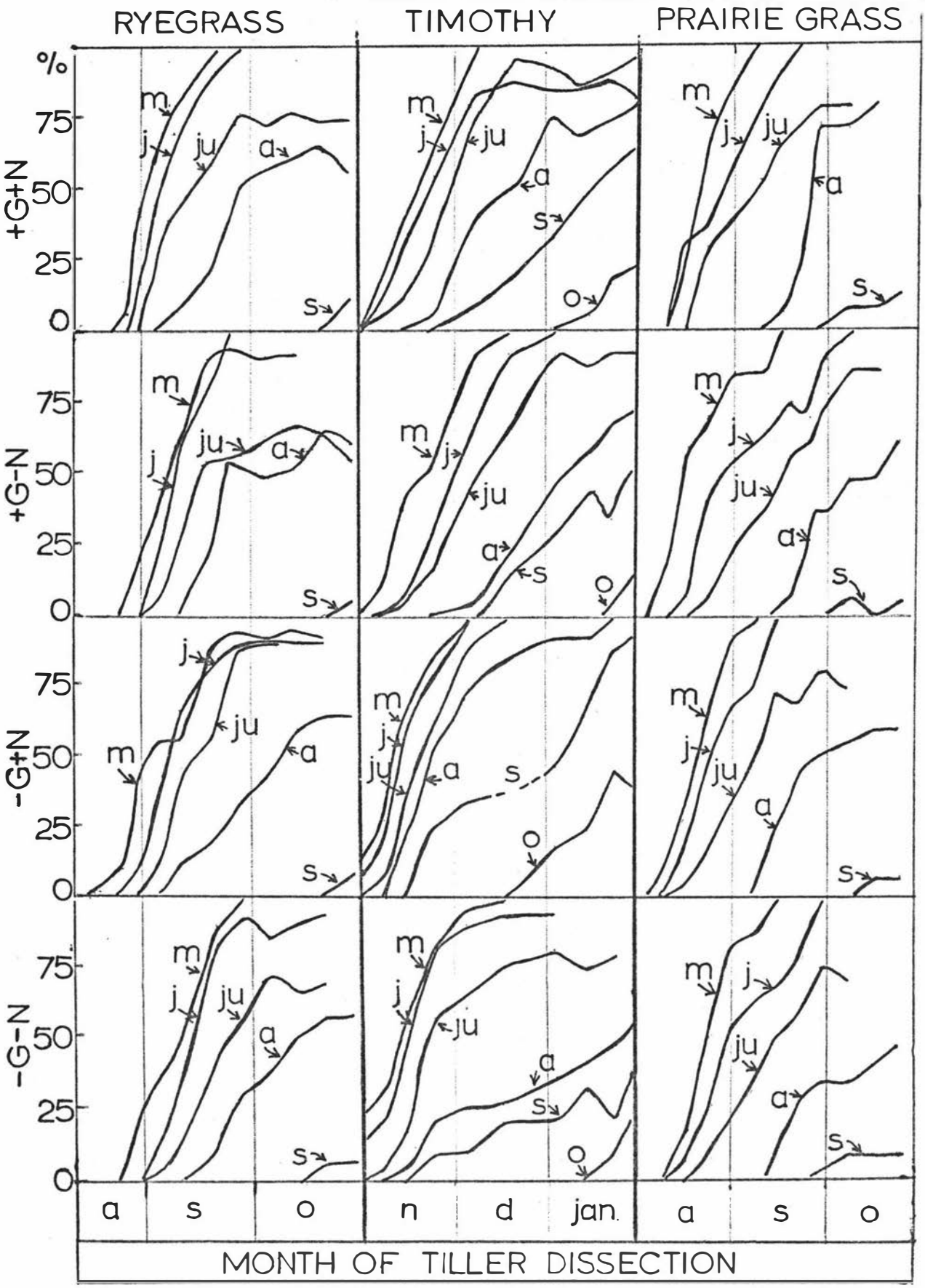
Floral Initiation of Tillers of Different Months of Origin

In spring, when grasses are starting reproductive growth, the crop consists ofaplant population comprising tillers varying in age and size according to their time of origin over the previous 6 months or more.

The results in Figure 9 and Appendix 4 show that earliest formed tillers in the first year (May tillers) were generally the first to initiate. Once floral initiation commenced it continued until all tillers originating in a particular month which were apparently capable of flowering had commenced floral development.

In ryegrass floral initiation of the earliest formed tillers (May) was first observed on 25th August. July formed tillers commenced floral initiation 11 days later, and tillers formed in August commenced initiation on the 12th September. This gave a mean spread of 18 days in observations of the onset of initiation of tillers originating in the months of May to August of the sowing year. Despite this however, there was a mean 31 day period between the time of complete initiation of May originated tillers and apparently full initiation of August formed tillers. This suggests that initiation in late-formed tillers occurs over a longer period than in early-formed tillers in ryegrass. A similar effect occurred in both timothy and prairie grass. In timothy an average of 29 days elapsed between the earliest onset of floral initiation in May and September formed tillers and at least 50 days between the time of complete floral initiation of May and September formed tillers. In prairie grass the mean relative durations for May to August formed tillers were 32 and 37 days respectively.These results indicate that while initiation in

FIGURE 9. PERCENTAGE OF REPRODUCTIVE TILLERS OF DIFFERENT MONTHS OF ORIGIN FOLLOWING APICAL DISSECTION, 1966.



KEY

m = may	s = september
j = june	o = october
ju = july	n = november
a = august	d = december

tillers of different ages occurred over an extended period (e.g. up to 12 weeks in timothy) the great majority were early-formed tillers which had growing-points beyond the spikelet or even floret-bud formation stages of development at a time when late-formed tillers were still in the earliest recognisable stages of floral development. This explains, in part at least, the spread in time of head emergence observed in these species.

The results suggest that during September in ryegrass and prairie grass, and October in timothy, some external factor necessary for floral initiation in each species became limiting. As a result subsequent tillers remained vegetative. Cooper (1952) has suggested that high spring and summer temperatures can inhibit inflorescence development in ryegrass. In addition, perennial ryegrass possesses an obligatory 'winter' requirement for low temperatures and short days before floral initiation is possible (Breese 1966). In timothy and prairie grass those tillers with the highest ear bearing capacity arose mainly during the winter months. This might suggest that some pre-treatment effect was indicated, were it not for the fact that both species have proved insensitive to seed vernalisation and subsequent short day treatment (Langer 1955, Cooper 1960, Lambert 1964 in timothy, and Karim 1961 in prairie grass). However, high temperatures have been shown to inhibit inflorescence development in timothy (Langer 1956, Cocks 1958b, Langer and Ryle 1959), resulting in a marked reduction in ears from late formed tillers (Wilson 1959). A similar effect has been observed in ryegrass (Cooper and Saeed 1949).

The lack of a low temperature induction requirement in prairie grass (Karim 1961) suggests that in this species some other factor is responsible for reduced ear bearing capacity of spring formed tillers.

It was of interest that nitrogen application appeared to slightly advance the date of onset of floral initiation of older tillers (in ryegrass in particular) and of the youngest tillers (those originating in August, September and October) in timothy. In addition nitrogen slightly reduced the time interval from onset to complete initiation of early tillers especially in prairie grass, and to a lesser extent in timothy.

No obvious effect from grazing occurred. However, it should be noted that in all species grazing was discontinued immediately prior to the onset of floral initiation. Had this not been done further grazing could well have influenced the rate and extent of floral initiation with an ultimate effect on seed yield as shown by Hill (1971).

As stated earlier (page 41) many primary tillers of prairie grass emerging within the first 5 weeks after sowing showed a high potential for spikelet development. Many heads formed at this time developed 'secondary' heads on the same tiller. Observations following apical dissection showed that these latter were not produced by bifurcation of the apex, but arose as a subsidiary basal branch from the node directly below the seedhead. This was a feature of primary tillers only, not being observed in higher order tillers at any time during the two years of the study.

Apex Length and Internodal Elongation

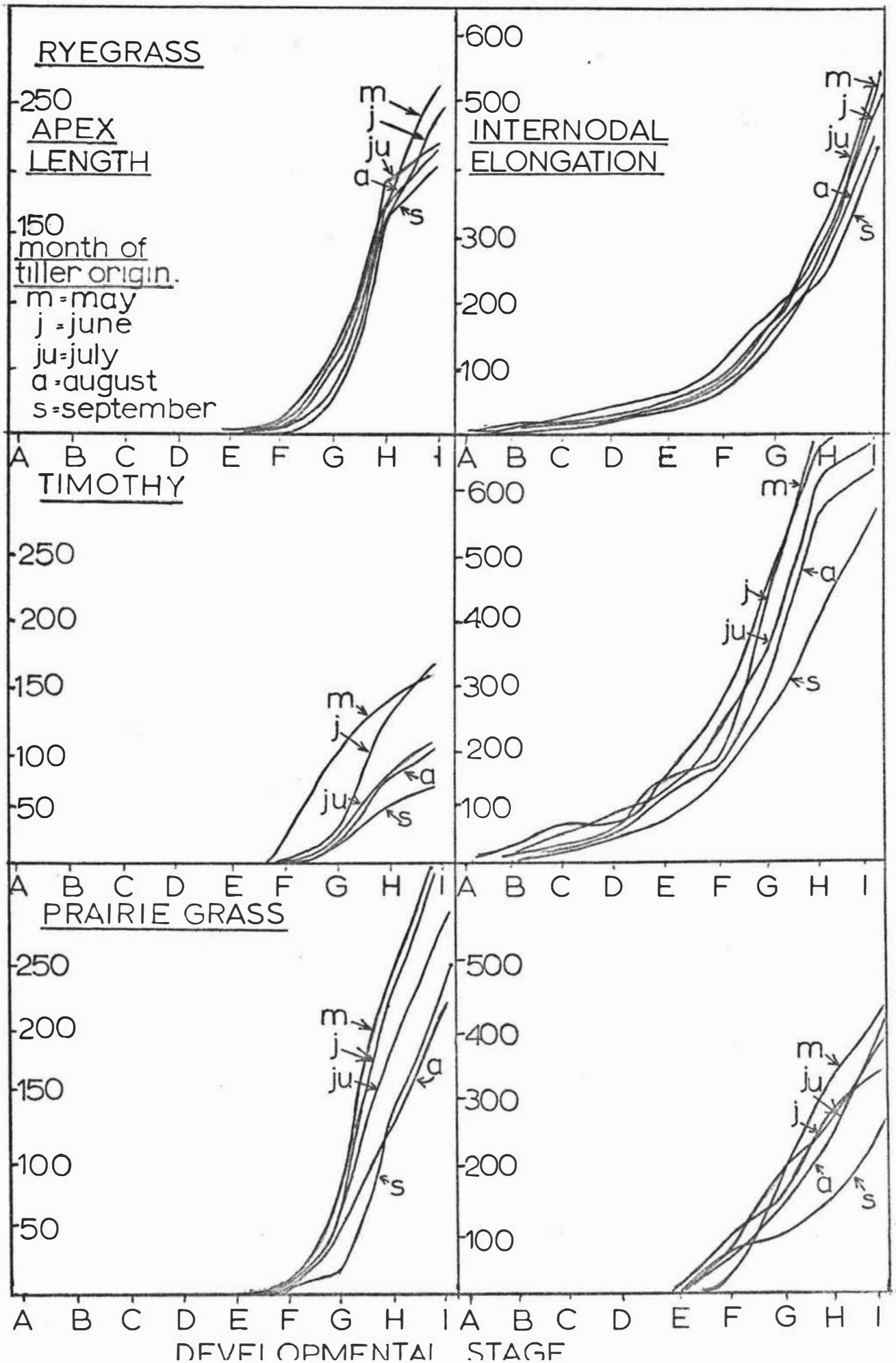
Measurements of apex length and distance of internodal elongation at ear emergence are presented in Table 3. A general picture of the developmental sequence is presented for the control treatment (-G-N) in Figure 10. Detailed measurements of these parameters at different stages of development for all treatments can be found in Appendix 5. The developmental stages (a-i) in both Figure 10 and Appendix 5 are identical to those previously described (page 46).

As shown in Table 3 there was a tendency for tillers in grazed treatments particularly in the absence of nitrogen to show both reduced apex length and reduced distance of internodal elongation at ear emergence than other treatments. This effect was particularly noticeable in timothy and prairie grass.

In ryegrass there was little apex length depression due to grazing alone except perhaps in late formed tillers. However, nitrogen application (particularly in the absence of grazing) consistently increased culm length and to a lesser extent head length at emergence compared with no nitrogen.

With timothy the major effect appeared to be a depression due to grazing. In this species grazed treatments, whether nitrogen had been applied or not

FIGURE 10 MEAN APEX LENGTH AND DISTANCE OF INTERNODAL ELONGATION (mm) AT DIFFERENT STAGES OF REPRODUCTIVE DEVELOPMENT (-G-N) 1966



generally developed fertile tillers which showed reduced apex and culm length compared with ungrazed treatments. In some cases this depression was partly overcome by the application of nitrogen to grazed plots.

TABLE 3 Mean Apex Length and Distance of Internodal Elongation at Ear Emergence (1966) (Extracted from Appendix 5)

	Month of Tiller Origin	Apex length (mm)				Distance of internodal elongation (mm)			
		+G+N	+G-N	-G+N	-G-N	+G+N	+G-N	-G+N	-G-N
Ryegrass	May	278	237	267	250	585	522	609	544
	June	224	217	260	231	576	506	646	517
	July	193	206	263	226	537	473	586	527
	August	176	211	249	212	462	426	513	453
	September	152	141	237	200	456	384	483	431
Timothy	May	146	124	153	158	797	638	863	814
	June	136	121	142	167	718	602	774	724
	July	108	92	130	107	693	517	738	672
	August	86	79	124	103	642	386	677	633
	September	81	63	77	76	537	407	636	574
Prairie Grass	May	302	271	297	340	392	255	477	431
	June	212	182	265	331	356	332	518	393
	July	217	177	207	208	274	296	455	405
	August	200	183	231	262	219	276	386	335
	September	126	162	237	251	211	298	371	261

In Figure 10 it appears that older tillers develop longer heads at ear emergence and longer culms than younger tillers. This was particularly the case in timothy and prairie grass. In all three species little apex elongation occurred until developmental stage g. At this stage ryegrass apices showed floret development with the glumes elongated. In timothy and prairie grass glume elongation had occurred on most of the apex with the floret buds becoming visible. Subsequently rapid apex elongation occurred in all species. These results support those of Evans (1960) who found that following the appearance of spikelet primordia in Lolium temulentum apex length began to increase, followed by subsequent exponential elongation.

In prairie grass, and generally in ryegrass there was no apparent internodal elongation before the growing point entered the reproductive phase. (Figure 10). During its vegetative phase the growing point remained close to the ground.

In ryegrass internodal elongation commenced at about the stage of vegetative apex elongation (Figure 10 stage B). This was at an earlier stage than that suggested by Cooper (1952). He stated that in perennial ryegrass internodal elongation did not occur until the late spikelet bud stage of reproductive development (equivalent to Figure 10 stage D).

In prairie grass internodal elongation did not occur until tertiary and quarternary primordia had become visible on the apex (Figure 10, stage E).

In timothy most tillers showed some internodal elongation prior to floral initiation, raising the apex above the soil surface before visible signs of reproductive development were seen. In addition a number of vegetative tillers were observed which showed extensive internodal elongation in timothy. These were considered sterile and were not included in assessments of internodal elongation. The maximum apex length observed in these 'sterile' tillers was in every case less than 1 m.m. However, internodal elongation was in many cases great (up to 270 m.m.). The majority of tillers showing this effect originated during the late winter and early spring (August and September) in the year of sowing. Internodal elongation without head initiation in timothy has been previously observed by Langer (1956) and Cooper (1958). They suggested an inhibitory effect of high temperatures on inflorescence development, no heads being formed if temperatures were high, even though photoperiod was adequate.

CONCLUSION

The sequence of floral development in all three grasses was the same, species differences being caused by the extent of branching of the inflorescence and the length of the internodes of various branch orders.

Tillers formed immediately following autumn sowing were first to commence reproductive development in the spring. Floral initiation of late winter-formed tillers occurred approximately 3 weeks later than autumn-formed tillers in ryegrass and up to 4 weeks later in timothy and prairie grass. Initiation extended over approximately a 9 week period in ryegrass and prairie grass, and up to 12 weeks in timothy. Nitrogen application slightly increased the rate

of floral development in older tillers.

Morphological studies indicated that late-winter and spring-formed tillers developed fewer and shorter seedheads, than autumn-formed tillers. Culm length was also reduced. Grazing and nitrogen effects were evident. In ryegrass nitrogen application increased head and culm length. The major influence in timothy was caused by grazing. This factor resulted in a reduction in both culm and seedhead length. In prairie grass the grazed treatment which had not received nitrogen produced shorter seedheads with reduced culm length compared with other treatments. Nitrogen application to grazed plots lessened this depression.

EAR EMERGENCE

INTRODUCTION

Since tillering in perennial grasses is a continuous process a heterogenous tiller population is exposed to conditions favourable for floral initiation. Consequently ear emergence occurs over a period of time. Studies were carried out on the relative emergence of seedheads produced from tillers originating in different months of the year and on fertile tiller production under different management treatments. In addition, the distribution of seedheads in different arbitrary emergence/time groups was determined, allowing analysis for individual seedhead characteristics within each group.

LITERATURE REVIEW

Ear emergence reflects the cumulative effect of environmental conditions at all stages of inflorescence development, although similar ear emergence dates among individuals and varieties may conceal large differences which occurred in their development to this stage (Griffiths *et al* 1967). The time of ear emergence varies from season to season, but the relative time sequence of emergence between varieties is rarely altered because of similarity in response. For example the effect of a cold spring is to delay ear emergence in all varieties, although relatively low temperatures and high insolation between spikelet initiation and ear emergence can result in larger ears being produced by most fertile tillers (Cooper 1952). Generally the interval from initiation to emergence is about 25-40 days, being generally shorter in late-heading than in early-heading grasses because of the higher temperatures experienced during their development (Griffiths *et al* 1967).

The use of ear emergence as a comparative measure of reproductive development in grasses has the advantages that it is easily recognised and requires no recording until heading occurs. However, as Cooper (1956) has pointed out, it has two main disadvantages. Being expressed on a calendar time scale it is strongly influenced by temperature, and varies between sites

and seasons. In addition, ear emergence does not measure the time of spikelet initiation directly, being also influenced by the rate of ear elongation. These two processes may often show different environmental responses. In Lolium, Cooper (1959b) observed considerable year to year variations in the date of ear emergence, which he attributed to differences in spring temperature once the critical photoperiod had been reached. He observed a tendency for a warm spring to accelerate heading and to increase the variance. Studies on ryegrass (Cooper 1959c) and S48 timothy (Bean 1967) have suggested the greatest variation within strains of each species was genetic in origin, but when climatic differences were small, selective effects of management, including the latest date of grazing in the spring, may be important in causing a shift in time of ear emergence.

Wilson (1959) showed for perennial and italian ryegrasses, cocksfoot and timothy that the date of ear emergence of tillers originating several months apart in the winter and early spring differed by only 7 to 10 days. Similar differences occur in ryegrasses (Cooper and Saeed 1949) and timothy (Langer 1956). In the species studied by Wilson (1959) high levels of nitrogen advanced the date of ear emergence by approximately 7, or in the case of cocksfoot 20 to 30 days.

Times from floral initiation to ear emergence in perennial and italian ryegrass are relatively constant at about 36-42 days (Cooper and Saeed 1949, Cooper 1952) although Wilson (1959) recorded minima of 30 and 21 days for these two species respectively. In Wilson's study (1959) timothy and cocksfoot both showed times decreasing from early to late formed tillers, to reach minima of 32 and 24 days respectively - the former result comparing favourably with the similar interval for timothy shown by Evans, Allard and McConkey (1935) and Sprague (1948). Wilson (1959) has also noted that leaf number at ear emergence decreased with later dates of tiller origin.

In timothy, Langer (1956) has shown that the inflorescence on primary tillers is longer and emerges earlier than those on secondary tillers.

Reduction in ear size of late formed tillers has been shown to result from decreased primary branch numbers in the ear and from fewer florets on each branch in cocksfoot (Ryle 1964). In ryegrass the decrease was in the number of spikelets on the shoot apex (Ryle 1964) and fewer florets per spikelet (Anslow 1963, Ryle 1965b). It has also been suggested (Ryle 1963) that variation in floret numbers in timothy heads may be due to the same effects.

Langer (1956) showed that seed yield in timothy was affected by the date of origin of the parent tiller. This was due mainly to a variation in seed number and not to differences in individual seed weight. However, Stoddart (1959) noted that seed weight in timothy declined with decreasing head length - that is, as heads emerged later.

In both cocksfoot and timothy dry weather at ear emergence reduced seed yield by limiting nutrient transfer to the ear (Evans 1953).

The point at which ear emergence is recorded varies in different investigations. These include the date on which the terminal spikelet is raised above the flag leaf (Evans, Allard and McConkey 1935, Cooper 1951, Langer and Ryle 1959), when half the head is extruded (Langer and Khatri 1965), or when the head is fully emerged from the leaf sheath (Sprague 1948). In investigations involving ear emergence date definition of the criterion used must be made.

MATERIALS AND METHODS

At approximately fortnightly intervals from the onset of ear emergence, (ryegrass 16.11.66, timothy, 21.12.66, prairie grass 15.11.66) all newly emerged heads in a selected row of each replicate of the trial were tagged. This procedure divided the spread of ear emergence in each species into 4 time groups (E1-E4) extending over an 8 week period. A different coloured plastic marker was used to identify heads emerged in each group. A seedhead was considered emerged when the entire head was visible above the flag. Approximately three weeks after tagging individual heads were divided into

groups bearing markers of the same colour. By this method it was possible to determine the contribution of heads arising from previously marked tillers of different months of origin to total head production and to determine total head numbers in each emergence group. In addition, heads produced by each species were divided into emergence groups (E1-E4) for analysis of head length, spikelet and floret numbers per head and total culm length. In timothy, because of the impracticality of counting total floret numbers per head, counts of total seed numbers per head were substituted. Records of the number of heads marked per unit area in each emergence group were kept for use in assessments of fertile tiller production.

RESULTS AND DISCUSSION

Seedhead Number

The total number of seedheads per row foot as presented in Table 4, reflect the response of each species to treatment combinations of grazing and nitrogen.

Table 4 Total Average Seedheads per Row Foot at Harvest

		+G+N	+G-N	-G+N	-G-N
1966	Ryegrass	301 Ab	262 Bc	324 Aa	210 Cd
	Timothy	103 Aa	79 Bb	98 ABa	90 ABab
	Prairie Grass	81 Aa	70 ABb	81 Aa	67 Bb
1967	Ryegrass	145 Aa	130 Bb	85 Cc	139 Aa
	Timothy	44 Bb	42 Bb	30 Cc	70 Aa
	Prairie Grass	37 Aa	24 Bb	35 ABa	38 Aa

In ryegrass, nitrogen application significantly increased seedhead production in 1966. However in the following year nitrogen application caused no such effect. Nitrogen severely depressed head numbers in ungrazed plots. This effect was due, at least in part, to the effect of nitrogen in promoting the ingress of weeds and the production of dense bottom growth which became severely infected with leaf spot (*Helminthosporium dictyoides* and *Ascochyta graminicola*) and rust (*Puccinia coronata*). Floating Sweetgrass (*Glyceria fluitans*) and Yorkshire Fog (*Holcus lanatus*) were the dominant grass weeds present in the second year. Grazing alone significantly increased head numbers in ryegrass in 1966 compared with the control treatment (-G-N). In

1967 grazing depression was completely overcome by the application of nitrogen.

In timothy, nitrogen alone had no effect on seedhead numbers in 1966. However grazing depression was effectively overcome by nitrogen application. In the following year grazing depression occurred irrespective of whether nitrogen had been applied or not. However nitrogen in the absence of grazing significantly reduced seedhead numbers, apparently for the same reasons suggested for ryegrass. The -G-N treatment produced significantly more heads than other treatments in 1967.

In prairie grass in 1966 the application of nitrogen significantly increased head numbers irrespective of the presence or absence of grazing. Although no grazing effect occurred it should be noted that grazing was discontinued at the onset of floral initiation. In 1967 nitrogen alone had no effect on seedhead numbers. The significant reduction in head numbers following grazing was overcome if nitrogen was also applied.

Fertile Tiller Production

The results in Table 5 express the percentages of fertile tillers produced per row foot.

Table 5 Percentage Fertile Tiller Production

		+G+N	+G-N	-G+N	-G-N
1966	Ryegrass	54 Aa	45 Bb	46 Bb	45 Bb
	Timothy	50 Aa	44 ABbc	40 Bc	46 Aab
	Prairie grass	62 a	62 a	59 a	61 a
1967	Ryegrass	48 Aa	23 Cc	12 Dd	30 Bb
	Timothy	10 Bb	9 Bb	5 Bb	18 Aa
	Prairie grass	33 Bb	34 Bb	28 Bc	44 Aa

These results, while showing the rapid decline in seed production potential from first year to second year, also reveal the extremely low fertile tiller production potential in the second season (1967). In timothy a $2\frac{1}{2}$-fold reduction in fertile tiller percentage was recorded in the control treatment (-G-N) and up to an 8-fold decrease in treatment -G+N.

In ryegrass, grazed plots receiving nitrogen produced a significantly higher fertile tiller population than other treatments in both years. While

no effect from grazing or nitrogen alone occurred in 1966 both caused severe fertile tiller reduction in the following year. However grazing depression was more than overcome if nitrogen was also applied in 1967.

In timothy grazing and nitrogen each significantly reduced percentage fertility in both years. When combined, however, grazing and nitrogen resulted in similar fertile tiller populations to the control (-G-N) in 1966. The control treatment was superior to all other treatments in terms of fertile tiller percentage in the following year.

While no management effect occurred in prairie grass in the first year, nitrogen and grazing both depressed fertile tiller percentage in 1967 compared with the control (-G-N). Nitrogen application was not effective in overcoming grazing depression in prairie grass in 1967.

The results suggest that despite the effect of nitrogen application alone in increasing total tiller production it had a severe depressing effect on the percentage of tillers which became reproductive. These findings are there similar to those of Langer and Lambert (1959) and Lambert (1964) but are not in agreement with those of some other workers for ryegrass (Evans 1937b, Evans 1954, Wilson 1959 and Roberts 1966), timothy (Evans and Calder 1931, Evans 1934, Lambert 1956b, Evans 1958, Roberts 1958b, Langer 1959b, Evans 1960c and Stoddart 1961) and prairie grass (Karim 1961) who found an increase in fertile tiller production following nitrogen application.

While grazing had no effect on fertile tiller percentage in ryegrass and prairie grass in 1966, significant grazing depression occurred in all three species in the second year. In ryegrass in both years and in timothy in 1966 nitrogen application was important in overcoming the depression caused by grazing. In ryegrass grazed plots receiving nitrogen produced a significantly higher percentage of fertile tillers than all other treatments, in both years. This correction of a potential depression in fertile tiller percentage, and ultimately in seed yield by the application of nitrogen to perennial ryegrass following grazing has been previously observed by Evans (1937a) and Roberts (1966).

The higher percentage of fertile tillers produced in the year of sowing (1966) in each species compared with the second year may be due to the high proportion of primary tillers in the crop. These tillers are regarded as being more fertile and persistant than secondary tillers. The results, indicate that the findings of Langer and Ryle (1959) for S215 Meadow Fescue and S37 Cocksfoot can be extended to include perennial ryegrass, timothy, and prairie grass. Particularly in the second year (1967) nitrogen application to ungrazed plots of ryegrass, prairie grass and timothy resulted in the production of a dense mass of tillers which were prone to severe frosting and rust attack during the winter. This may have contributed to the reduced number of fertile tillers in this treatment. A further possible explanation lies in the severe ingress of annual grass weeds which occurred in the second year and which may have depressed fertile tiller production through competition.

One of the difficulties in using a single figure to describe the percentage of fertile tillers in grass-seed crops is inherent in the method used. Most methods express fertile tiller number as a percentage of the total tillers present at seed harvest (Langer 1957a) or at a particular previous time, e.g. at the onset of floral initiation (Lambert 1963a). As Lambert (1966) has suggested these methods are only estimates at best, inaccuracy occurring because no allowance is made for the production of new tillers or for reduction through tiller death.

Perhaps the most realistic expression of the percentage of tillers which produce seedheads is the number of heads present at harvest as a percentage of tillers capable of reproductive development. As shown previously (Table 1) in 1966 only tillers formed from sowing (April) through to September were capable of producing seedheads in ryegrass and prairie grass. The corresponding period in timothy was from sowing to November. In 1967 only tillers originating during the months January to August in ryegrass and prairie grass and January to December in timothy were capable of reproduction

(see Table 2). Accordingly, only total tillers formed during the above specified periods were included in assessments of fertile tiller production (Table 5).

Proportion of Heads in Emergence Groups

Table 6 shows the influence of treatments on the percentage of seedheads contributed by each emergence group. In all species most heads generally occurred in emergence group 2, in both years, and in 1966 the sum of heads in groups 1 and 2 contributed the major proportion of total heads (87% in ryegrass, 77% in timothy and 86% in prairie grass). In 1967 heads in emergence groups 1 and 2 contributed the major proportion of total heads in grazed treatments of ryegrass and prairie grass only. In ungrazed treatments of ryegrass and prairie grass, and in all treatments in timothy, emergence groups 2 and 3 contributed the major percentage of heads at harvest. In ryegrass and prairie grass in 1967 therefore grazing caused a shift towards higher numbers of early emerged heads which was not apparent in the year of sowing, this effect occurring whether nitrogen had been applied or not. Over both years however the results emphasise the importance of the contribution of heads in emergence group 2 to total seed yield, and stress the futility of waiting for seed on late-emerged heads (group E4) to ripen at the expense of reduction in seed number by shedding from early-emerged heads. This is particularly important since early-emerged heads generally outnumber late-emerged heads in a crop.

In 1966 in all three species heads in emergence group 1 (earliest emerged heads) originated primarily from tillers formed in the months of May and June (Appendix 6). Heads in emergence group 2 originated mainly from tillers formed in May, June and July. In ryegrass and prairie grass June, July and August formed tillers contributed most heads in emergence group 3, while in timothy this group comprised heads from tillers originating from June to October. The last heads to emerge (group 4) arose from tillers formed during the months July to September in ryegrass and prairie grass and August to

TABLE 6

PERCENTAGE CONTRIBUTION OF SEEDHEADS IN EACH EMERGENCE GROUP

	Percentage of heads in each emergence group			
	E1 early	E2	E3	E4 late
PRAIRIE GRASS		1966-7		
+G+N	44.1	41.6	12.7	1.6
+G-N	25.0	59.6	14.1	1.3
-G+N	43.3	43.6	9.4	3.7
-G-N	16.0	69.7	12.4	1.9
PERENNIAL RYEGRASS				
+G+N	29.0	57.3	11.3	2.4
+G-N	27.0	61.5	7.9	3.6
-G+N	22.1	59.8	16.4	1.7
-G-N	26.9	67.1	4.8	1.2
TIMOTHY				
+G+N	24.5	50.2	13.4	11.9
+G-N	19.9	61.6	9.9	8.6
-G+N	22.0	53.3	21.4	3.3
-G-N	18.7	57.0	16.7	7.6
		1967-8		
PRAIRIE GRASS				
+G+N	19.7	65.3	13.9	1.1
+G-N	30.5	64.7	4.0	0.8
-G+N	15.3	60.0	22.6	2.1
-G-N	5.0	65.5	24.6	4.9
PERENNIAL RYEGRASS				
+G+N	36.1	48.3	13.5	2.1
+G-N	23.9	66.3	8.5	1.3
-G+N	8.8	66.5	21.6	3.1
-G-N	5.5	74.4	19.5	0.6
TIMOTHY				
+G+N	4.8	62.6	14.0	18.6
+G-N	11.7	47.4	27.6	13.3
-G+N	5.0	36.5	39.2	19.3
-G-N	8.3	51.0	28.9	11.8

November in timothy.

In 1967 (Appendix 6) tillers formed in the summer (January) and through into the autumn (March and April) contributed most of the early emerged heads (E1) in the crop in each species. Emergence group 2 was mainly composed of heads produced from tillers formed during the summer, autumn and winter (January-May in ryegrass and prairie grass, January-July in timothy). Autumn and winter tillers provided most heads in emergence group 3 in ryegrass and prairie grass with an additional contribution from spring tillers in timothy. (March-July tillers in ryegrass and prairie grass, January-October/November tillers in timothy). The last heads to emerge (E4) were produced from tillers originating in the late autumn and winter in ryegrass and prairie grass and including spring tillers in timothy. (April-August in ryegrass, June-November in timothy, June-August in prairie grass).

In both years heads formed from tillers originating in the winter and spring were the last to emerge.

Percentage of Heads Contributed by Tillers of Different Ages

From records of the number of ears in each monthly ringed tiller category, values were derived for the percentage contribution to the total seedhead population of various monthly groups of tillers. These results are presented in Table 7.

The most striking feature was the important contribution of the earliest tiller categories to the final population of seedheads.

In all species tillers originating in the late autumn and winter months following an April sowing made the major contribution to total seedhead numbers at harvest. In ryegrass spring formed tillers (September) produced only approximately 2% of the total heads at harvest. In timothy and prairie grass the figures were approximately 20% (September-November tillers) and 5% respectively.

TABLE 7 Percentage of Total Seedhead Population Contributed by Tillers of Different Ages

	Treatment	Month of Tiller Origin (1966) May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Ryegrass	+G+N	14	21	40	23	2	-	-	-
	+G-N	16	25	35	22	1	1	-	-
	-G+N	18	21	38	21	1	1	-	-
	-G-N	18	26	36	18	2	-	-	-
Timothy	+G+N	20	17	20	21	12	4	6	-
	+G-N	23	18	23	18	11	5	2	-
	-G+N	20	8	21	24	12	5	9	1
	-G-N	21	11	27	23	7	5	6	-
Prairie Grass	+G+N	44	14	18	16	8	-	-	-
	+G-N	53	11	21	13	2	-	-	-
	-G+N	46	17	18	12	7	-	-	-
	-G-N	51	13	21	12	3	-	-	-

		Dec/ Jan.	Feb.	Mar.	Apr.	Month of Tiller Origin (1967) May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Ryegrass	+G+N	23	21	18	13	9	6	4	2	4	trace	-	-
	+G-N	21	20	19	18	10	6	3	trace	3	-	-	-
	-G+N	18	18	22	19	9	5	4	3	2	-	-	-
	-G-N	23	15	16	22	14	4	3	1	2	-	-	-
Timothy	+G+N	10	11	14	12	15	13	9	8	5	2	1	trace
	+G-N	13	16	15	7	11	15	6	8	7	2	trace	-
	-G+N	16	13	12	10	12	11	9	5	8	2	2	-
	-G-N	13	15	14	14	13	8	8	7	5	1	2	-
Prairie Grass	+G+N	33	27	16	6	8	8	1	1	-	-	-	-
	+G-N	35	25	8	8	12	11	-	1	-	-	-	-
	-G+N	38	23	14	10	8	3	3	1	-	-	-	-
	-G-N	36	20	17	13	8	4	2	trace	-	-	-	-

In the second year the major contribution to total head population at harvest was from tillers formed in the late summer, autumn and winter months. As in the first year the relative contribution of spring formed tillers was low, being approximately 3%, 9% and 0% respectively in ryegrass, timothy and prairie grass.

The results for both years support the findings of other workers who have stressed the importance of the oldest tillers in a crop and the progressive decline in head numbers produced through succeeding monthly generations of tillers (Langer 1956, 1957b, Langer and Ryle 1959, Wilson 1959, Lambert 1966 in timothy; Langer and Lambert 1959, Lewis 1969 in meadow fescue; Langer and Lambert 1959, Lambert 1963bin cocksfoot). Langer and Lambert (1959) have suggested that this decreasing ear bearing capacity with later tiller formation is apparently inherent in the organisation of the plant since it occurs irrespective of the time of sowing. However, any discussion of decreasing ear bearing capacity must take into account the fact that this may not be solely an age effect. As Langer (1956) has pointed out time of origin is closely correlated with tiller position on the parent plant. The later the date of origin the greater the number of preceding tillers on the plant. In addition Langer and Ryle (1959) have shown that tillers inserted on the main stem tend to have a higher chance of flowering than other tillers on the plant which appear at the same time.

The results in Table 7 indicate that although seedhead production generally declined with successively later dates of tiller origin it was possible for tillers to produce a head if they were formed before mid October in ryegrass, December in timothy and October in prairie grass following an autumn sowing. In second year crops only tillers formed before September in ryegrass and prairie grass and before December in timothy were capable of contributing to the seedhead population at the next harvest. Presumably at these times some factor conducive to reproductive development ceased to operate. In timothy Langer (1956) has suggested daylength as a limiting factor inhibiting

ear formation after mid July (U.K.). Possibly other factors such as defoliation and mineral nutrition (Langer 1957b) are also involved. The results in the present study with New Zealand Kahu timothy are generally similar to those reported by Langer (1956) in S48 timothy in the United Kingdom.

A large number of tillers formed in the spring and early summer of 1966 survived into the following year. None of these vegetative tillers apparently survived long enough to bear heads in the 1967 harvest. Langer (1956) showed in S48 timothy that no single generation of tillers exceeded a mean age of 1 year. In the present study tillers formed in the spring and early summer either died before harvest, or remained vegetative into the following year thereby ensuring the survival of the plant. As previously discussed (page 40) none of these tillers apparently survived longer than the following autumn (April). This suggests their function is one of ensuring perenniality rather than contributing to seedhead production.

Analysis of Individual Seedhead Components at Ear Emergence

Measurements and counts of individual seedhead components are presented in Appendix 7. Analysis of variance data derived from these results, (Tables 8-11) is presented in its entirety in Appendix 8 and shows the effect of treatments and emergence groups on head length, spikelet and floret number and mean total culm length for 1966 and 1967. (Head length was measured in cm from the point of exsertion of the basal branch to the inflorescence tip).

Head Length

TABLE 8 Head Length Variation Between Treatments and Emergence Groups

		Treatment				Emergence Group			
		+G+N	+G-N	-G+N	-G-N	1	2	3	4
Ryegrass	1966	18 a	18 a	19 a	18 a	24 Aa	19 Bb	17 Bc	12 Cd
	1967	21 Aa	18 Bb	20 ABa	20 ABa	24 Aa	20 Bb	17 Cc	17 Cc
Timothy	1966	12 a	11 a	12 a	13 a	15 Aa	15 Aa	10 Bb	8 Bc
	1967	9 a	9 a	11 a	10 a	11 a	9 a	10 a	9 a
Prairie Grass	1966	38 a	35 a	40 a	37 a	60 Aa	45 Bb	24 Cc	20 Cc
	1967	25 ABb	21 Bc	31 Aa	26 ABb	28 Aa	28 Aa	25 ABab	22 Bb

Results in Table 8 show that in 1966 there was no treatment effect on head length. However, in all species a significant reduction in head length occurred between early (E1) and late (E4) emerged heads. With the exception of timothy, treatment effects on head length became apparent in the second year. In both ryegrass and prairie grass, grazing depressed head length. The application of nitrogen to grazed plots fully overcame this depression. However nitrogen did not significantly increase head length in ungrazed plots of ryegrass. In prairie grass and ryegrass, heads in emergence groups 1 and 2 were longer than those in groups 3 and 4. No such effect occurred in timothy in the second year.

Variations in length between heads in early and late emergence groups can perhaps be explained in terms of the time of tiller formation. Any tiller originating late enough to be exposed soon after its formation to environmental conditions suitable for floral development will initiate a seedhead earlier in its morphological development than a tiller formed some months prior to the flowering period. Under these conditions head length would be most likely to be reduced, a factor which might also influence the number of spikelets and florets produced per head. The results tend to support findings by Stoddart (1959) and Langer (1959b) for timothy in the first year (1966). This is shown by the significant reduction in head length of this species in groups E3 and E4, compared with Groups E1 and E2. In the second year, however, lack of significance tends to negate Stoddart's conclusion that timothy heads can be

divided into groups according to time of ear emergence purely on head length. Analysis of timothy heads in each emergence group into arbitrary head length categories (Appendix 9) shows that in the second year while there were more short heads (less than 5.0 cm length) in emergence groups E3 and E4 than in E1 and E2, there were still a number of heads in the later emerged groups which were over 10.0 cm in length, and a small number over 15.00 cm in length. It is likely that these longer heads in late-emergence groups were responsible for failure to detect a statistical head length reduction gradient from E1 to E4 in the second year.

TABLE 9 Spikelet Number Variation Between Heads in Different Treatments and Emergence Groups

		Treatment				Emergence Group			
		+G+N	+G-N	-G+N	-G-N	1	2	3	4
Ryegrass	1966	19 a	19 a	20 a	20 a	21 Aa	19 ABb	20 ABab	17 Bc
	1967	20 a	18 a	21 a	22 a	21 a	22 a	20 a	18 a
		(Seed Number per Head)							
Timothy	1966	308 BCb	264 Cc	373 Aa	346 ABa	376 Aa	357 ABa	311 Bb	247 Cc
	1967	308 a	267 a	292 a	284 a	324 a	305 a	290 a	234 a
Prairie Grass	1966	25 a	21 a	31 a	23 a	43 Aa	25 Bb	18 Bbc	13 Bc
	1967	20 Bb	14 Bc	31 Aa	21 Bb	26 a	24 a	18 a	19 a

The results in Table 9 show the effect of treatments on spikelet number and spikelet number variation between ear emergence groups. (Seed number per head was used in timothy because of difficulty in distinguishing individual spikelets).

In ryegrass in both years treatments had no significant effect on spikelet number.

The application of nitrogen appeared to increase spikelet number per head in prairie grass, this effect reaching significance in the second year. Grazing tended to reduce spikelet number, particularly in the second year, but the application of nitrogen to grazed plots tended to overcome this depression.

Seed number per head in timothy tended to be depressed by grazing but stimulated by nitrogen. This nitrogen stimulus was most evident in the presence of grazing in the first year.

Emergence group records of spikelet number in both ryegrass and prairie grass and seed number per head in timothy showed a reduction from early-emerged

(1) to late-emerged (4) heads in the sowing year (1966). No emergence group differences were detected in the second year.

The results in Table 9 stress the depression of spikelet number by grazing prairie grass, and the value of nitrogen in the management of this species for seed production. The results also reinforce claims by other workers (Evans 1937a, 1962) and Roberts (1966) that ryegrass, because of its lack of response to treatment combinations of grazing and nitrogen, is a flexible species, able to withstand the effects of defoliation without depression in spikelet numbers per head. Nitrogen applied up to the time of floral initiation apparently did not influence spikelet numbers.

As spikelet branches develop from the shoot apex it is not surprising that their number should be influenced by the size of the vegetative apex at the time of floral initiation. As Langer (1957b) has pointed out tillers formed in the summer and autumn develop ears at about the same time in the spring. Spikelet numbers per head is greatest in these tillers. Those arising on later dates bear shorter heads and progressively fewer spikelets until the minimum number is found on heads produced from tillers actually formed under floral-induction and initiation conditions in the late winter and early spring. This difference may arise from the greater number of leaf primordia accumulated on the shoot apices of older tillers, infering that more sites are available for spikelet initiation.

Floret Number

TABLE 10 Floret Number Variation Between Heads in Different Treatments and Emergence Groups

		Treatment				Emergence Group			
		+G+N	+G-N	-G+N	-G-N	1	2	3	4
Ryegrass	1966	114 ABa	87 Cb	120 Aa	96 BCb	138 Aa	111 Bb	91 Cc	78 Dd
	1967	120 a	97 a	114 a	111 a	155 Aa	117 Bb	87 Cc	83 Cc
		(Seed number per head)							
Timothy	1966	308 BCb	264 Cc	373 Aa	346 ABa	376 Aa	357 ABa	311 Bb	247 Cc
	1967	308 a	267 a	292 a	284 a	324 a	305 a	290 a	234 a
Prairie Grass	1966	80 Aab	57 Ab	107 Aa	82 Aab	146 Aa	76 Bb	58 Bb	46 Bb
	1967	93 ABb	75 Bb	163 Aa	95 ABb	152 a	121 ab	80 b	78 b

A sufficient supply of mineral nutrients must be available to allow individual heads to grow to maximum size. It was not surprising therefore, that nitrogen application in the present study exerted a strong positive effect on the number of florets formed on individual heads, as shown in Table 10.

In all species in both years grazing generally depressed, and nitrogen application increased total floret production, these effects generally reaching significance in the first year. The ability of nitrogen to partly or completely overcome the deleterious effect of grazing on floret numbers is reflected in the number of florets produced in the treatment +G+N.

In all species the main overall effect of nitrogen application was to increase the number of florets developed per spikelet without in many cases significantly increasing the number of spikelets. Ryle (1964) has however shown that in ryegrass, meadow fescue and cocksfoot, conditions of soil nitrogen deficiency can result in the number of primary branches in the ear being reduced. The effectiveness of nitrogen in increasing floret number has been previously observed by Langer (1959c) and Ryle (1965b).

Two other factors which exert an effect on ear size are temperature and daylength. In single plants of timothy (Ryle and Langer 1963) and ryegrass (Ryle 1965a) the total floret numbers per head decrease as daylength or temperature is increased.

The date of emergence of individual heads affects the number of florets developed (Table 10). Thus in ryegrass early emerged heads (1 and 2) contained more florets per spikelet than heads emerging later in the season (3 and 4). In prairie grass, ears developed on early emerged heads were larger not only because of a greater number of spikelets but also because each spikelet generally developed more florets. This latter effect was particularly the case in 1967.

In timothy the morphology of the ear precluded distinctions being drawn between spikelet and floret numbers. However seed number per head dropped

significantly from early-emerged to late-emerged heads in the first year with a similar trend occurring in the second year.

Similar effects on the reduction in floret numbers with later ear emergence have been recorded by Anslow (1963) and Ryle (1964, 1965b) in ryegrass, Ryle and Langer (1963) in timothy, and Ryle (1965b) in meadow fescue and cocksfoot.

Culm Length

TABLE 11 Culm Length Variation Between Heads in Different Treatments and Emergence Groups

		Treatment				Emergence Group			
		+G+N	+G-N	-G+N	-G-N	1	2	3	4
Ryegrass	1966	83 a	80 a	84 a	86 a	90 Aa	84 Aa	88 Aa	72 Bb
	1967	87 a	71 a	91 a	87 a	93 a	84 a	81 a	77 a
Timothy	1966	99 Bc	101 Bb	114 Aa	111 Aa	117 Aa	119 Bb	103 Cc	97 Dd
	1967	92 b	92 b	99 a	101 a	99 Aa	101 Aa	95 ABa	89 Bb
Prairie	1966	92 Ab	88 Ab	134 Aa	126 Aa	135 Aa	127 Aab	99 Abc	80 Ac
	1967	88 BCb	80 Cb	123 Aa	113 ABa	117 Aab	117 Aa	97 ABbc	73 Bc

The results in Table 11 show that culm length at ear emergence in both timothy and prairie grass was reduced by grazing. Similarly, in these species there was a reduction gradient in culm length from early-emerged (1) to late-emerged (4) heads. In ryegrass however, little apparent relationship between treatment, or time of ear emergence, and culm length occurred.

CONCLUSION

Grazing and nitrogen supply strongly influenced seedhead number in all species. Grazing was not generally deleterious to seedhead number per row foot provided nitrogen was also applied. In ryegrass and timothy, particularly in the second year, ungrazed plots to which nitrogen had been applied yielded fewer heads than the control treatment.

Percentage fertile tiller production declined in the second year compared with the percentage of fertile tillers produced in the year of sowing. This was particularly evident in timothy, fertile tiller percentage being reduced as much as 8 times in ungrazed treatments to which nitrogen had been applied, and yielding a final fertile tiller percentage of only 5% in 1967. The application of nitrogen generally had a depressing effect on the percentage

of tillers which became reproductive. However, nitrogen application did increase total tiller numbers, resulting in a greater between-treatment percentage of tillers producing heads. Grazing and nitrogen reduced fertile tiller percentage in timothy and prairie grass in the second year. In ryegrass, nitrogen application overcame the depression in fertile tiller production caused by grazing. This indicates that in this species useful grazing could be obtained without reduction in seedhead production provided nitrogen was also applied.

In the sowing year (1966) early-emerged seedheads (emergence groups 1 and 2) contributed over 85% of the total heads formed in ryegrass and prairie grass and 77% in timothy. In the second year the corresponding figures were approximately 80% in ryegrass and prairie grass and 55% in timothy. In 1967 grazing caused a shift towards earlier ear emergence, increasing the contribution of seedheads in emergence group 1 at the expense of those in emergence group 3. The major proportion of seedheads generally fell in the first two emergence groups. These heads originated almost exclusively from tillers formed in the autumn and early winter of the year of sowing and during the immediate post-harvest period, autumn and early winter in the second year. The contribution of tillers formed in the spring to total seedhead percentage was low. Heads formed from tillers originating during this latter period generally contributed to the numerically smaller number of late-emerged seedheads (emergence groups 3 and 4) in the crop.

The results of analysis for selected seedhead components show the major trend in all species as a general depression in head length, spikelet and floret number, and culm length with grazing. These effects were in most cases partly or completely overcome by the application of nitrogen. The major effect of applied nitrogen, however, was to increase floret number per head. The results again reflect the tolerance of ryegrass to management systems incorporating grazing and nitrogen, the intolerance of prairie grass to grazing and positive response to nitrogen, and the deleterious effect of

grazing on the number of seeds per head in timothy stands in the sowing year.

In all species most seedhead components varied according to time of ear emergence. Early-emerged heads were generally longer, bore more spikelets and more florets per head and had a greater culm length than late-emerged heads.

ANTHESIS

INTRODUCTION

In all species the progress of anthesis (anther exsertion) was observed to determine the time of peak anthesis in the field. The information obtained was necessary for the measurement of the duration and extent of subsequent stages of seed development. As it was intended to study anthesis in both ryegrass and prairie grass in more detail at a later stage intensive observation of anthesis in these two species was not carried out. However, closer examination of timothy plants under glasshouse conditions was undertaken to provide some information on anthesis and seed formation.

LITERATURE REVIEW

The term 'anthesis' is widely used to describe the process of blooming in grasses. This process begins when anthers and stigmas are exposed to the pollinating agent(s), either because the flower opens or because the organs protrude from a closed flower, and ends when the same floral organs are no longer available to the pollinating agent(s). In cleistogamous flowers there is, by definition, no anthesis (Faegri & Pijl 1966).

The morphology of the grass flower has been described by a number of workers (Mosher 1918, Bews 1929, Armstrong 1937, Wheeler & Hill 1957). Others have observed the daily pattern of anthesis in grasses (Evans 1916, Gregor 1928, Beddows 1931, Jones and Brown 1951, Grabe 1956, Johnston 1960, Anslow 1963).

The time of day at which anthesis occurs varies between species and daily according to weather conditions. The environmental conditions influencing anthesis in grasses are reviewed in a following section (Page 141). Generally anthesis is most active between 5 a.m. and 9 a.m. but some species bloom more freely towards the middle of the day e.g. Lolium and Festuca (Beddows 1931, Cocks 1958c, Dotzenko and Stegmeier 1959), and in rare cases during the hours of darkness e.g. Phleum (Evans 1916).

In most grasses individual heads shed pollen over 6 to 8 days, the limits being approximately 3 to 11 days (Gregor 1928, Jones and Newell 1946, Anslow 1963,

Griffiths et al 1967) depending on species and the number of florets on each inflorescence (Jones and Brown 1951).

Some workers studying seed development in grasses have recorded the emergence of anthers as a datum line for measuring the subsequent development of seeds (Grabe 1956, Stoddart 1959, Baltensperger and Kalton 1959, Hyde et al 1959, Anslow 1963 and Bean 1965). The use of this criterion has reduced variability within an inflorescence and allowed conclusions on the germination capacity and the increase in weight of individual seeds. In studies with Bromus inermis Grabe (1956) suggested that since individual florets remain open for only a few hours the date of anthesis could be regarded as the date of pollination.

In ryegrass anthesis proceeds in a regular manner from the apex downwards. Within the spikelet the reproductive organs of the basal floret mature first, and anthesis continues extremely regularly upwards (Gregor 1928). The daily period of anthesis varies, with the majority of florets generally open between 11 a.m. and noon. Anthesis does not generally commence before 9.30 a.m. and all florets have closed before 5 p.m. (Gregor 1928). Beddows (1931) concluded that, in perennial ryegrass, stigma and anther exsertion were simultaneous. Gregor (1928) also found that stigmata were freely exposed at the time of anther dehiscence.

The first indication that a timothy floret has commenced anthesis occurs when the glumes open slightly and the tips of the anthers become visible. After anther emergence the filamets continue to extend to their full length. At about this time the tips of the stigmas elongate, spread laterally, and become feathery in appearance (Evans 1916). Anther sacs remain closed until after the filaments and stigmas have become fully extended. There is therefore, an interval after the stigmas are fully exposed before pollen liberation occurs. The glumes close soon after the anthers are exserted. At dehiscence, each half of the anther opens longitudinally from tip to base. After the anther sacs have partially dehisced, any slight movement of the culm will set free quantities of pollen. Following dehiscence the filaments wilt. The stigma remains

attached to the floret and gradually dries and shrivels after anthesis is completed. The terminal florets begin anthesis first on a timothy head. On successive days florets lower down on the spike bloom.

The amount of literature on the details of anthesis in prairie grass is limited. Several workers, however, have made general observations on anthesis in this species (Beddows 1931, Smith 1944, Langer & Wilson 1965). Prairie grass produces both chasmogamous and cleistogamous flowers. In response to environmental conditions (day and soil moisture in particular) Langer and Wilson (1965) have shown that chasmogamy in prairie grass occurs early in the spring, to be followed by the production of cleistogamous flowers in the summer. Chasmogamy is attended by greater anther length but later anthesis than occurs in the cleistogamous condition. (Chase 1918, Madge 1929). Physiologically, the type of flower produced appears to be a matter of delicate balance which Harlan (1945) attempted to explain by assuming that conditions would have to reach and maintain a certain threshold before chasmogamous flowers could be formed, otherwise cleistogamy would result. Both types of flowers may occur on the same spikelet. (Uphof 1938, Ragonese and Marco 1941, Langer and Wilson 1965). Apart from Bromus spp. cleistogamy has also been observed in other grasses including Stipa leucotricha (Brown 1952) and Danthonia spp (Dobrenz and Beetle 1966).

In the case of chasmogamous florets of prairie grass anthesis apparently follows a sequence similar to that for ryegrass, anthers being exserted from the floret prior to dehiscence (Beddows 1931).

MATERIALS AND METHODS

The progress of anthesis in each species was recorded approximately daily by examining 100 heads in each treatment in the field experiment and recording the number of heads with exserted anthers. Examination was made at 8 a.m. for timothy and at 11 a.m. for ryegrass and prairie grass to reduce inaccuracies due to diurnal fluctuations in anther exsertion.

In another study five clones of 'Grasslands Kahu' timothy were obtained from single plants grown at the Grasslands Division, D.S.I.R. Palmerston North, and

after potting were placed in a glasshouse for observation of anthesis. On selected heads the number of anthers exserted was recorded. Two periods of study were used, one covering the hours of darkness (8 p.m. - 8 a.m.) and the other covering the period 8 a.m. - 8 p.m. The number of exserted anthers present at 8 p.m. and 8 a.m. respectively was recorded and all exserted anthers then removed.

In addition, ten timothy heads were enclosed in plastic bags prior to anthesis to determine the ability of timothy to develop seed following selfing. At seed maturity individual heads were dissected, the total number of florets counted and seed numbers recorded. The results obtained were compared with similar records made on ten heads which had not been bagged.

To obtain information on the relative fertility of florets in different positions on timothy heads five seedheads each of 10.0 cm in length were chosen and divided into four regions, each of 2.5 cm. These regions were recorded 1-4 from the top of the head to the base. On each head the progress of anthesis was observed and the total florets which flowered in each region recorded. Approximately 20 days after the completion of anthesis the heads were harvested and dissected to obtain figures for both the total florets and the number of seeds formed in each region.

RESULTS AND DISCUSSION

(a) Field Experiment

From the results of field observations of anthesis presented in Figure 11, (raw data in Appendix 10) it is evident that in all species there was little treatment effect in the first year (1966) but a more marked treatment effect in the second year (1967).

In ryegrass in the first year the range in date of onset of anthesis, date of peak anthesis and duration of anthesis between treatments was only 4, 4 & 3 days respectively. Treatment effects were more marked in the second year. In 1967 the onset of anthesis occurred later in grazed than ungrazed plots. However, the influence of nitrogen application to grazed plots was clearly shown by the onset of anthesis in +G+N being advanced 7 days compared with

FIGURE 11

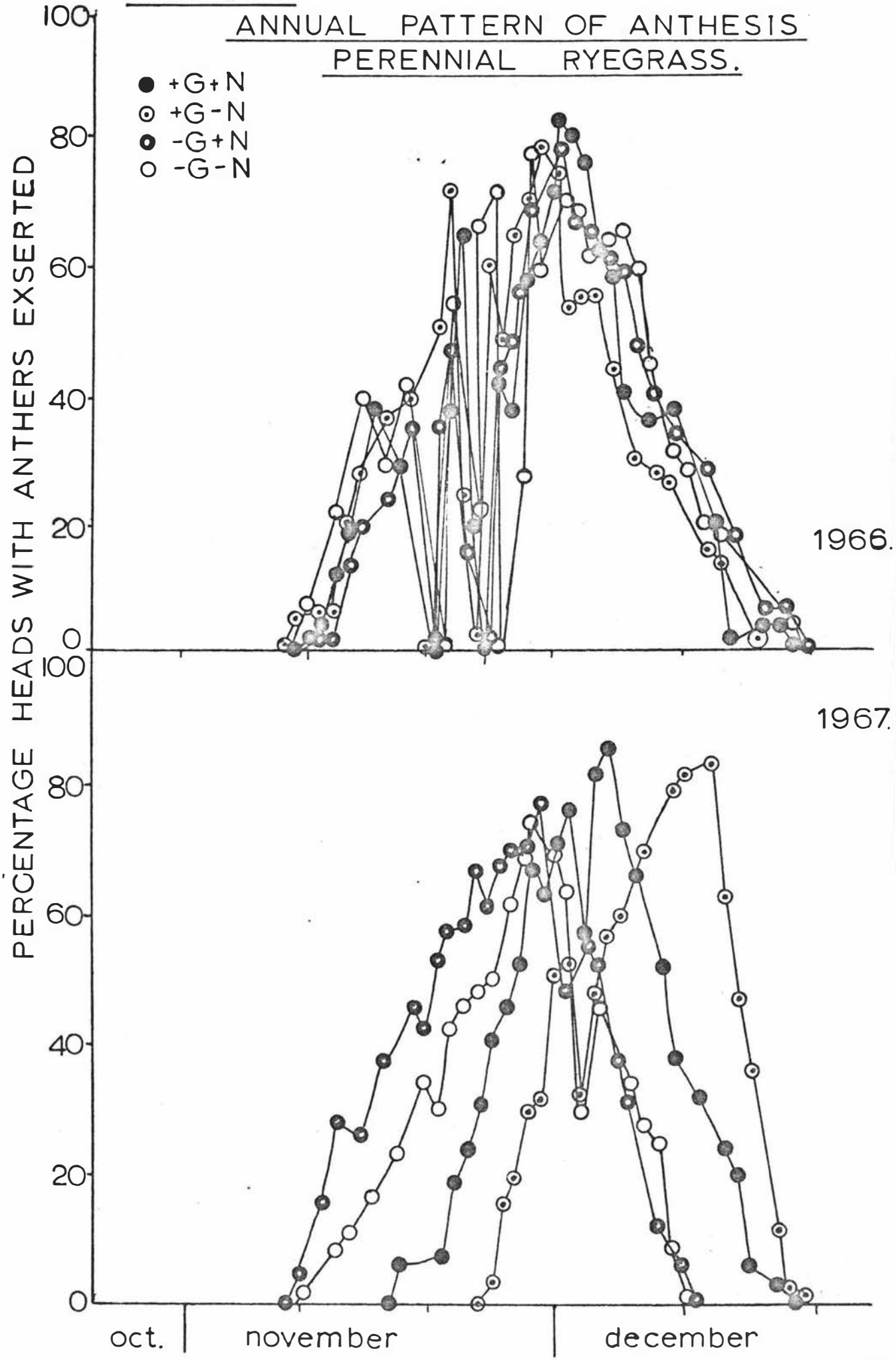

ANNUAL PATTERN OF ANTHESIS
PERENNIAL RYEGRASS.
● +G+N
⊙ +G-N
◉ -G+N
○ -G-N
PERCENTAGE HEADS WITH ANTHERS EXSERTED
100
80
60
40
20
0
1966.
1967.
oct.
november
december

FIGURE 11 continued

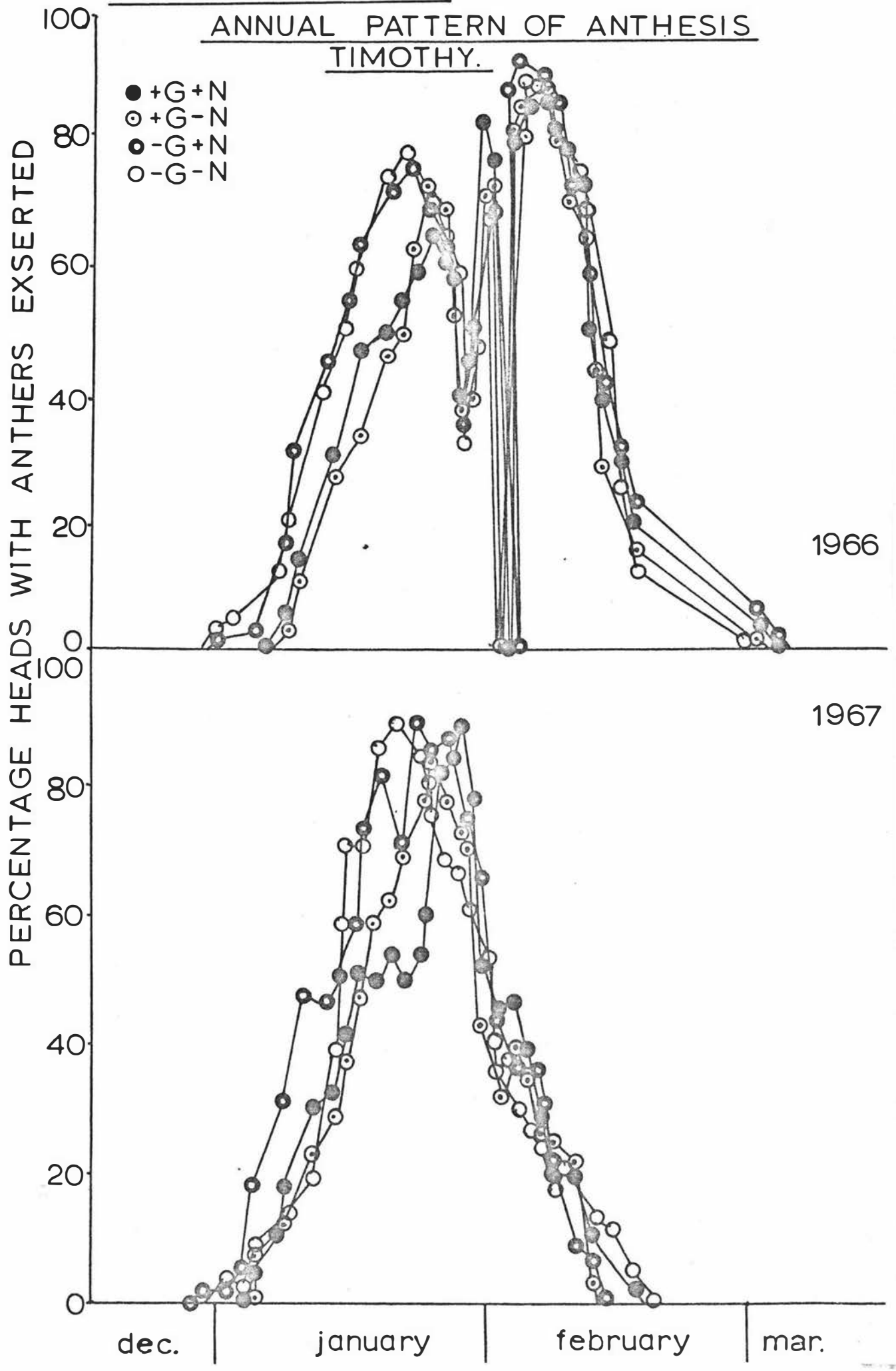
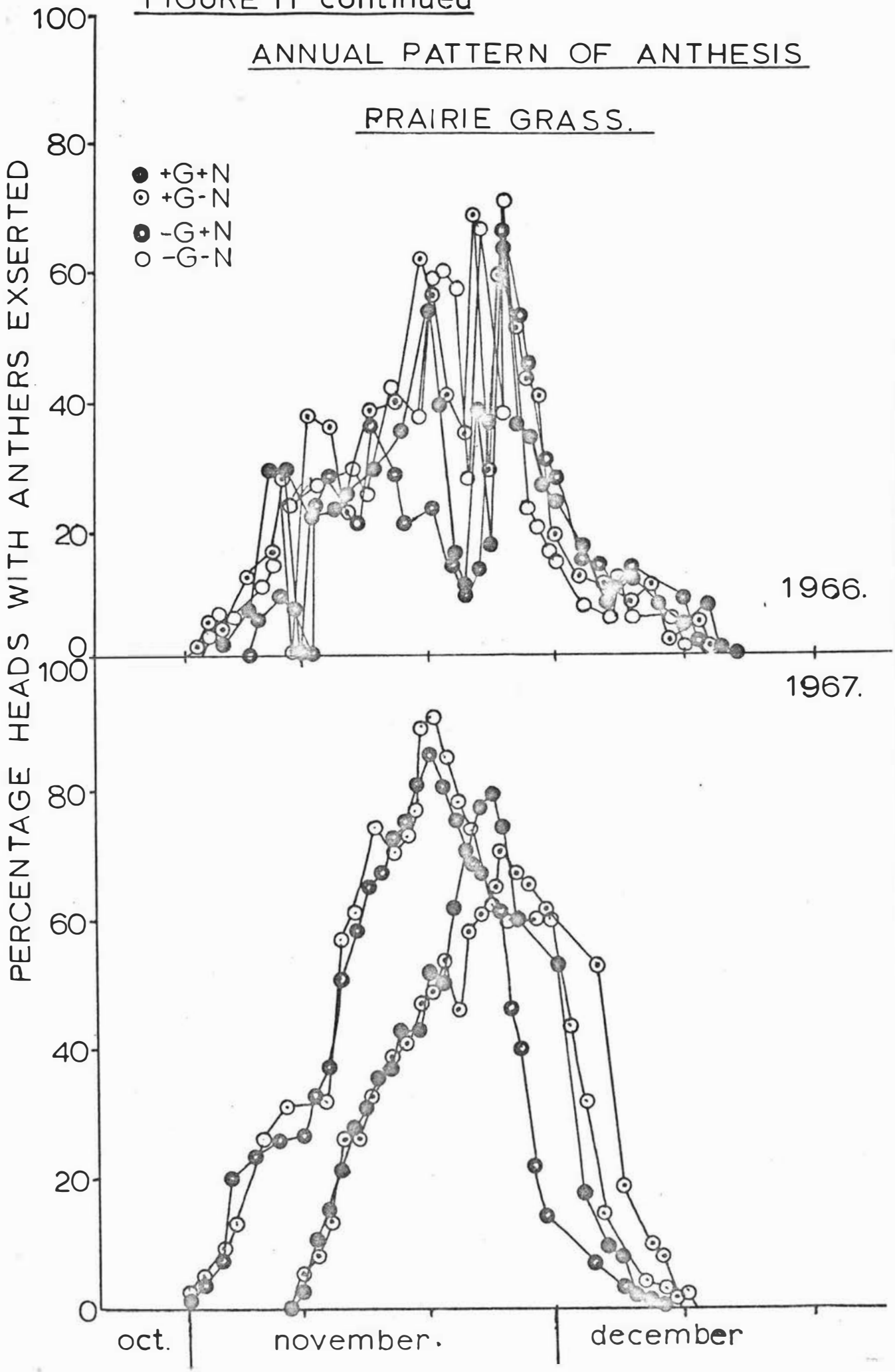


FIGURE 11 continued



treatment +G-N. The number of days to peak anthesis was reduced in grazed plots and apparently increased slightly in ungrazed plots which had received nitrogen. The duration of anthesis in all treatments in the first year was 41 to 43 days compared with a duration of only 27 to 32 days in the second year.

In timothy a delay in the onset of anthesis of grazed plants occurred in the first year. The range in the onset and duration of anthesis was 7 and 8 days respectively over all treatments. Anthesis extended for up to 74 days during unfavourable weather in the first year. No apparent difference between the date of peak anthesis in different treatments could be detected. In the second year, there was considerable variation in the onset and duration of anthesis in different treatments. As with ryegrass, but to a lesser extent, anthesis commenced earlier in ungrazed plots while the addition of nitrogen tended to delay the time to peak anthesis. The range in the onset of anthesis, date of peak anthesis, and duration of anthesis was 8, 8 and 10 days respectively. Despite an 8 day delay in the onset of anthesis in grazed plots heads in these treatments reached peak anthesis more quickly and completed anthesis over a shorter period than plants in ungrazed plots.

In prairie grass the percentage of seedheads showing exserted anthers on each day of observation was counted. This is a facultatively cleistogamous species some florets being chasmogamous and others cleistogamous. The results presented here may not be considered completely accurate as they do not take into account heads with florets which flowered cleistogamously and were not observable in the field. The results therefore include only those heads flowering chasmogamously.

In prairie grass, in the first year, the onset of anthesis was apparently delayed in treatments receiving nitrogen. However the time between the onset of anthesis and peak anthesis in all treatments remained relatively constant between 21 and 23 days. Similarly the total duration of anthesis in prairie grass ranged from 40 - 42 days over all treatments. No apparent effect from grazing occurred in the first season.

In the second year grazing had a considerable effect on both the date of onset of anthesis and on the number of days required to reach peak anthesis. Despite an 11 day delay in the onset of anthesis in grazed compared with ungrazed plots, the time from onset to peak anthesis was only 17 days in grazed treatments versus approximately 21 days in ungrazed treatments. The duration of anthesis for all treatments was 36 to 42 days, with plants in grazed plots completing anthesis over a slightly shorter period than plants in ungrazed plots. By comparison the addition of nitrogen had little effect on these processes.

Anthesis occurred over an extended period in all species in the first year. This was apparently due to environmental conditions over the months of November, December and January. Strong winds, low temperatures, and frequent rain caused inhibition of anthesis on a number of days and caused apparent depression in the number of florets which exserted anthers on several occasions. In the second year warm, fine weather allowed a more contracted anthesis period and resulted in the date of peak anthesis being more clearly defined in each treatment. The variation of anthesis between years was particularly marked in the case of timothy; the mean duration of anthesis for all treatments in the first year being 71 days, compared with only 45 days in the second year. This emphasises the important role of environmental conditions on the anthesis of grasses, the influence of protracted anthesis being subsequently reflected in uneven seed development and ripening throughout the crop.

Observations were also made of the duration of anthesis of 50 individual heads of each species in the first year. The average figures for ryegrass and prairie grass were 9.4 and 9.2 days respectively. In timothy the duration of anthesis per head varied from 6-17 days. This variation in timothy may have been caused by variation in head length as reported by Evans (1916) and Wheeler and Hill (1957).

(b) Glasshouse Experiment (Timothy)

The results in Table 12 show the progress of daily anthesis in 5 selected timothy heads under glasshouse conditions.

TABLE 12 Progress of Daily Anthesis in Selected Timothy Heads

	Day Number	Number of florets with exserted anthers Night (8 p.m. - 8 a.m.)	Day (8 a.m. - 8 p.m.)
(18.1.67)	1	17	0
	2	0	0
	3	383	7
	4	362	113
	5	25	1
	6	277	57
	7	854	240
	8	42	0
	9	22	1
	10	568	1
	11	610	16
	12	143	0
	13	91	17
	14	58	0
	15	95	0
	16	293	0
	17	39	0
	18	26	0
	19	17	0
	20	12	0

The results confirmed that anthesis occurred mainly during the night, as suggested previously by Robbins (1924) and Beddows (1931). However, under warm humid conditions (as recorded by thermohygrograph) on days 4, 6 and 7, anthesis continued intermittently during the day.

Emecz (1961) and Lambert (1966) have both discussed the environmental requirements for anthesis in S48 timothy. They state that anthesis will only occur when the temperature is at least 62°F and light intensity at least 1200 ft. candles. These two minimum values must be exceeded for at least 10 hours before anthesis can occur. A wind velocity of 8 m.p.h. or more can also inhibit anthesis. Observations showed that the whole process of anther exsertion, and pollen dehiscence in timothy occupied a variable period from as little as 30 minutes up to several hours. This is in line with observations by Evans (1916) and Robbins (1924) who quoted a duration of anthesis of between 1 and 2.5 hours in individual timothy florets.

By enclosing a number of seed heads in plastic bags prior to anthesis comparisons of the number of seeds formed following self-pollination were made with the number of seeds formed following crossing.

TABLE 13 Seed Numbers Produced on Timothy Heads Following Self and Cross Pollination

	Average floret number per head	Average seed number per head	Average percentage seeds per head
Self Pollination	1683	4	0.24
Cross Pollination	1885	517	27.43

The results in Table 13 confirm statements by Gorman (1950b) that although self-fertilisation can occur in timothy, the average percentage of florets producing seed is much less with self-pollination than with cross-pollination. These findings show that timothy may be regarded as an open pollinating species, the contribution of self-pollination to total seed yield being negligible.

Studies on the fertility of florets in different positions on timothy seedheads, results of which are presented in Appendix 11 and summarised in Table 14 show that although there was no significant difference in the total number of florets formed in each region a higher proportion of florets completed anthesis and formed seeds in the middle regions than in the basal and terminal areas of the head.

TABLE 14 Summary of Anthesis and Seed Development Data in Different Regions of Timothy Heads

Region	Av. Florets	Av. Florets Flowered	Percentage Total Florets Flowered	Av. Florets Forming Seed	Percentage Seed Formed
1	450a	184	40.0b	75	16.7b
2	504a	263	52.2a	110	21.8a
3	435a	235	54.0a	100	23.0a
4	510a	191	37.5b	70	13.7b
TOTAL	1899	873	45.9	355	18.8

Despite the large number of florets formed per head the number of florets which completed anthesis and eventually developed seed was low. This could be interpreted as being caused either by a low genetic fertility effect or possibly a strong dependance on specific environmental conditions which were absent in the present experiment. Nevertheless, the results show that the middle two regions of timothy heads are capable of a higher seed yield potential than florets situated on the basal and terminal areas of the head. This finding

disagrees with Kahre's (1964) suggestion that in timothy, seeds are developed uniformly over the entire length of the head.

CONCLUSION

In ryegrass, timothy and prairie grass grazing generally delayed the onset of anthesis compared with ungrazed treatments. This effect generally occurred irrespective of whether nitrogen had been applied or not although in ryegrass the addition of nitrogen tended to reduce this delay. Despite the delay in onset, anthesis was generally completed in seedheads in grazed plots more quickly than in ungrazed plots, particularly in ryegrass and prairie grass in the second year.

Strong winds and low temperatures caused inhibition of anthesis in all species. The results presented emphasise the importance of environmental conditions in regulating the duration of anthesis within a crop.

In timothy anthesis occurred mainly during the hours of darkness, but some florets exserted anthers during the day, mainly between 8 a.m. and 11 a.m. Self-pollination resulted in far fewer seeds being formed than occurred following crossing. Within individual timothy heads florets in the central area were potentially more fertile and produced more seeds than florets from basal and terminal regions of the seedhead.

SEED DEVELOPMENT

INTRODUCTION

Following anthesis and seed set (successful fertilisation) seed development commences. Cell division continues until the embryo has a full-developed scutellum, a stem apex and root initials. Accompanying this development various physiological changes also occur. These changes include variations in seed moisture content, increase in seed weight, biochemical changes in various components, colour changes in the caryopsis and seedcoat and the onset and increase in seed germination capacity. The object of this section of the study was to follow some changes occurring during seed development of ryegrass, timothy and prairie grass in the field. The term "seed development" as used in this study covers the period from seed 'set' through to seed maturity, this latter term being reached at the point at which maximum seed dry weight is first attained.

LITERATURE REVIEW

In several studies on the course of seed development in grasses, (Hyde 1950, Grabe 1956, Hyde et al 1959 and Anslow 1964) most attention has been paid to two main aspects, the relationship of moisture content to dry weight, and the development of viable seed from the time of anthesis to seed maturity.

As Grabe (1956) has pointed out, few attempts have been made to define seed 'maturity' in the literature. He quotes Aldrich (1943) who describes maturity as the point at which maximum grain development is first obtained. Also, the terms 'physiological' and 'morphological - maturity' have been used by Shaw and Loomis (1950) and Anderson (1944) respectively, to describe the point at which maximum seed dry weight occurs.

Following fertilisation, the ovule begins to undergo changes which result in seed formation and development. Each seed consists of three major parts - embryo, endosperm and seedcoat. The embryo has a single cotyledon or scutellum, lying in contact with the endosperm and which utilises food from it. This food is passed on by the scutellum to the growing parts of the embryo. The surface of the scutellum comprises a layer of cells which secrete enzymes by which starch and protein in the endosperm is digested or

rendered soluble. The endosperm of grasses consists of two portions; the aleurone layer, which is a layer of large cells inside the seedcoat and the starchy endosperm consisting of large, elongated, thin-walled cells filled for the most part with starch grains. The seedcoat is developed from the integument(s) of the ovule (Wheeler and Hill 1957). The development of the embryo does not continue indefinitely. Cell divisions gradually decrease and ultimately cease when the embryo is fully developed. At this stage the seed may be termed mature (James and Clapham 1935).

Hyde (1950) and Hyde et al (1959) recognised three stages of seed development in white clover and ryegrass. In the latter species these stages may be described as:

1. A Growth Stage lasting for the first 10 days after pollination and characterised by rapid increase in seed weight and high seed moisture content (75-80%). Seed harvested during this stage is not viable.

2. A Food Reserve Accumulation Stage lasting for a further 10-14 days. This stage is characterised by a slow increase in seed dry weight, reaching a maximum at the end of the stage. The amount of water in the seed changes little but the percentage of moisture falls steadily. Seed attains full viability during this stage.

3. A Ripening Stage lasting for 3-7 days. During this stage dry weight remains approximately constant, but moisture content falls from approximately 40% to equilibrium with the atmosphere.

Determination of the stage at which seed development continues independent of attachment to the parent plant has been discussed by Stoddart (1965). He recognised two stages of seed independence. The first was partial (described as 'root independence' or the earliest stage at which continued development ceased to depend on functional connection between the culm and the root system). The second stage Stoddart suggested, was absolute (the point after which the seed no longer required functional connection with the parent plant).

Keller (1943) demonstrated that inflorescences of Bromus inermis could form viable seed when culms detached immediately after anthesis were kept in

water. Confirmation of this effect was later obtained with Phalaris tuberosa (McWilliam and Wardlaw 1965). These findings illustrated the ability of the culm to act as a carbon and nitrogen source for viable seed formation. However, as Stoddart (1965) pointed out, they do not demonstrate root-independence during ripening as this, by definition, also required continued development in the absence of external moisture. In physiological terms this second stage commenced when transport of metabolites across the pedicel ceased, due to the formation of an abscission layer or atrophy of the conducting elements. Stoddart (1965) found this latter point to coincide in Lolium temulentum with the 'late-dough' stage endosperm. He suggested that because of this, seed could not be detached from the standing culm before this point was reached without deteriment to seed yield.

Hyde (1950) has listed three important aspects of seed quality which are affected by the stage of seed development - viability, seedling vigour, and storage life. Full viability was acquired 14 days after pollination in perennial ryegrass (Hyde et al 1959). However, at this stage translocation of food materials to the seed was just beginning. Earlier work with white clover (Hyde 1950) indicated that the vigour of seedlings from immature seeds suffered through inadequate food reserves. Perennial ryegrass seed harvested 14 days after pollination would therefore possess viability, but not high seedling vigour. This latter was not gained until about 24 days after pollination. Similarly, Hyde (1950) showed that immature seed deteriorated rapidly in storage, and suggested this was one of the main factors reducing the quality of many commercial seedlines.

MATERIALS AND METHODS

The changes occurring during seed development in 1966 were studied by making sequential harvests at approximately weekly intervals from peak anthesis. Because of the lack of treatment effect on the date of peak anthesis in all three species in 1966 harvesting of seed of each species was carried out at regular intervals from the mean date of peak anthesis for all treatments.

(30.11.66 for ryegrass, 6.2.67 for timothy and 25.11.66 for prairie grass). At each harvest a 2 foot swath was cut by hand across 10 rows in each treatment and total fresh-weight determined. Immediately following cutting two subsamples were taken. The seed on one subsample was immediately removed from the stalks, total seed fresh weight determined, and a sample retained for moisture assessment. The seed was then spread out to dry or in the case of high moisture content seed artificial drying was carried out (Materials and Methods page 16). The remaining subsample was spread out to dry for approximately 10 days. Seed was then stripped from the stalks, weighed and air dried.

This procedure allowed two seed samples from each harvest - a sample (designated 'direct') equivalent to that obtained following direct harvesting and a sample (designated 'swath') equivalent to that which would be obtained following mowing and swathing and harvesting after a 10 day period of drying in the field. Six sequential harvests were taken for both timothy and prairie grass, and seven for ryegrass. Rain caused difficulties in harvesting in 1966, but despite this only harvest five in ryegrass was seriously affected. At each harvest date records were kept of changes in seed moisture content, seed weight, seed and seedhead colour changes and chlorophyll and anthocyanin content of the floret determined by biochemical extraction. Observations of endosperm consistency of the seed were also made. In addition, samples of seed were air dried and tested for germination following approximately 3 months storage.

Seed moisture content, purity and germination tests were determined as previously described (pages 17-18).

At each harvest date in 1966 100 heads were removed at random in each treatment and divided into head colour categories - entirely green (G), heads showing some greenness but with some florets yellow (G-Y) and heads which were entirely brown (B). The percentage of heads showing loss of seed through shedding was also recorded (S). The seed was then rubbed from the heads and the percentage of seeds in each colour category determined.

Measurements of quantitative changes in both the chlorophyll and anthocyanin content of florets at various stages from ear emergence through to

seed ripeness were undertaken using methods described by Stoddart (1964c) (Appendix 12). At each sampling one foot lengths of row were cut in each treatment. The florets were stripped from the heads to provide material for analysis. Four subsamples (1 gram samples for ryegrass and timothy, and 2 grams each for prairie grass) were taken for duplicate estimations of chlorophyll and anthocyanin content. To overcome possible errors due to diurnal variations in pigment content, samples were taken at the same time each day (1 p.m.) Extraction commenced within 60 minutes.

RESULTS AND DISCUSSION

The major physiological changes studied during seed development included changes in:

1. Moisture content.
2. Seed weight.
3. Seed colour changes.
4. Endosperm consistency.
5. Germination capacity.

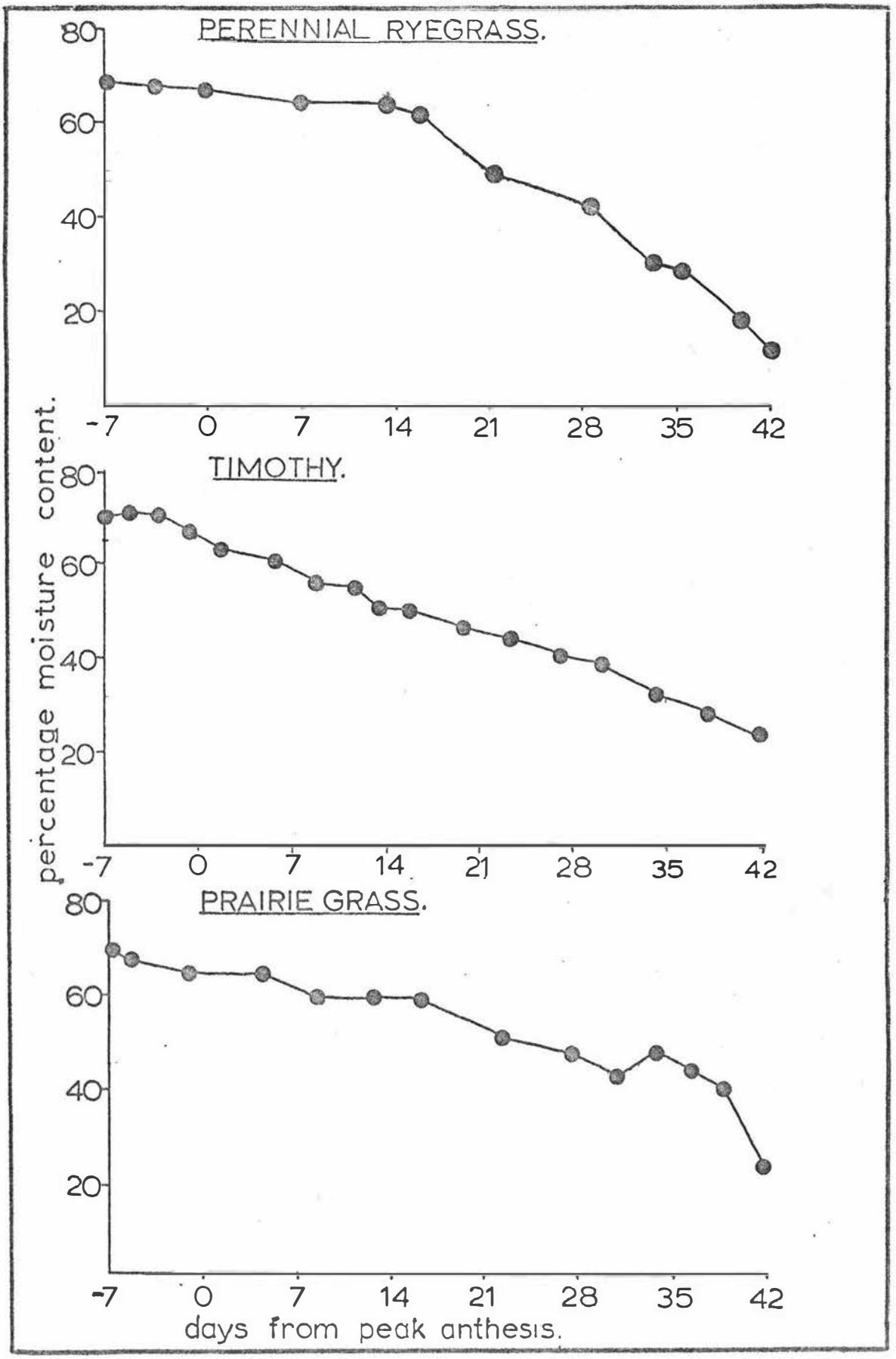
These factors are discussed below.

1. Moisture Content

Mean results for each species are presented in Figure 12 while individual treatment effects are contained in Appendix 13.

Following ear emergence the mean moisture content of the floral organs in all species remained high (60-70%) for some time. Coincident with a point approximately 14, 0 and 5 days after peak anthesis for ryegrass, timothy and prairie grass respectively, gradual loss of moisture began. This loss continued during seed development with minor fluctuations possibly due to variable weather conditions. As shown in Appendix 13 little between-treatment variation was observed although quite high fluctuations in seed moisture content were recorded between observations due to heavy and frequent rain during December and early January. The excessive rainfall over this period reduced the natural drying rate of the seed in ryegrass and prairie grass. At a point 30 days after peak anthesis the average seed moisture content in

FIGURE 12. CHANGES IN SEED MOISTURE CONTENT.



these two species was 44% and 43% respectively. Timothy on the other hand contained seed with a mean moisture content of approximately 40% at this time. The hot, dry weather in February apparently allowed more rapid drying of timothy seed.

In the second year (1967) with hot, dry weather during December, January and February the respective mean seed moisture contents for ryegrass, timothy and prairie grass 30 days after peak anthesis were approximately 40%, 31% and 43%. This between-year variation in seed moisture content at comparable stages of seed development stresses the influence of prevailing weather conditions on the rate and extent of natural drying of seed in the field.

2. Seed Weight

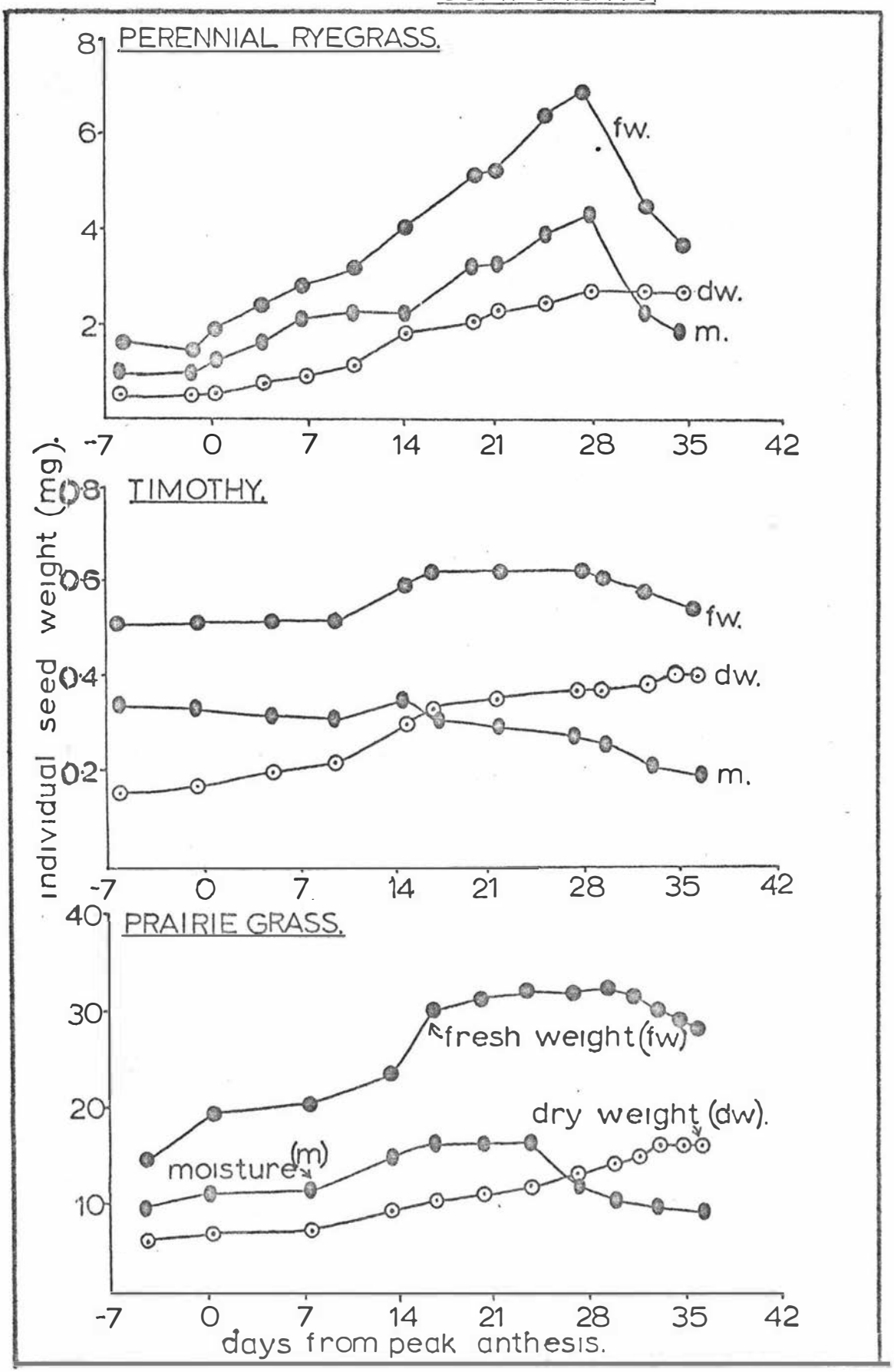
Bushel weight is one of the criterions of high seed quality in commercial trade. One of the objectives of seed production therefore should be to produce the greatest number of seeds per unit area, and to ensure that these seeds are of maximum weight. This is important since ability to germinate and subsequent seedling vigour is related to seed weight and to the amount of food reserves contained in the seed (Grabe 1956). Seed dry weight could therefore be a useful indicator of seed maturity and possibly seed quality.

The results in Appendix 14 show that in all species the dry weight of seed increases from peak anthesis to maturity. The mean results for all treatments in Figure 13 show that in ryegrass seed maturity was reached approximately 28 days after peak anthesis compared with approximately 35 days in timothy and 32 days after peak anthesis in prairie grass.

In ryegrass maximum seed dry weight was first achieved at a point where it comprised approximately 41% of total fresh weight, compared with relative figures for timothy and prairie grass of 59% and 57% respectively.

The final dry weight of seed formed was influenced by different management factors in each species (Appendix 14). Nitrogen application increased seed weight in ryegrass, while in prairie grass grazing depressed seed weight unless nitrogen was also applied. In timothy however, neither nitrogen application nor grazing significantly influenced final seed dry

FIGURE 13. CHANGES IN SEED WEIGHT COMPONENTS.



weight.

The maximum weight of individual seeds of ryegrass has been shown to occur at approximately the same time in early and intermediate emerged heads being reached about 26 days after maximum anthesis. (Anslow 1964). This is in close agreement with the present study and also with the 28 days quoted by Hyde et al (1959).

Hyde (1950) states that seed weight is a useful indicator of maturity. He also points out that thousand-seed weight is used in some European countries as a criterion of quality in agricultural seeds.

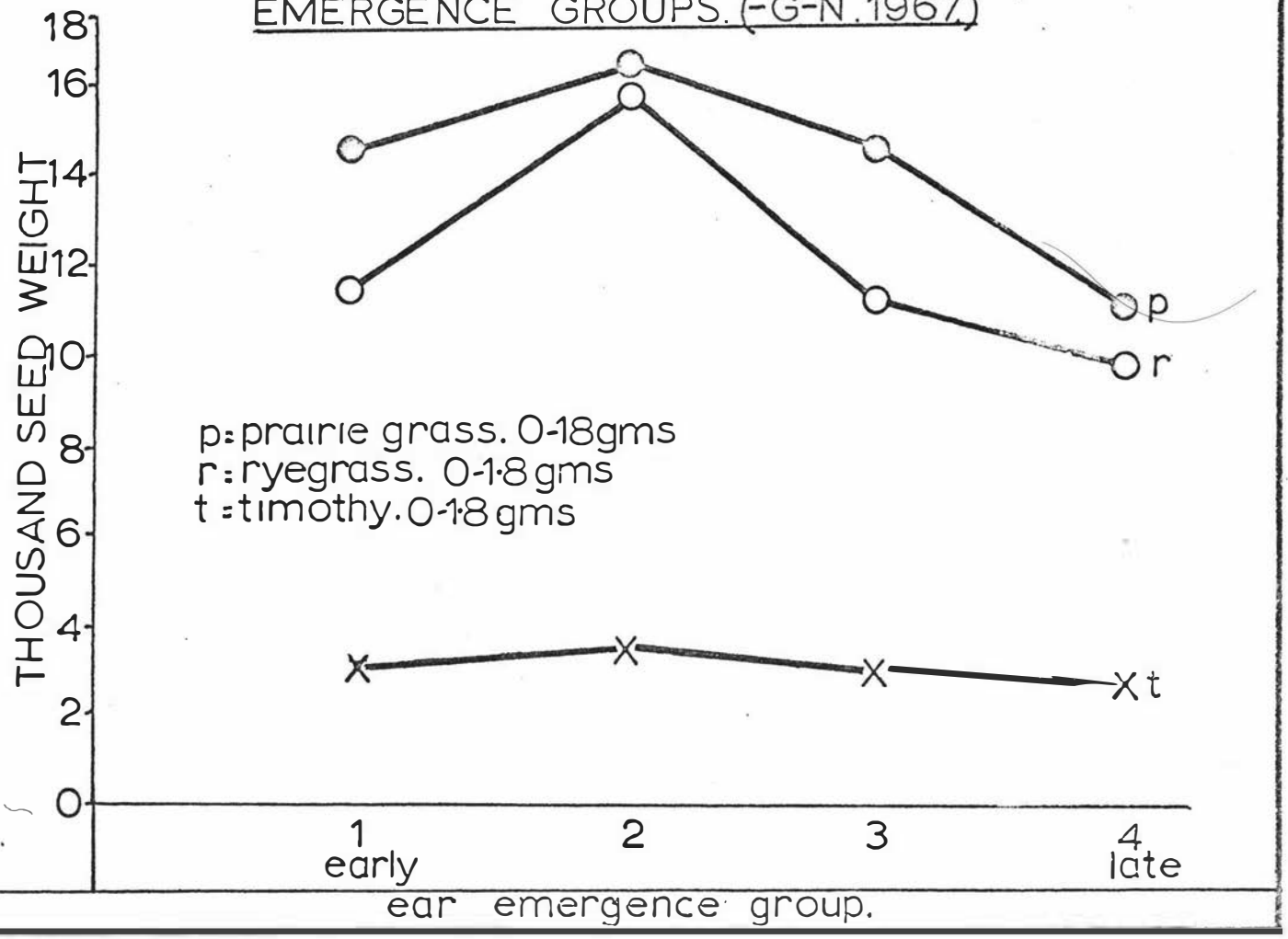
In addition, Anslow (1964), has shown that seed weight within individual heads may vary due to spikelet position and by the position an individual seed occupies within the spikelet. He has shown that, within one spikelet, there is a considerable fall in seed weight from the basal floret to the terminal one.

It is relevant to include at this stage data relating to seed weight in the different ear emergence groups previously considered in an earlier section (page 59). Figure 14 shows differences in seed weight between heads from different emergence groups in the control treatment (-G-N). Date for all treatments is presented in Appendix 15.

The results in Figure 14 support earlier findings that heads in emergence group 2 contribute the major proportion of total seed yield in each species. When the summation of relative yield figures for emergence groups E1 and E2 is considered in relation to the weight of seed present in each group the major influence of early-emerged heads is fully expressed, as heads in these two groups have been shown to contribute between 75% and 85% of the total heads formed in a crop (page 64).

The reduced yield of seed formed on late-emerged seedheads may be influenced not only by individual seed weight as suggested by Stoddart (1959) and Anslow (1964) but also by a reduction in seed number as shown by Langer (1956) in timothy. This latter contention is supported by results previously

FIGURE 14 SEED WEIGHT DIFFERENCES BETWEEN HEADS FROM DIFFERENT EMERGENCE GROUPS. (-G-N.1967)



presented (page 72) which have shown that floret number per head is significantly reduced in late-emergence heads in all species.

The results in Appendix 15 show the influence of grazing and nitrogen application on seed weight in each species.

In ryegrass grazing increased seed weight in early-emerged heads (E1 and E2) and also in late-emerged heads (E3 and E4) if nitrogen was also applied. Nitrogen generally increased seed weight in late-emerged heads. In timothy grazing generally increased seed weight in heads in emergence group 1 at the expense of late-emerged heads (E4). Neither nitrogen nor grazing had a major effect on seed weight in heads from different emergence groups of

prairie grass.

It has been suggested by various workers that variability in seed weight in the same species is largely influenced by competition of assimilates between florets of seedheads on the same plant (Salisbury 1942 , Donald 1954 , Lambert 1956a , Sonneveld 1957). Generally, whether this competition is for moisture, nutrients or for the products of photosynthesis is not clear. Anslow (1964) has however, emphasised the influence of competition between inflorescences for light. This latter effect is perhaps supported by observations in the present study where late-emerged heads were shaded by earlier and taller heads. This effect was particularly marked following lodging in ryegrass and to a lesser extent in prairie grass. The ability of late-emerged heads to actively photosynthesise could therefore have been reduced. This could explain the reduced seed weight found in late-emerged heads, individual seed weight being less than that possible in full daylight.

Also, nitrogen supply has been shown to influence the final weight of individual seeds (Lambert 1956b, Sonneveld 1957). Frequently, however, the same factor has been observed to have opposite effects in different experiments, (Ryle 1965b).

3. Seed Colour Changes

Seed colour is probably the most widely used criterion used in judging the stage of development of grass seed crops. A seed is generally not considered mature until it has lost all traces of greenness. Hyde et al (1959) Evans (1961) and Stoddart (1964a, 1964c) have noted however that in some years seed maturity may be attained while the seedcoat is still green. Under such circumstances crops can give every appearance of immaturity. Their findings suggest the determination of seed maturity and ripeness purely on seed or seedhead colour can be unreliable. However, it was felt that the ease with which a colour criterion could be used in the field was sufficient important to warrant study of this aspect of seed development.

Initially the study was conducted on a field scale, attempts being made to follow the proportion of heads and the percentage of seeds in different

colour categories.

In addition, studies were undertaken to follow quantitative changes in the levels of chlorophyll and anthocyanin in the florets of each species during seed development (method described page 90).

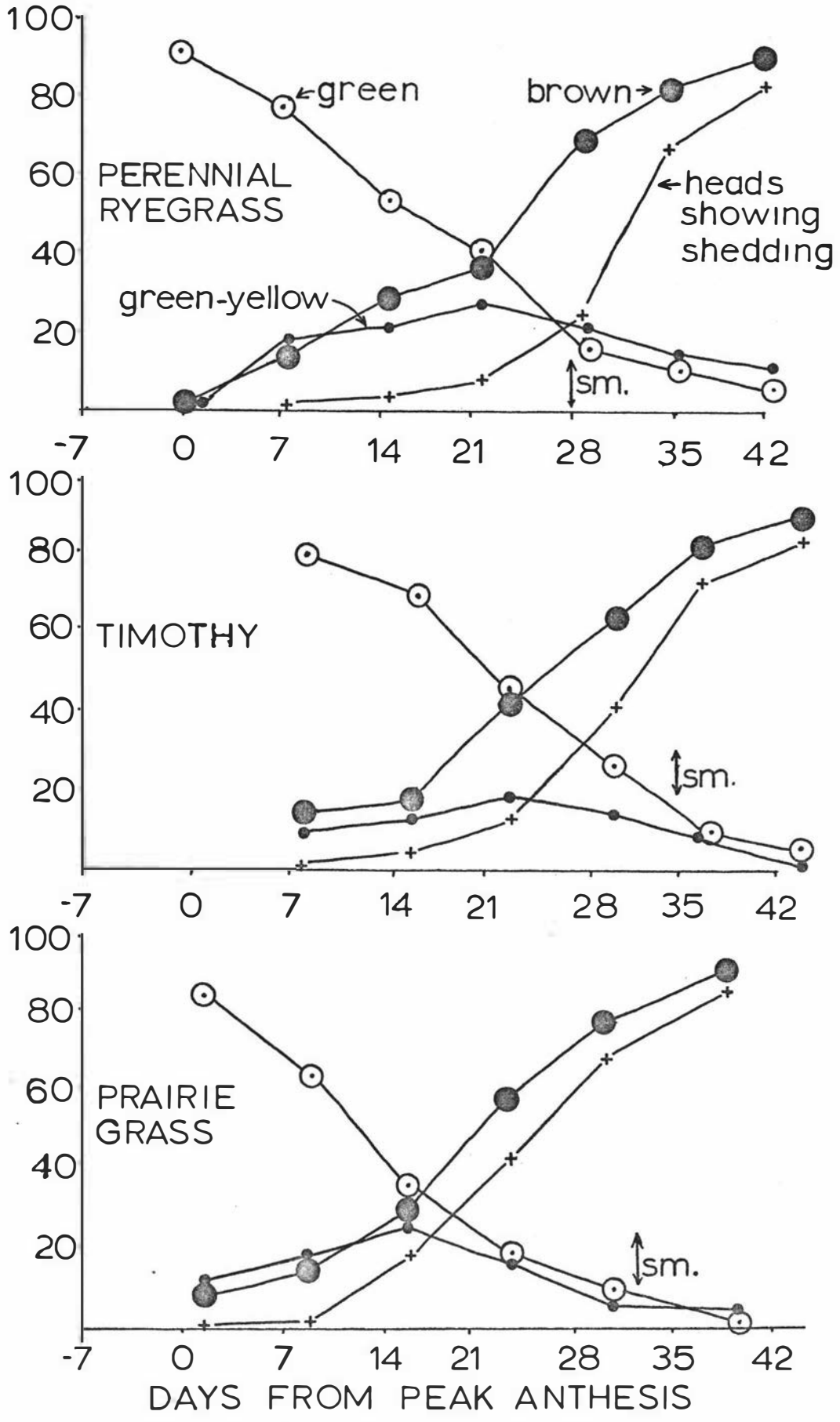
Variation in the percentage of seedheads and seeds in colour categories in the field was not sufficiently marked in the species studied to enable treatment effects to be determined. Although the results obtained in each treatment in the first year are presented in Appendices 16 and 17, those shown in Figures 15 and 16 are mean values for all treatments in each species. These results show that colour changes in the seed closely follow those occurring in the glumes of the floret. Hence the external appearance of the seedhead can be used to follow colour changes within a crop without removing seed from the glumes.

The percentage of seedheads in a crop which had turned brown in colour at the time of seed maturity (S.M.) varied between species (Figure 15). In ryegrass approximately 65% of the heads in the crop were brown, irrespective of the treatment. In timothy and prairie grass the corresponding figures were approximately 70% and 80% respectively.

At this stage approximately 28% of heads in ryegrass were showing seed shedding losses. In timothy and prairie grass the corresponding figures were approximately 55% and 70%. The percentage of heads in a particular colour category emphasises that although the rapidity of colour changes in the seedhead may vary between species, the role of climatic conditions should also be considered. Under high rainfall conditions loss of greenness might be more gradual than under hot dry conditions. This infers that yearly variations in climate during seed development may make it difficult to use colour changes of the seedheads in a crop to provide precise visual criteria for assessing the attainment of seed ripeness for harvest, as reported by Crosbie (1964).

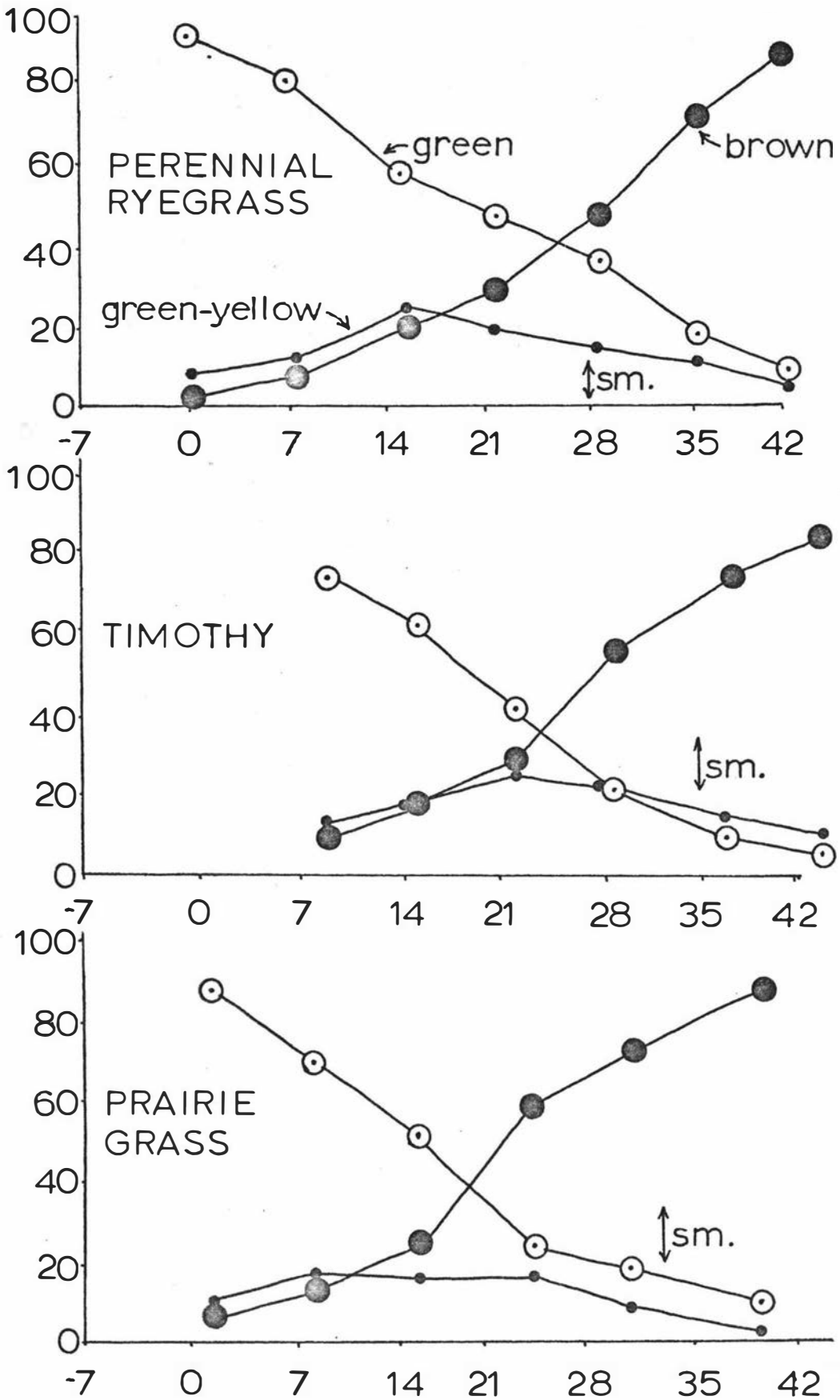
Results in Figure 16 show that at the point of seed maturity approximately 50% of ryegrass seeds were brown in colour. In timothy and prairie grass at

FIGURE 15 PERCENTAGE OF HEADS IN DIFFERENT COLOUR GROUPS DURING SEED DEVELOPMENT



sm = seed maturity

FIGURE 16 PERCENTAGE OF SEEDS IN DIFFERENT COLOUR GROUPS DURING DEVELOPMENT



sm=seed maturity

this stage the respective percentages were approximately 65 and 70.

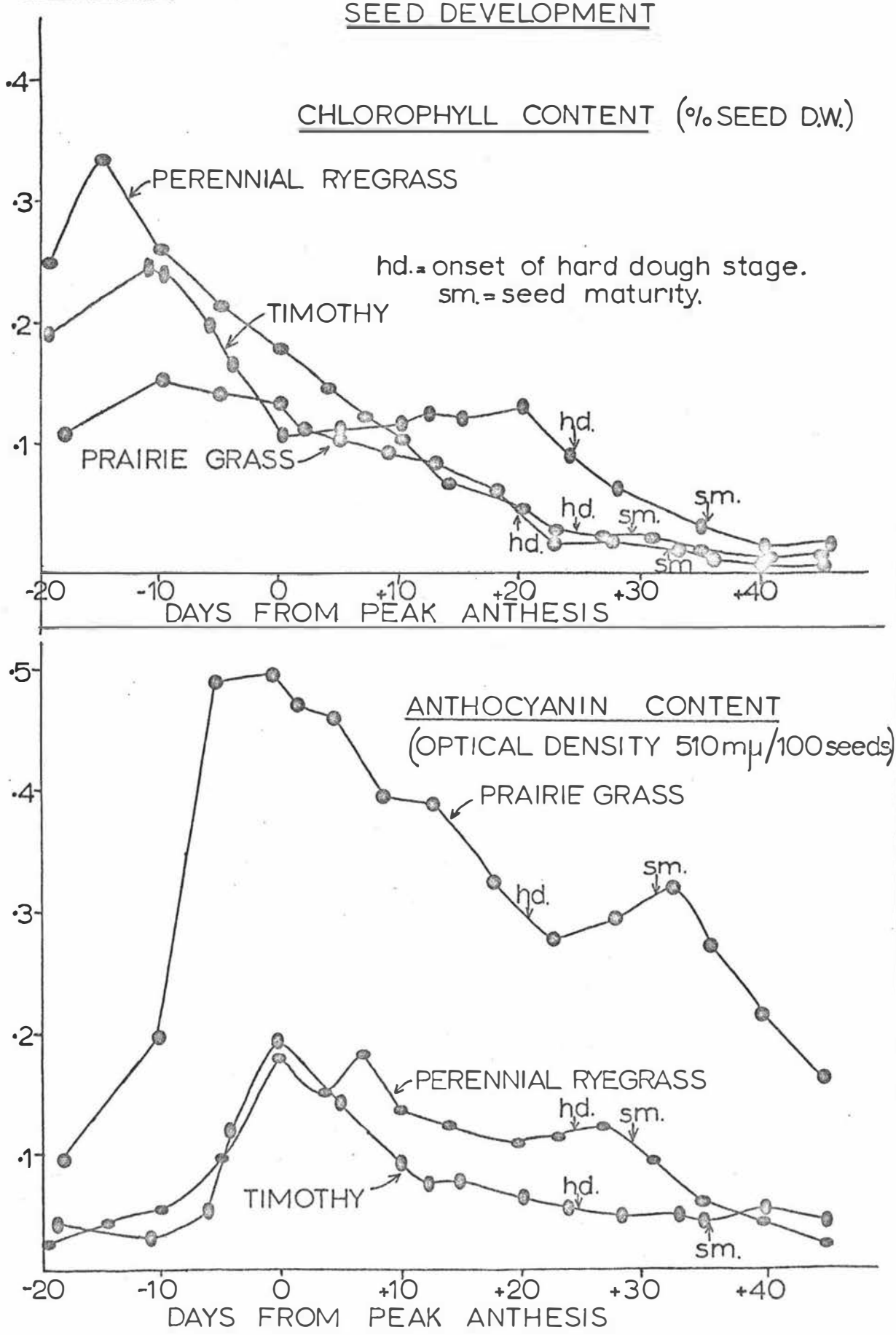
Colour changes in perennial ryegrass seed from green to yellow or purple have been shown by Hyde et al (1959) to commence about the 20th day after anthesis. This was approximately 8 days prior to the point of maximum seed dry weight. The data presented by Hyde et al (1959) was collected in different years and was combined to form a 'single season' assessment of changes occurring during seed development. Because of this, these workers stated that comparison between species or with overseas results, in the rates of seed colour changes and seed development must take this into account.

The results of determinations of changes in both chlorophyll and anthocyanin content of florets from ear emergence through to seed maturity (S.M.) and ultimately to a point approximately 45 days after peak anthesis are presented in Appendix 18. Results showing mean values for all treatments are presented graphically in Figure 17.

A. Chlorophyll

In all species there was a progressive reduction in chlorophyll content of florets commencing prior to peak anthesis. As anthers apparently contain little green pigment any increasing contribution to the dry weight of the floret due to anther development and maturation would cause a corresponding fall in chlorophyll content expressed as a percentage of total dry weight. Similarly, during seed development increases in seed weight would be reflected in a reciprocal decline in chlorophyll content of the floret as a unit. From a point corresponding approximately to the onset of the 'hard dough' (hd) stage loss of chlorophyll in ryegrass and prairie grass was almost complete. In timothy a further fall in chlorophyll content occurred to a stage following seed maturity (S.M.) reaching low levels approximately 45 days after peak anthesis. Eventually the percentage of chlorophyll in the floret would presumably reach zero. Unfortunately this final degradation phase is a gradual one being difficult to utilise as a precise visual criterion of seed ripeness.

FIGURE 17 PIGMENT CHANGES DURING SEED DEVELOPMENT



Stoddart (1964c) has suggested that the detection of extensive chlorophyll degradation in the seed and glumes could be regarded as an indication that abscission layers were fully formed and that ripening processes requiring continued connection with the parent plant were completed.

B. Anthocyanin

Determinations of changes in anthocyanin content were considered necessary because, especially in prairie grass and to a lesser extent in ryegrass, the glumes and the seedcoat developed red pigmentation during seed development.

The results in Figure 17 show there was little anthocyanin present in the inflorescences of the three species at ear emergence, being virtually absent in timothy and prairie grass and visible only as a slight red nervation on the surface of the glumes in ryegrass. Soon after seedhead emergence there was a rapid rise in anthocyanin content due to the production of anthocyanin in the anthers. The close relationship between anthocyanin production and anther maturation has been previously observed by Onslow (1925).

Following anthesis anthocyanin content fell sharply due to anther dehiscence. At the completion of anthesis the pigment content gradually fell to a level similar to that obtained from freshly emerged heads. Anthocyanin content remained relatively high in prairie grass through to seed maturity (S.M.) and to a lesser degree in ryegrass and timothy. This trend was also observed by Stoddart (1964c) in S321 perennial ryegrass, and was due he suggested, to the production (or lack of degradation) of anthocyanin in the seedcoat, resulting in a dark purple caryopsis. In prairie grass however anthocyanin appeared to be concentrated in the glumes, little if any pigment being observed in the seedcoat. The final degradation of anthocyanin corresponded approximately to the point of seed maturity in both ryegrass and prairie grass (28 and 32 days after peak anthesis respectively).

The unreliability of seed chlorophyll and anthocyanin as a guide to seed maturity is evident. In all species seed maturity was generally reached at a point when the seed had lost the majority of these pigments. However, precise

demarcation or rapid loss of chlorophyll or anthocyanin was generally not sufficiently marked to be readily detected by eye in the field. Because anthocyanin content of the floret rises to a peak at the point of anthesis in all species changes in the level of this pigment could perhaps be useful in determining peak anthesis in the field.

As Stoddart (1964c) has pointed out, two factors detract from the usefulness of pigment components in the field assessment of seed maturity and ripeness. First it is necessary to begin determinations well before the anticipated harvest date to detect accurately the attainment of physiological ripeness. Secondly, the facilities necessary for actual chemical determinations will seldom be available.

It is of interest that New Zealand 'Grasslands Ruanui' perennial ryegrass and 'Grasslands Kahu' timothy showed similar sequential changes in both chlorophyll and anthocyanin content to those found in Aberystwyth bred strains S321 perennial ryegrass and S352 timothy by Stoddart (1964c). In 'Grasslands Ruanui' ryegrass however the proportion of both chlorophyll and anthocyanin present in the floret was approximately twice as high as the levels found by Stoddart in S321. The quantity of both pigments in 'Grasslands Kahu' timothy appeared comparable to that found in S352 (Stoddart 1964c).

4. Endosperm Consistency

The changes in endosperm consistency during seed development can be described as 'milky', 'soft dough', and 'hard dough' (Griffiths et al 1967). During the initial rapid phase of seed growth, the endosperm consists of a predominantly clear fluid, but the ensuing milk and soft dough stages are not sharply separated, and throughout the early 'soft dough' stage it is possible to observe quantities of milky fluid by pressing the immature endosperm between the fingers. In the late 'soft dough' stage the endosperm tends to yellow, especially in ryegrass, and becomes more viscous. During the final stages of seed maturation the endosperm hardens to a granular consistency (Evans 1960a).

While seeds in a crop obviously cover a range of endosperm development the overall maturity of seed in each species was attained in ryegrass, timothy and

prairie grass approximately 28, 35 and 32 days after peak anthesis respectively. Observations showed that the onset of the hard-dough stage occurred approximately 24, 24 and 20 days respectively in the same species (see Figure 15).

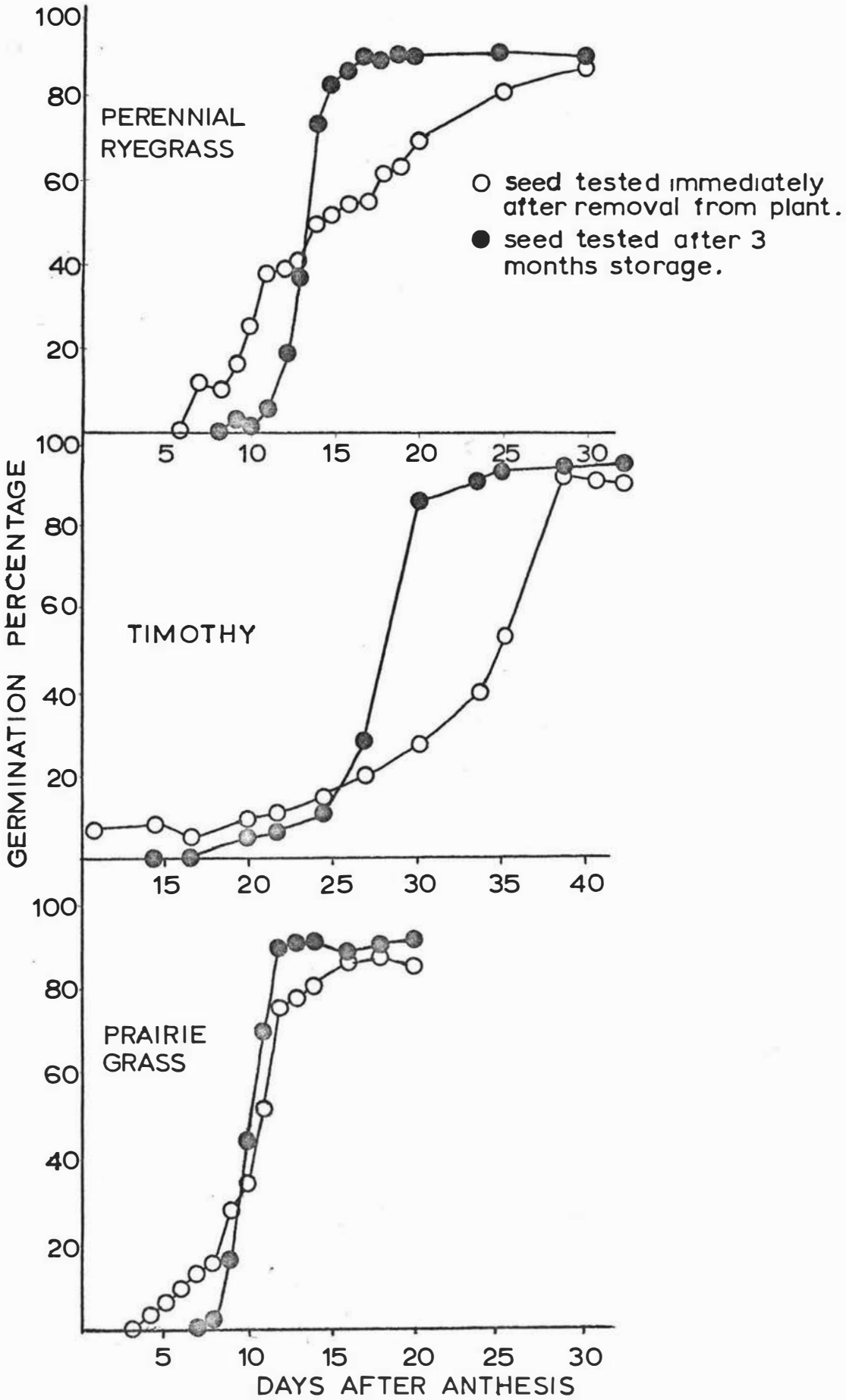
Stoddart (1959) has suggested that solidification of the endosperm and the cessation of translocation should indicate there can be little further increase in seed weight. This is probably true in cases where seed is devoid of photosynthetic tissue at the onset of the 'hard dough' stage. Under these conditions the presence of a hard endosperm could be used as an indicator of seed maturity. The figures quoted above, however, indicate that in all three species increase in seed dry weight continues for some time following endosperm solidification. This is attributed to the fact that at the time of onset of the 'hard dough' stage in ryegrass approximately 47% of the heads were entirely green in colour. In timothy the corresponding figure was approximately 24% and in prairie grass 40%. The mean values for increase in dry weight of seed in each species following the onset of the hard dough stage through to seed maturity (maximum dry weight) were approximately 18% in ryegrass, 4% in timothy and 19% in prairie grass. It appears that the amount of photosynthetic pigments present over this period, although declining, may still be an important contributor to the pool of carbohydrate materials in the developing seed.

5. Germination

Seeds were removed from seedheads at known intervals following anthesis. At each sampling date a germination test and a tetrazolium test was immediately carried out. The latter was undertaken using methods described by Hyde (1952) for ryegrass and Wharton (1955) for timothy and prairie grass. The results were used to determine viability of seed immediately following removal from the plant. The remaining seed in each sample was stored in paper bags at room temperature. Following three months storage a further germination and tetrazolium test was conducted.

The results in Figure 18 (raw data presented in Appendix 19) show the germination percentage of ryegrass, timothy and prairie grass at varying intervals following anthesis.

FIGURE 18 GERMINATION CAPACITY OF SEED HARVESTED AT DIFFERENT INTERVALS AFTER ANTHESIS



In ryegrass, germination was observed as little as 7 days after anthesis reaching a maximum approximately 23 days later. In samples which had been stored for 3 months however, the onset of germination was delayed to a point 9 days after anthesis, but full germination capacity was reached on the 17th day. A similar trend was observed in both timothy and prairie grass.

In all three species germination and tetrazolium test results were closely related. This infers that low temperature pretreatment of the seed prior to the germination test effectively broke dormancy, which can cause anomalous results in the germination of freshly harvested seed.

In many studies on seed development one of the major aspects considered has been the time of onset and rate of increase of the germination capacity of seed following anthesis. Workers generally agree that in a number of species the onset of germination occurs at an early stage of seed development e.g. 10 days after anthesis for perennial ryegrass (Hyde et al 1959), 6 days for barley (Harlan and Pope 1922) 5 days for Bromus inermis (Grabe 1956) and 4 days for oats (Frey et al 1958). Hyde et al (1959) observed that in perennial ryegrass viability was acquired with great rapidity, the first viable seeds being observed only 10 days after anthesis, and full germination potential being reached 14 days after anthesis. In contrast however, Stoddart (1959) found that in timothy the increase in germination percentage was a gradual process beginning approximately 10 days after anthesis and increasing slowly over the next 30 days to over 90%. This suggests that species vary in their rate of attainment of maximum seed viability following anthesis. The results obtained in this experiment also suggest that germination tests on immature seed immediately following harvest can yield very different results when compared with tests carried out after 3 months storage.

It seems likely that a number of immature seeds in all species which were capable of germination soon after anthesis contained insufficient food reserves to maintain their viability during a three month storage period. Similar conclusions have been reached by Grabe (1956) in Bromus inermis,

Hyde et al (1959) in perennial ryegrass, Hyde (1950) in white clover and McAlister (1943) in a number of pasture grasses. As a result, some ryegrass, timothy and prairie grass seeds harvested as little as 7, 10 and 4 days respectively after anthesis would possess viability but would show a limited storage life. Such seed, being light and immature, would probably be removed during commercial cleaning.

The major difficulty in a discussion of the results shown in Figure 18, is to explain the increased germination gradient and earlier attainment of full viability of seed after 3 months storage. The figures on germination percentage after 3 months storage of ryegrass seed, closely follow those obtained by Hyde et al (1959). Under these conditions the rapid increase in germination capacity commencing on the 9th day after anthesis and reaching a maximum on the 17th day relates to the 10th and 14th day values quoted by Hyde et al (1959). In prairie grass the rate of attainment of full germination capacity is also rapid, commencing on the 8th day after anthesis and rising to a maximum value on the 12th day. In timothy seed following 3 months storage germination onset began 20 days after anthesis, reaching a maximum approximately 15 days later. This latter figure corresponds reasonably well with the 40 days quoted by Stoddart (1959).

As a possible explanation for this variation in the rate of attainment of full germination capacity it is suggested that a post-harvest change in the seed may occur. Such an after-ripening effect may allow a greater number of seeds to germinate at an earlier stage of development than occurs in the case of freshly harvested seed. This suggestion is supported by the fact that tetrazolium staining patterns in freshly harvested seed of all three species showed marked variation in intensity. In some seeds the coleorhiza was only lightly stained, compared with the intense red staining of the scutellum and coleoptile. These lightly stained areas, while classed as normal in freshly harvested seed, were not evident following tetrazolium treatment of seed after 3 months storage.

Because of the emphasis previously placed on the importance of heads in different ear emergence groups to seed yield it was thought desirable to include germination records for seed from heads in each ear emergence group.

The results shown in Figure 19 are mean values of germination percentages for all treatments except at E4 where individual treatment differences are also shown. (See Appendix 20)

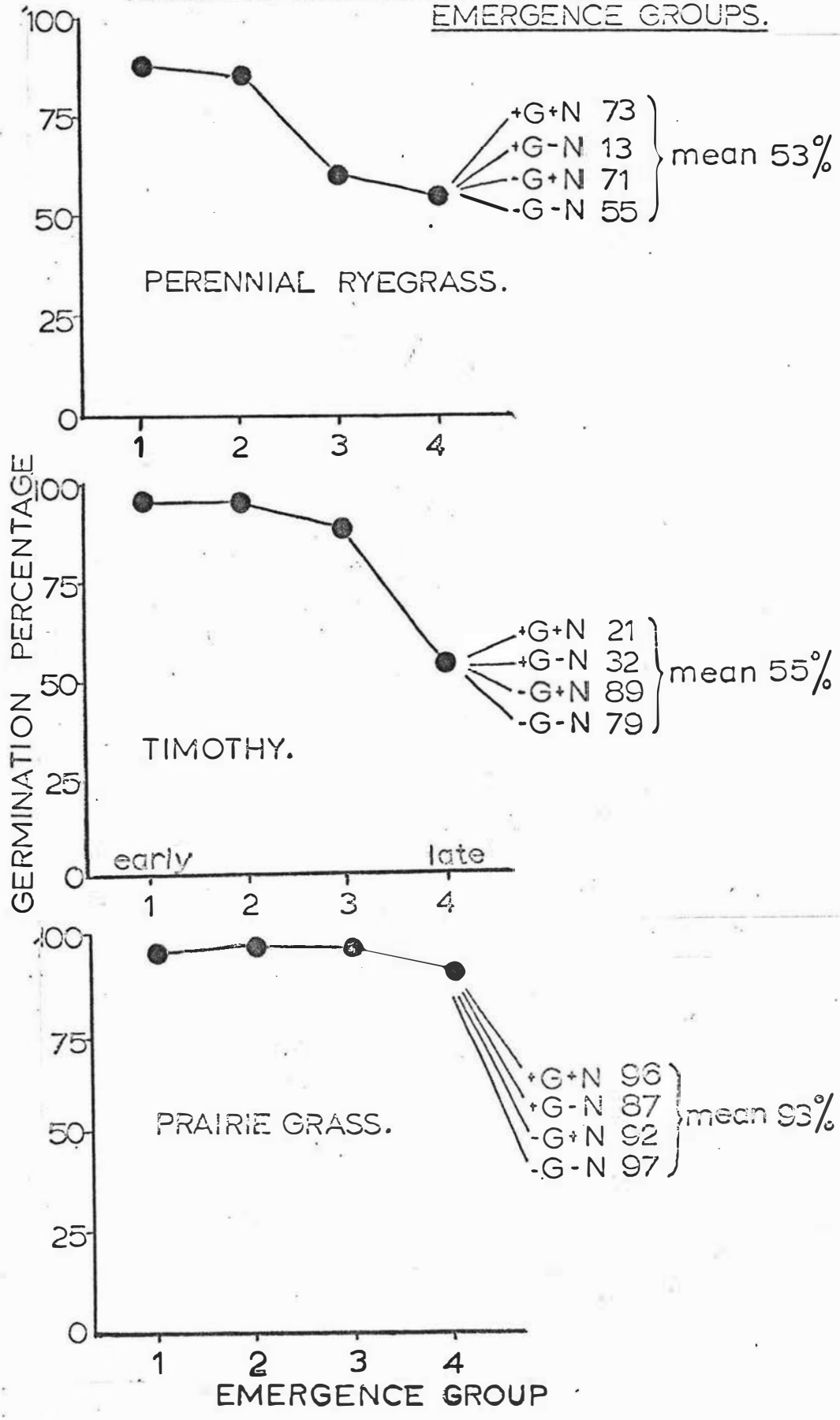
The results stress that in ryegrass there was a germination reduction gradient between seeds formed on early-emerged heads (E1) to late heads (E4). Seeds from late heads (E3 and E4) had 25-30% lower mean germination than seeds from early heads (E1 and E2). Similarly in timothy, seed from late-emerged heads (E3 and E4) had a 12% and 31% lower germination respectively than seeds from early-emerged heads (E1 and E2). In prairie grass, however, little germination reduction occurred. In this species mean germination of seeds from early-emerged heads (E1 and E2) and seeds from late-emerged heads (E3 and E4) was 98% and 96% respectively. The speed of germination of seeds from late heads was slower than that of seed from early-emerged heads.

The nitrogen and grazing treatments presented in Figure 19 show that in ryegrass, nitrogen application increased the germination percentage of seed from late-emerged heads. Grazing alone reduced seed viability. In timothy, grazing again had a deleterious effect on the germination capacity of seed from late-emerged heads while the nitrogen effect was less obvious. In prairie grass the effects of grazing and nitrogen on germination capacity of seed from heads in E4 were relatively small compared with the other species.

Anslow (1964) observed similar variations in germination capacity of seeds on early, intermediate and late emerged heads of ryegrass. Germination capacity was lower on average in late heads. In addition, he found that seed from spikelets in the middle of ryegrass heads gave the highest germination and that the terminal seeds in each spikelet were also of lower germination than the basal ones.

The results in the present section together with those presented in previous sections (Pages 64 and 92) emphasise the relative contribution and

FIGURE 19 GERMINATION CAPACITY OF SEEDS FROM HEADS IN DIFFERENT EMERGENCE GROUPS.



value of seed from early-emerged and late-emerged heads. They show that the number of heads emerging early is greater; their seed weight higher and their germination capacity greater than those emerging late.

CONCLUSION

The sequence of seed development involves initially rapid cell division, resulting in an increase in seed size and weight. Thereafter rate of cell division progressively declines, food reserves are accumulated in the developing seed and seed germinability is attained. Finally seed reaches maximum dry weight at maturity.

In the present study the sequence of development was considered by measurement and observations on changes in seed moisture content, weight, colour, endosperm consistency and germination capacity.

Initially seed moisture content is high (60-70%) after anthesis. At varying periods after peak anthesis (14, 0 and 5 days for ryegrass, timothy and prairie grass respectively) moisture content began to fall. The rate and extent of loss of moisture was affected by seasonal weather conditions.

Maximum seed dry weight (maturity) was reached approximately 30 days after peak anthesis in all species. Nitrogen application increased final seed weight in ryegrass, while grazing reduced the weight of seed formed in prairie grass. In timothy, neither nitrogen application nor grazing significantly reduced final seed weight. This suggests the importance of considering the management of individual species to maximise seed weight rather than the use of common management systems for different species sown for seed production.

The major contribution to total seed weight was made by early-emerged heads, seed weight being reduced with time of subsequent ear emergence.

The rate of floret and seed colour changes from green to brown in a particular species was variable. The influence of weather on this factor suggested it was difficult to use seedhead colour changes or measurements of loss of chlorophyll or anthocyanin from the floret to obtain precise

assessments of seed maturity. Anthocyanin content of the floret was considered a potentially useful measurement of peak anthesis in a crop.

At maturity the endosperm of the seed was already in the 'hard dough' stage. The onset of this stage was reached 4, 11 and 12 days prior to the point of maximum seed dry weight in ryegrass, timothy and prairie grass respectively. Increases in seed dry weight therefore continue for some time following endosperm solidification.

Studies on the rate of onset of germination capacity following anthesis showed that variation could occur depending on whether germination tests were conducted immediately following removal from the plant or following storage (3 months). Immature seeds removed from the plant as little as 7, 10 and 4 days after anthesis in ryegrass, timothy and prairie grass respectively were capable of germination when dormancy was broken. These immature seeds however, did not retain viability after 3 months storage. In cases where seed was germinated after storage viable seeds were first detected in samples taken 9, 20 and 8 days respectively in the three grasses after anthesis. An increased germination gradient and earlier attainment of full viability was characteristic of seed stored for 3 months after sampling when compared with viability tests on seed immediately after removal from the head. Maximum viability of ryegrass, timothy and prairie grass seed tested immediately after harvest occurred 30, 38 and 16 days after anthesis compared with 17, 35 and 12 days respectively when germination testing was delayed for three months.

Seed from early-emerged heads showed superior germination speed in all species and a higher final germination than seed from late-emerged heads. Nitrogen caused a substantial increase in germination percentage in ryegrass, while grazing tended to depress seed viability, particularly in timothy.

SEED RIPENING, HARVESTING AND YIELD

INTRODUCTION

In the present study the term "ripening" refers to changes occurring from seed maturity until the seed has dried to a moisture content suitable for harvesting. Weather conditions vary from year to year and the time taken for seed to ripen changes accordingly. Stages of development and their relationship to the external appearance of the head remain approximately the same, but the time occupied by each stage is apparently influenced by the environment, particularly rainfall.

The present study includes consideration of the effect of harvest method and of grazing and nitrogen application on seed yield and quality; of moisture changes in the seed and methods employed to assess the point of harvest ripeness and hence of optimum harvest time.

Work by Arnold and Lake (1965) has raised doubts as to whether direct threshing of grass seed crops can be carried out early enough to avoid considerable shedding losses without impairing seed viability. If seed is removed from the plant before it comes away easily, germination is inevitably impaired. In contrast, high quality seed can be obtained over a relatively longer period when it has dried prior to threshing. For these reasons it was decided to study whether improvement in seed quality results from natural drying of the seed in the standing crop only, or whether the same result could be obtained by cutting the crop prior to seed maturity before seed shedding losses became severe and allowing the seed to mature and dry on the cut straw. This study was also prompted by work by Stoddart (1965) which showed that the later stages of seed maturity were able to proceed to completion without requiring the culm to be functionally attached to the root system.

LITERATURE REVIEW

The rate of moisture loss in seed during natural drying is variable, and is apparently related to seasonal weather conditions, particularly rainfall. (Evans 1960a, Anslow 1964). In addition the range of ripeness occurring in a seed crop depends on genetic constitution and differences in the age of

individual seedheads (Columbus-Jones 1959). The rate of development of the seed, in terms of both size and the accumulation of reserve products, largely determines the onset of final drying. Shaw and Loomis (1950) for example, distinguish between 'physiological maturity' of maize seed at 30-40% moisture content (at which stage dry matter accumulation is complete), and 'harvest maturity' at about 20% moisture content which occurs by moisture loss.

Studies by Stoddart (1959) on timothy and by Evans (1960a) on cocksfoot, meadow fescue and meadow foxtail, have indicated that seed in the late-dough stage appears to be ripe in all respects, even though the seedcoat and glumes may be still predominantly green. A crop containing seed at this stage would not be judged ripe by present criteria, which demand a yellow or light brown seedcoat and a hard endosperm. This emphasises the need for greater understanding of the state of 'ripeness' in seed of herbage grasses (Stoddart 1964a).

Many workers have suggested methods for determining the precise point of seed ripeness for harvest in grass seed crops. Most of these methods have involved the use of visual criteria. The long-used techniques of sweeping a hat through the standing heads, pulling a few heads through the fingers or rubbing seed out of the head in the palm of the hand are still employed by many seed growers. These methods are apparently designed to give some indication of the physical condition of the seed and suitability for harvest and have been recommended by many workers (Evans 1937b, Stuart 1957, McPherson 1957, Barrer 1957, Jolly 1957, Smith 1957, Harbord 1957, Morris 1959, Richards 1961, Delahunty 1962). The first visual evidence of shedding in grass seed crops has been suggested by some workers as indicative of optimum harvest date (Palmer 1937, Wheeler 1950, Hadfield 1957, Harbord 1957, Stoddart 1959, Delahunty 1962, Kahre 1964, Gwynne 1966).

Loss of greenness from the seed and/or the straw have both been suggested as useful indicators of seed ripeness at harvest (Cockayne 1913, Jolly 1946, Whatman 1956, Culbertson and Kommedahl 1956, Wheeler and Hill 1957, Smith 1957,

Columbus-Jones 1959, Culbertson et al 1960, Richards 1961, Gwynne 1966), and the consistency of the endosperm one of the major anatomical components of the seed, apparently can provide a usable and reliable guide to seed ripeness (McPherson 1957, Richards 1957, Jolly 1957, Smith 1957, Stoddart 1959, 1964a, 1964b, and Richards 1961).

Relatively few workers have suggested determinations of seed weight and/or seed moisture content as useful methods to assist in the assessment of crop ripeness, (Wheeler and Hill 1957, Crawford 1960, Koopman 1963, Anslow 1964, Griffiths et al 1967, and Nellist and Rees 1968).

In practice a seedcrop consists of a population of inflorescences covering a wide maturity range, which means that problems arise in determining the most accurate impression of overall crop ripeness.

Anslow (1964) suggests that the relationship between seed weight and moisture content, as one of the more consistent factors in seed development, could be a useful method of assessing crop ripeness.

When using percentage moisture as a field criterion of ripeness, two difficulties occur. The first is that the relationship between percentage moisture and viability varies according to season, and the second is that precipitation can influence the values obtained. However, in the later stages of maturity these difficulties largely disappear, and seed moisture measurements can be a valuable additional guide for deciding the best time for direct combining of crops. (Griffiths et al 1967).

Moisture may be associated with seed in two ways, firstly as surface moisture which is quickly lost by evaporation, and secondly as internal moisture. (Hill and Crosbie 1966). Removal of internal moisture requires that the water be moved to the seed surface before evaporation can occur and explains why the process of seed ripening may be a rapid or gradual process depending upon the prevailing environmental conditions. Klein (1967), however, quotes the average loss of moisture in the standing crop of a wide range of grasses as being from 1-4% per day.

Stoddart's (1964b) studies on changes in total free amino acids in seed during development have shown that the patterns of fluctuation in timothy and perennial ryegrass are similar to those he described for total soluble carbohydrate (T.S.C.) (Stoddart 1964a). However, he concluded that, from a practical standpoint, the determination of T.S.C. content appeared to be a more convenient method of seed ripeness assessment.

Changes in seed respiration rate have been investigated as a possible criterion for estimating the earliest point of seed ripeness. (Stoddart 1961). Unfortunately, during seed maturation, infection by sub-epidermal fungi such as Alternaria spp. almost invariably occurred, giving false respiratory values and nullifying the potential usefulness of seed respiration measurement in the determination of ripeness.

Many grass seed crops can be harvested at moderately high moisture levels (Grabe 1956 quotes 47% for Bromus inermis, Hyde et al (1959) and Klein (1967) quote 40% for perennial ryegrass. The stage of maturity of the seed at these moisture levels does not appear to be critical in affecting the viability and bushel weight of commercial seedlots. In many crops the seed has reached maximum dry weight and is able to germinate and produce vigorous seedlings before it is dry enough to combine (Grabe 1956). In such cases then, the problem is really one of eliminating excess moisture from the seed before it is put into storage.

Klein (1967) observed that in a range of grasses the seed moisture content of the standing crop was nearly the same at the highest yield point in successive years and therefore was a good index of best mowing time. In general, seed moisture is high in the immature crop - usually 60%-70%. As seed ripens the moisture drops eventually to about 10%. Klein has therefore suggested it is possible to draw 'drying curves' for each grass species. The drying curve for each type of seed has a characteristic shape as to slope or drying rate. During hot weather, the slope of the curve would temporarily increase, while during cool or rainy weather the curve would flatten. Such seed moisture content curves have been used by Klein (1967) to predict

the proper mowing date of seedcrops of a number of species.

While more reliable techniques for evaluating the stage of ripeness of seedheads for harvesting may assist in minimising seed losses through shedding, the problem of uneven seed ripening in many perennial grass crops remains to be overcome. Selection and breeding for seed retention appears to be a most promising line of enquiry likely to lead to a solution of this problem. (Bean 1965).

In addition Stoddart (1959) has shown that in timothy endosperm solidification corresponds with the complete formation of abscission layers and is associated with seed dehydration. At this stage even slight mechanical disturbance can cause extensive seed shedding.

Similarly, Bonin and Goplen (1963a) in Phalaris arundinacea found that shedding involved the release of the seed from the glumes, disarticulation occurring just below the floret.

Field conditions which promote shattering are extremely variable. For example, Bonin and Goplen (1963b) observed that shattering stress in Phalaris arundinacea was most severe on the windward side of a crop. Further, a difference of one or more days in anthesis date could compound differences in shattering percentage between clones if heavy winds or rain were experienced just as some clones were beginning to shatter and before others had commenced shattering. (Bonin and Goplen 1963b).

While seed retention can apparently be improved by appropriate selection techniques (McWilliam 1963), it remains to be seen whether easier separation of seed and glumes can be selected for simultaneously (Baltensperger and Kalton 1959).

The physiological control of abscission layer formation at the point of seed attachment to the pedicel has been shown to have a hormonal basis (Griffiths et al 1967). It was found by Jewiss (1961) that spraying timothy seedheads with synthetic auxin (naphthylacetic acid) 20 days after anthesis increased seed retention, and more recently Mullet (1966) reported improvements

in both seed yield and seed retention in Phalaris tuberosa with auxin sprayed before and at anthesis. However, until varieties with a high seed-retaining capacity are developed, early harvesting still remains the best method of minimising seed shedding losses. (Griffiths et al 1967, Evans et al 1962).

Grass seed which is harvested as soon as maximum viability is attained usually has a low thousand-seed weight, a fluid endosperm with a high moisture content and consequently a very limited storage life. (Hyde et al 1959). The seed is also extremely difficult to remove from the inflorescence which means that threshing must be so severe that seed is damaged in the process. As Stoddart (1964a) pointed out, such factors become less extreme with increasing maturity, and it is theoretically possible to select a harvest date which is late enough for them all to exceed minimum tolerances, but sufficiently early to preclude losses due to shedding.

Normally grass seed is sold by weight and it stops increasing in weight while it is still green and before it is fit for safe harvesting. It has been suggested by Compson (1959) that it is wrong to think that maturing in the field, either in the standing crop or on the cut straw, results in increases in seed weight. He suggests the object of conditioning is to allow the outside of the seed to die and wither, rendering the seed safe for storage. The problem is apparently to kill the seedcoat without damaging the embryo, sunshine presumably being important in this conditioning process. Whatman (1956) suggests, however that the importance of allowing a cut grass seed crop to lie in a swath for several days is simply to facilitate moisture loss from the seed to prevent the seed heating in storage. Crosbie (1964) notes that whereas many growers thresh grass seed up to 14 days after mowing, in fact the weather conditions 2-4 days prior to threshing are more important, for these will determine the seed moisture content at threshing.

Timothy is acknowledged as being a difficult crop to harvest. This is partly because the seed can be difficult to remove from the head but mainly because it is enclosed in a double chaff. (Gwynne 1966). The inner chaff

envelopes the seed and should, if possible, be left intact. This single seed with its chaff is enclosed in two glumes which are much larger. The problem is to separate the seed contained in the inner chaff from the outer glumes without 'skinning' the seed. Seed merchants require the presence of the inner chaff or skin as evidence that the seed has not been damaged during harvesting (Gwynne 1966). Also such hulled seeds have a reduced storage life, Lampeter (1958) recording a loss of viability of 70% in hulled timothy seed 3 months after harvest.

Harvesting and threshing of herbage seeds at an early stage of maturity often reduces germination capacity. Jensen (1968) has shown that the reduced germination capacity of early harvested seed is mainly caused by mechanical damage at threshing.

A number of workers have carried out studies involving the sequential harvest of various grass seed crops at stages of development ranging from a few days after anthesis through to seed ripeness. (Grabe 1956, Hyde et al 1959 , Lawrence 1960, Anslow 1961, Kahre 1964, Rebischung et al 1964, Stoddart 1964a, Arnold and Lake 1966 and Jensen 1968). Their studies have shown that seed weight, germination capacity, and seed storage ability are all markedly affected by harvest date. Once seed is mature all these factors are maximal and harvesting can proceed at any time during the ripening stage provided that, if threshing is carried out while the seed is of high moisture content, care be taken to avoid mechanical damage to the seed during threshing, and to remove moisture from the seed by drying to a level suitable for safe storage.

Although it is not within the scope of this review to discuss harvesting machinery and methods it should be pointed out that excellent discussions on the techniques of harvesting (direct - and swath - harvesting and double threshing) have been produced by a number of workers (Arnold and Lake 1965, 1966, Nellist and Rees 1967, 1968, Nellist 1966, 1967, Griffiths et al 1967).

The amount of literature on the effect of nitrogen on seed yield is extensive. The application of nitrogen has been shown to increase seed yields in ryegrass (Evans 1937a, Evans 1954, Evers and Sonneveld 1955a 1955b, Lobb 1955, Wilson 1959, Evans 1960c, Greaves 1964, Roberts 1966); in timothy (Wheeler 1950, Hagsand 1955, Lambert 1956b, Huq and De Long 1958, Wilson 1959, Langer 1959b, Evans 1960c, Stoddart 1961, Lewis 1961, Björklund 1962 and Greaves 1964); and in prairie grass (Saxby 1956, Karim 1961, Langer 1963). Conversely, some workers have found no significant increases in seed yield following nitrogen application (Evans 1953 and Lambert 1964 in timothy and Lobb 1955 and Anslow 1962 in ryegrass). Lambert (1961, 1963a) found significant seed yield reduction in S48 timothy in separate experiments following the use of nitrogen.

This variability in seed yields from studies on timothy to which nitrogen has been applied indicates that other factors may modify the effect of nitrogen on seed yield in this species (Lambert 1966). Evans (1953) and Lambert (1961, 1963a) have both suggested that dry weather, particularly at ear emergence reduced the yield of timothy by limiting nutrient transfer to the ear. The anomalous behaviour of timothy in its response to nitrogen, compared with other herbage grasses may well be that it initiates and develops ears later and is therefore the species most liable to encounter dry conditions during ear formation. Lambert (1963a) has therefore suggested that supplementary water may be an important adjunct to the efficient use of nitrogen in the management of timothy for seed.

The timing of grazing in relation to both plant growth rate and season is also important in influencing subsequent seed yield. Evans (1937a) and Roberts (1958c) have shown that seed yields of perennial ryegrass, timothy and cocksfoot are not generally reduced by winter grazing, except when followed by a dry period in the spring. This latter effect may be caused by conditions being unfavourable for aftermath recovery. Spring grazing on the other hand reduced seed yields through the formation of smaller inflorescences. Results

by Evans (1937b), Langer (1957b), Roberts (1958c) and Langer and Ryle (1959), have shown that spring grazing of perennial ryegrass and timothy seriously reduced seed yield. Particularly in perennial ryegrass, spring grazing resulted in permanently reduced ear numbers. Roberts (1966) observed yield reduction following grazing one week after inflorescence initiation. In Tama ryegrass Davies (1969) has shown that defoliation should cease in October or seed yield reduction can occur.

Evans (1962) and Roberts (1966) have both suggested the possibility of correcting a potential depression in seed yield following grazing in the autumn, winter and early spring period by optimum applications of nitrogen. With nitrogen application, perennial ryegrass has been shown to be capable of producing as much seed after spring grazing (Evans 1937a, Roberts 1966). Their results support the contention that perennial ryegrass is a flexible species, responding positively to defoliation coupled with nitrogen application in the production of seed.

In a discussion on timothy management Davies (1960) noted that lenient grazing may be continued until stem formation begins without deleterious effects on seed yield. Saxby (1956) has also stated that timothy will persist for many years under sheep grazing, provided this is not close or continuous.

While defoliation, whether by grazing or cutting does not appear to enhance seed yield in timothy Lambert (1966) has pointed out that claims made for benefits from defoliation were "based on individual satisfaction with the yields obtained rather than on any measured increases in yield in a comparison of defoliation versus no defoliation". Therefore, he suggested that where seed production was the only concern, defoliation was of no benefit in this species. On the other hand, where livestock and seed production were integrated in the farm programme the problem was different. If properly timed and controlled, useful grazing could be obtained without marked reduction in seed yield. This was particularly so in the case of grass species which had

a winter dormancy (e.g. timothy and cocksfoot). In such cases, Lambert suggested, yield probably would not be affected unless the plants were damaged by pugging.

MATERIALS AND METHODS

The harvesting methods used in 1966 have been previously described in detail (page 89). Briefly, in the first year sequential harvests commenced at, or soon after, peak anthesis and continued for six or seven weeks at approximately seven day intervals. Half of the harvested material was immediately threshed and seed yields determined. The remainder was left for 10 days as a swath and then threshed. Seed shedding losses were determined by recording the percentage of heads on which shedding had occurred at various intervals after peak anthesis.

In the second year (1967), although large scale sequential harvests were not carried out, yield determinations were obtained using direct-harvesting and swath-harvesting methods for ryegrass and prairie grass 30 days after peak anthesis and for timothy 35 days after peak anthesis in each treatment.

RESULTS AND DISCUSSION

A. Seed Yield

Seed yields for ryegrass, timothy and prairie grass obtained at different harvests in 1966 are presented in Table 15 (over) (raw data in Appendix 21).

Although both ryegrass and timothy failed to show significant treatment effects the trend nevertheless in the sowing year was for grazing and nitrogen to increase yields in ryegrass and depress yields in timothy. In prairie grass, irrespective of harvesting method, nitrogen application was important in overcoming yield depression in treatments incorporating grazing. Highest yield of prairie grass seed was obtained from plants in ungrazed plots receiving nitrogen. Results for prairie grass stress the detrimental effect of grazing and the promoting influence of applied nitrogen on the seed yield of this species.

TABLE 15 Seed Yields 1966 (Means in lb/ac at 15% seed moisture content)

Treatment	Yield Direct Harvest	Yield Swath Harvest	Days After Peak Anthesis	Harvest	Yield Direct Harvest	Yield Swath Harvest
Ryegrass						
+G+N	668 a	844 a	0	H1	436 Cb	430 Bc
+G-N	654 a	630 a	7	H2	470 Cb	584 ABbc
-G+N	666 a	750 a	14	H3	770 ABa	960 ABab
-G-N	606 a	624 a	21	H4	810 ABa	1236 Aa
			28	H5	930 Aa	Not Recorded
			35	H6	540 BCb	650 ABbc
			42	H7	404 Cb	410 Bc
Timothy						
+G+N	190 a	258 a	10	H1	140 Cbc	292 ABbc
+G-N	218 a	267 a	17	H2	325 Aa	383 Aa
-G+N	173 a	206 a	24	H3	302 ABa	354 ABab
-G-N	236 a	279 a	31	H4	215 BCb	261 Bc
			38	H5	127 Cc	133 Cd
			45	H6	119 Cc	91 Cd
Prairie Grass						
+G+N	2444 ABa	4620 Bb	3	H1	804 Cd	1780 De
+G-N	1740 Bb	3660 Cc	10	H2	1096 Cd	2670 Cc
-G+N	2814 Aa	5466 Aa	17	H3	2350 Bc	3186 Bb
-G-N	2420 ABab	4236 Bb	24	H4	2950 ABb	4020 Aa
			31	H5	4450 Aa	4346 Aa
			39	H6	2260 Bc	2080 CDde

The yield figures following swath harvesting (Table 15) show that increased yield can be obtained particularly in ryegrass and timothy by cutting the crop prior to seed maturity and allowing seed development and ripening to continue on the cut straw. This technique allowed higher seed yields to be obtained than the use of direct-harvesting methods.

Sequential harvests carried out in the sowing year (1966) indicate that maximum seed yield was obtained at different times after peak anthesis in each species. This was a reflection of species variation in the time taken for seed to mature.

Maximum yield data (expressed as a mean value at 15% seed moisture content) for the second year (1967) is presented in Table 16 (raw data in Appendix 22).

The results stress the influence of management on each species.

TABLE 16 Seed Yields 1967 (Mean values lb/ac. at 15% seed moisture content).

	Treatment	Yield	
		Direct Harvest	Swath Harvest
Ryegrass	+G+N	530 Aa	596 Aa
	+G-N	505 Aa	528 Aab
	-G+N	385 Bb	256 Bbc
	-G-N	308 Bb	334 Bc
Timothy	+G+N	83 Cc	82 Cc
	+G-N	124 BCc	87 Cc
	-G+N	210 ABb	213 Bb
	-G-N	285 Aa	272 Aa
Prairie Grass	+G+N	1000 Cc	781 Cc
	+G-N	277 Dd	380 Dc
	-G+N	2672 Aa	2406 Aa
	-G-N	1836 Bb	1731 Bb

While nitrogen application failed to reveal major yield increases in ryegrass, grazing was beneficial to seed yield. Approximately a 60% increase in yield was obtained in grazed plots irrespective of whether nitrogen had been applied or not, compared with the control treatment (-G-N).

Timothy showed marked grazing and nitrogen application effects in depressing seed yield in the second year. In this species the control (-G-N) was superior to all other treatments. In contrast to the previous year the 1967/8 season was very dry during January-March. Perhaps, as suggested by Lambert (1963), under such conditions timothy plants developed a smaller root mass at high nitrogen levels. This could explain the depressing effect of nitrogen on seed yield in timothy in the second year.

In prairie grass, as in the year of sowing, treatment figures show the detrimental effect of grazing on seed yield. In both years highest yields were obtained in the treatment -G+N, +G-N being inferior to all other combinations. In the second year, the application of nitrogen to grazed plots failed to overcome yield depression caused by grazing as was the case in the sowing year.

Mean maximum yield over all treatments showed a marked reduction between years. Maximum yields in 1967 were approximately 15% to 70% less than those in the previous year depending on species and harvesting method. The highest yield reduction (68.5%) occurred in prairie grass while direct-harvested

timothy showed only a 14.8% reduction in 1967 compared with 1966. Probably the major reason for yield being reduced in all species in the second year was the marked fall in fertile tiller percentage which occurred in 1967 compared with the first year (page 61). In addition weed growth and poor aftermath recovery may have contributed to the reduced seed yields occurring in the second year.

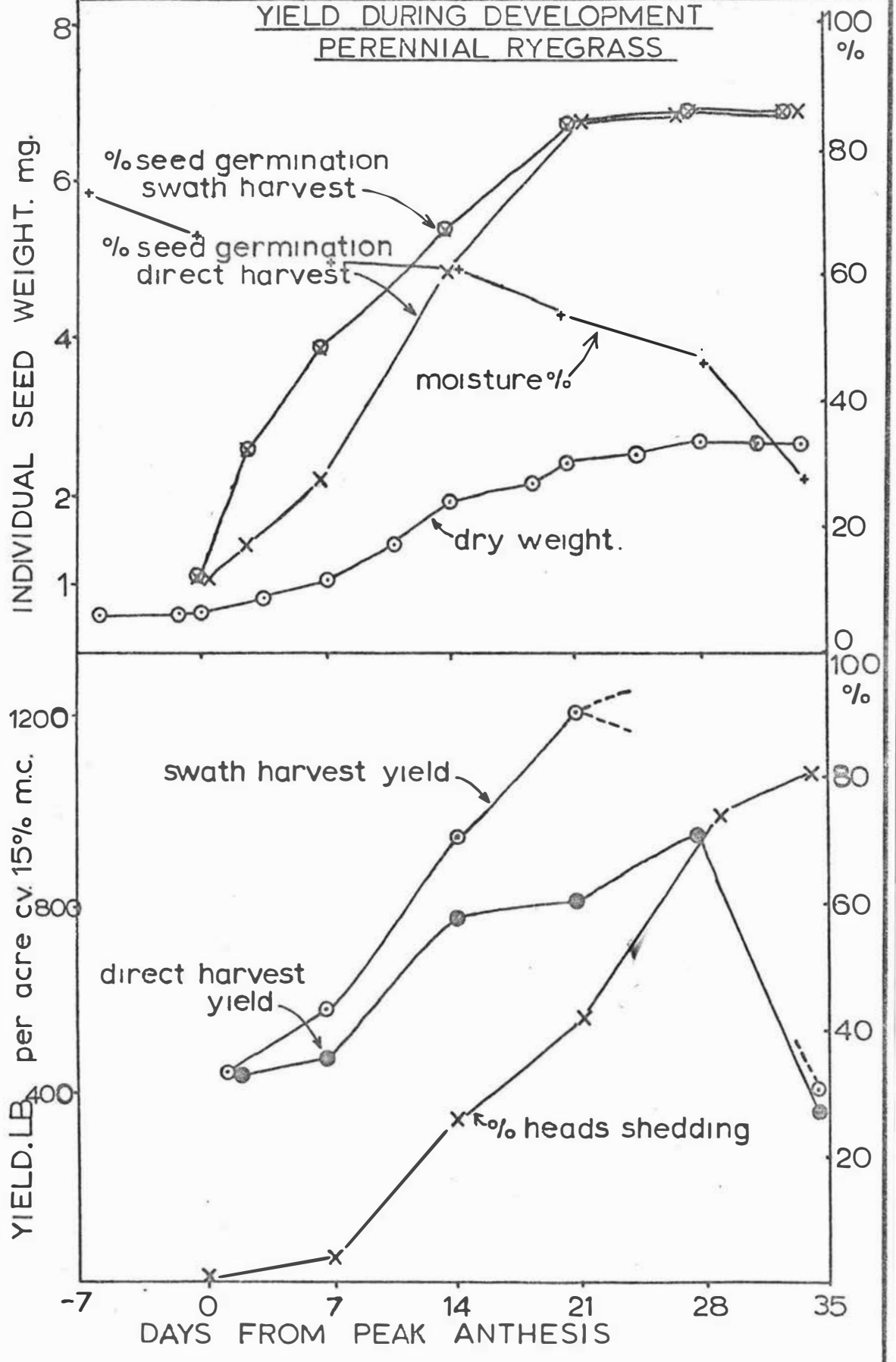
B. Seed Quality

In all species studied the improvement in seed quality exhibited at successively later harvests up to the point of maximum yield was associated with both an increase in seed weight and germination capacity not only within the uncut crop but also within the swath. A similar pattern has been found by Lawrence (1960) in a comparison of direct - and swath-harvesting of Russian wild rye (Elymus junceus Fisch) and by similar comparisons by Nellist and Rees (1967b) in S24 ryegrass.

By incorporating data on seed yield from Table 15 with germination results, seed weight (Figure 13) and seed moisture levels (Figure 12) at successive harvests a comparison of harvesting methods on the rate of attainment of maximum seed quality (maximum weight and germination capacity) was obtained (data in Appendix 23). Results for ryegrass, timothy and prairie grass are shown in Figures 20, 21 and 22 respectively.

In ryegrass (Figure 20) maximum yield following direct-harvesting was attained at harvest 5 (28 days after peak anthesis) with a mean yield of 930 lb/ac. At this point seed germination and dry weight were maximal having been reached 21 and 28 days after peak anthesis respectively. At harvest 5 seed moisture content was approximately 47% and a mean value of 75% of heads showed some shedding losses. Unfortunately yield data obtained after 10 days natural drying (swath-harvesting) following cutting 28 days after peak anthesis is not available as heavy rain caused samples to deteriorate following cutting. Unfortunately this makes yield comparisons between direct-harvest and swath-harvest data at harvest 5 impossible. It should be noted, however, that cutting samples at harvest 4 (21 days after peak

FIGURE 20 CHANGES IN SEED COMPONENTS AND YIELD DURING DEVELOPMENT PERENNIAL RYEGRASS

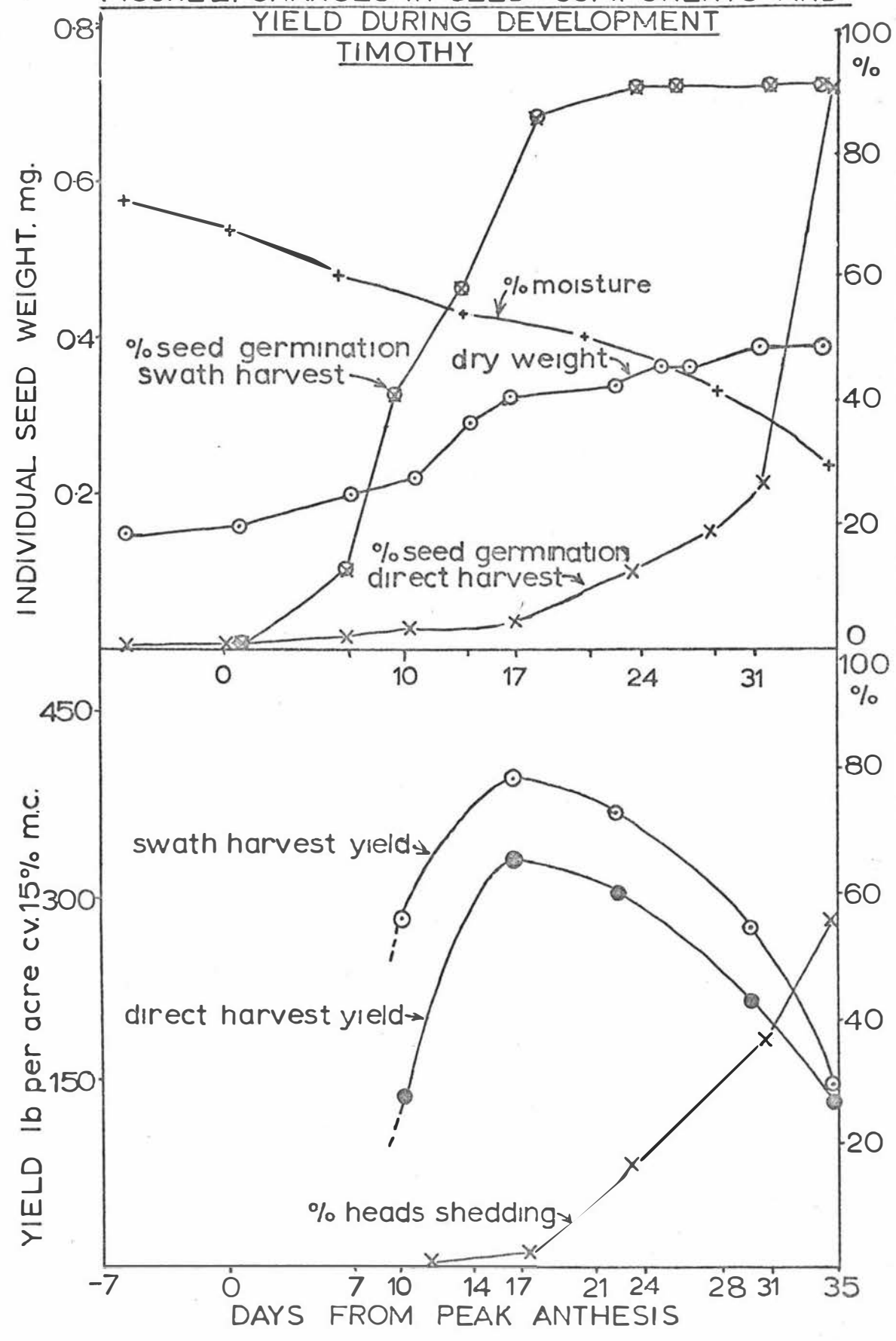


anthesis) and removal of seed 10 days later resulted in a mean yield increase of over 300 lb/ac. compared with the yield obtained by direct-harvesting 28 days after peak anthesis. Direct-harvesting at harvest 4 (21 days after peak anthesis) would have resulted in seed being threshed 7 days prior to the attainment of maximum seed dry weight even though this point coincided with the attainment of full viability. The inference from these results for ryegrass is that high yields can still be obtained even when the crop is cut slightly before seed maturity and allowed to continue maturation and ripening on the culm prior to threshing. In contrast harvesting at harvest 3 (14 days after peak anthesis), resulted in seed yields following direct-harvesting and swath-harvesting of 770 and 960 lb per acre respectively. While these yield figures are quite high seed harvested at this stage would be of low weight (approximately 70% of final seed weight) and reduced germination capacity (approximately 65%). In addition such seed, as well as being of poor quality would have a reduced storage life.

The data for timothy (Figure 21) is of interest in that maximum yield was reached at harvest 2 (17 days after peak anthesis) irrespective of the harvesting method used. At this point neither seed germination capacity nor seed weight were at their maximum. Seed direct-harvested 17 days after peak anthesis showed a mean germination of only 5%, whereas seed obtained by swath-harvesting the crop 17 days after peak anthesis had a mean germination value of approximately 82% compared with a final value of 95%. This early yield maximum occurred at a point approximately 18 days prior to seed maturity, and at a mean seed moisture content of 51%.

From the maximum yield point 17 days after peak anthesis, yields fell progressively at successive harvests, despite a gradual increase in individual seed weight for a further 18 days. This reduction appeared to be a reflection of seed losses through shedding. The results indicate that timothy is not suitable for direct-harvesting. The reason for this is that peak mean yield

FIGURE 21 CHANGES IN SEED COMPONENTS AND YIELD DURING DEVELOPMENT TIMOTHY



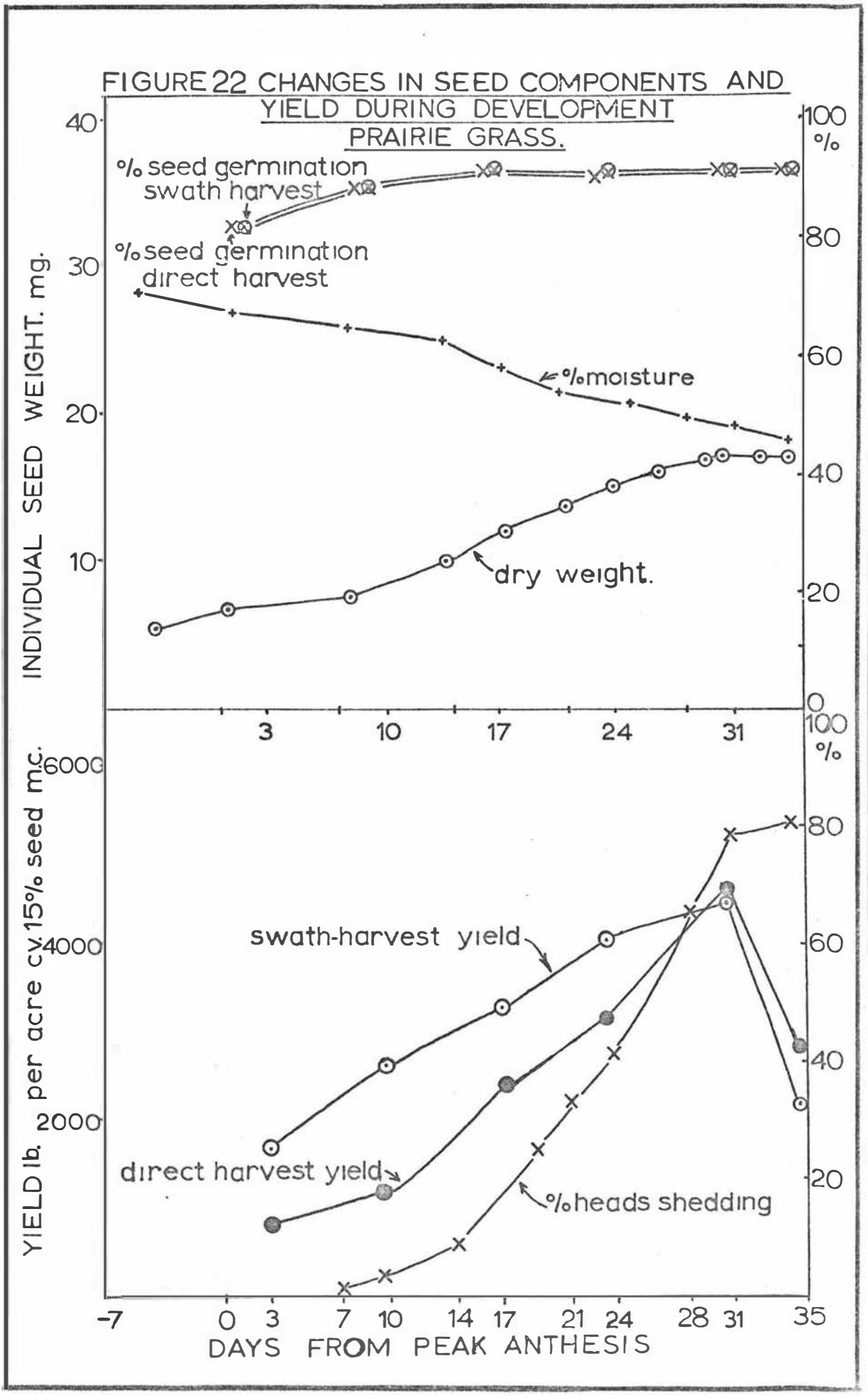
(325 lb/ac) was attained while the seed was of very low germination capacity. Delaying direct-harvesting until harvest 5 (38 days after peak anthesis) when maximum seed weight and germination capacity were reached resulted in severe yield reduction (198 lb/ac) through shedding.

In 1966, it is suggested that the protracted period of anthesis in the crop (66-74 days) may have allowed early-emerged heads to develop seed to a stage where their number contributed markedly to yield prior to the development of seed from intermediate and late emerged heads. The effect of this could have been to allow yield maximum to be reached earlier following peak anthesis than would normally occur.

In timothy cutting the crop prior to seed maturity (24 days after peak anthesis at a moisture content of 47%) and allowing the seed to dry on the culm prior to threshing resulted not only in a high seed yield but also in the harvesting of seed of high germination capacity.

In prairie grass (Figure 22) maximum yield occurred at harvest 5 (31 days after peak anthesis) irrespective of harvesting method (4450 lb/ac and 4346 lb/ac for direct - and swath-harvesting respectively). In prairie grass, therefore, direct-harvesting appears to be satisfactory despite the fact that at peak yield, 31 days after anthesis, approximately 80% of seedheads showed some signs of shedding. In addition, seed moisture content at maximum yield was approximately 48% so that seed direct-harvested at this point would require artificial drying prior to storage. Swath-harvesting, because it allowed seed to dry naturally to a moisture content of between 12 and 15% overcame this objection. The disadvantage of this latter harvesting technique was the risk of seed losses prior to threshing through inclement weather. Peak yield, 31 days after anthesis, in prairie grass coincided with the attainment of maximum seed dry weight, germination maximum having been reached 14 days earlier (17 days after peak anthesis).

FIGURE 22 CHANGES IN SEED COMPONENTS AND YIELD DURING DEVELOPMENT PRAIRIE GRASS.



C. Optimum Harvest Time

Following presentation of data in the previous sections on seed yield and quality it was thought desirable to attempt to relate these factors to the optimum point in the ripening sequence at which seed was suitable for harvesting to achieve maximum quantity of highest quality seed. Accordingly seed drying curves were prepared (Figures 23, 24, 25) using data for 1966 (Appendix 23). In addition sequential seed yield and germination assessments at 16, 23, 30, 37 and 43 days after peak anthesis and seed moisture determinations in 1967 allowed similar drying curves to be drawn incorporating data for the second year (Appendix 24). The results presented are mean values for all treatments in each year. The mean rate of seed moisture loss in the standing crop for all treatments was related to viable seed yield, the point of highest yield of viable seed being designated as the optimum mowing time.

The regularity of the rate at which all species lost moisture with time and the relationship between both seed yield and quality suggested that the moisture content of seed was a reasonable indication of mowing time which could be used as a basis for the commencement of harvesting operations. From the difference between results in each of the two years, however, it can be seen that rates of seed moisture loss in the standing crop can vary, presumably in response to environmental conditions. Sunshine hours, evaporation, wind speed and rainfall have all been shown to influence rate of reduction of seed moisture (Dodds and Pelton (1967)). Despite this, however, it seems feasible that the use of drying curves could be used to predict the date of commencement of harvesting at least a few days in advance.

The best mowing dates for each species varied slightly from year to year. Hence, as Klein (1967) has pointed out, 'calendar time' is not an adequate index of mowing time. Results in the present study show, however, that seed moisture content in the standing crop is similar at the highest yield point within each species and, therefore, is a good indicator of optimum mowing time.

FIGURE 23 SEED DRYING CURVES. PERENNIAL RYEGRASS.

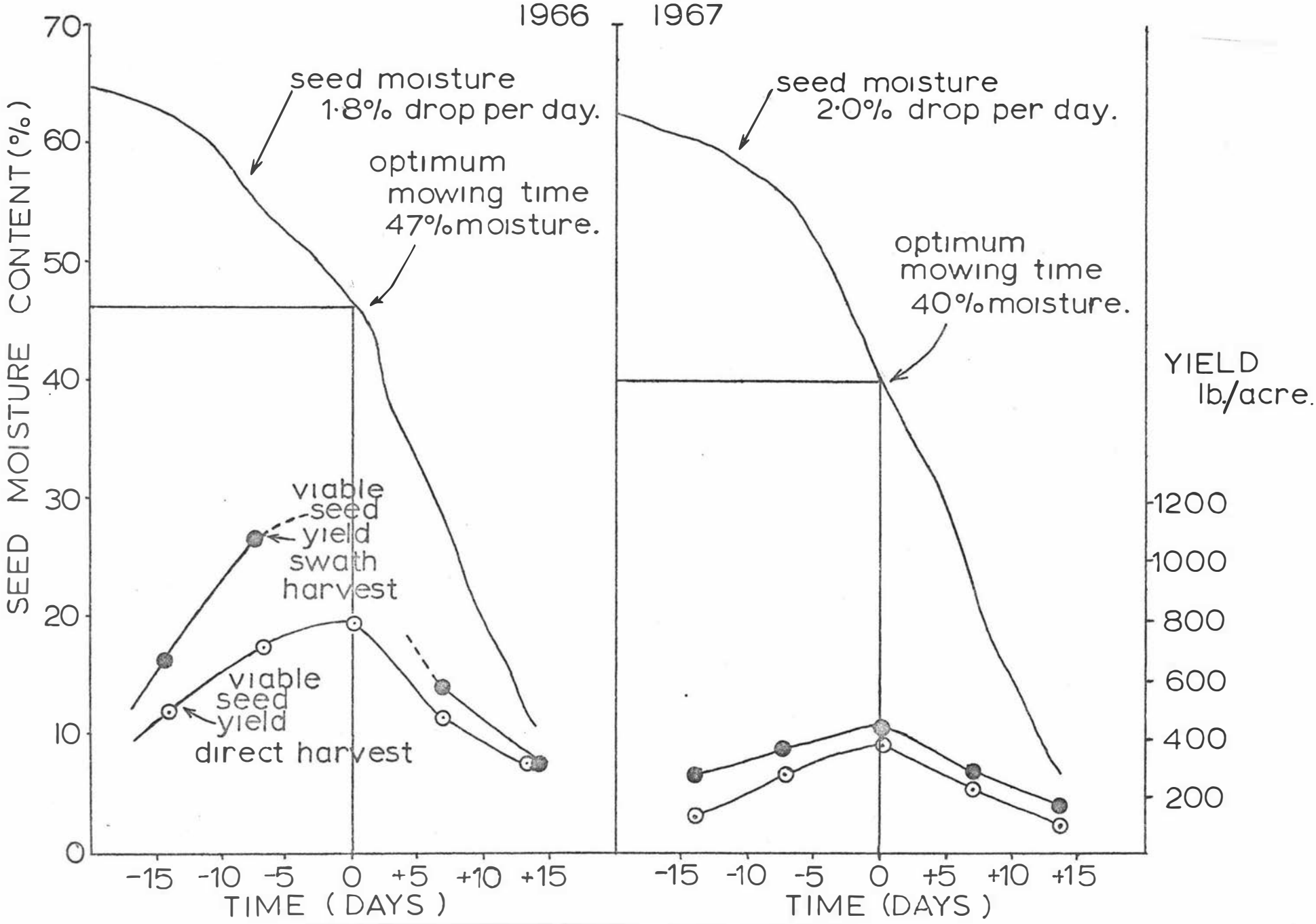


FIGURE 24 SEED DRYING CURVES. TIMOTHY.

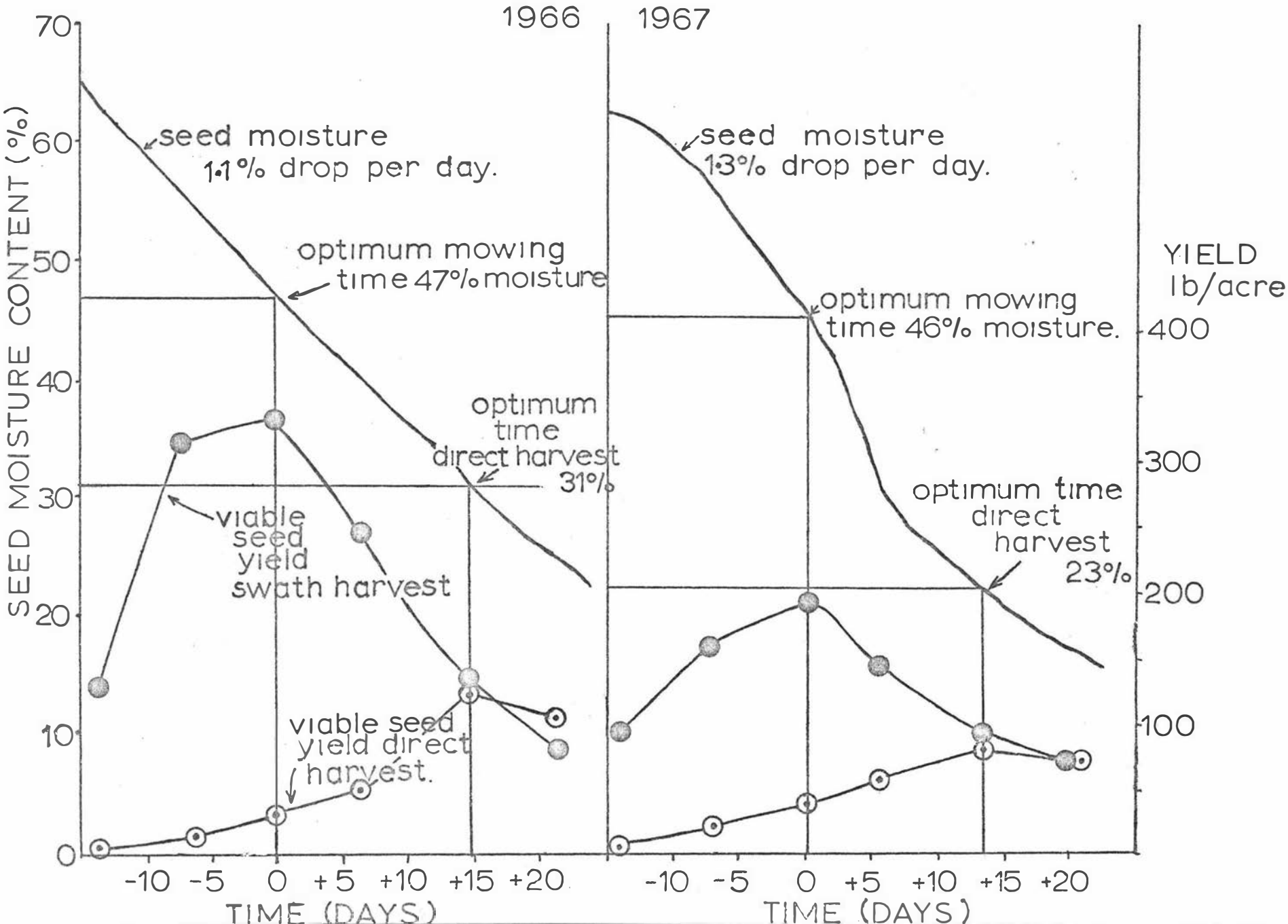
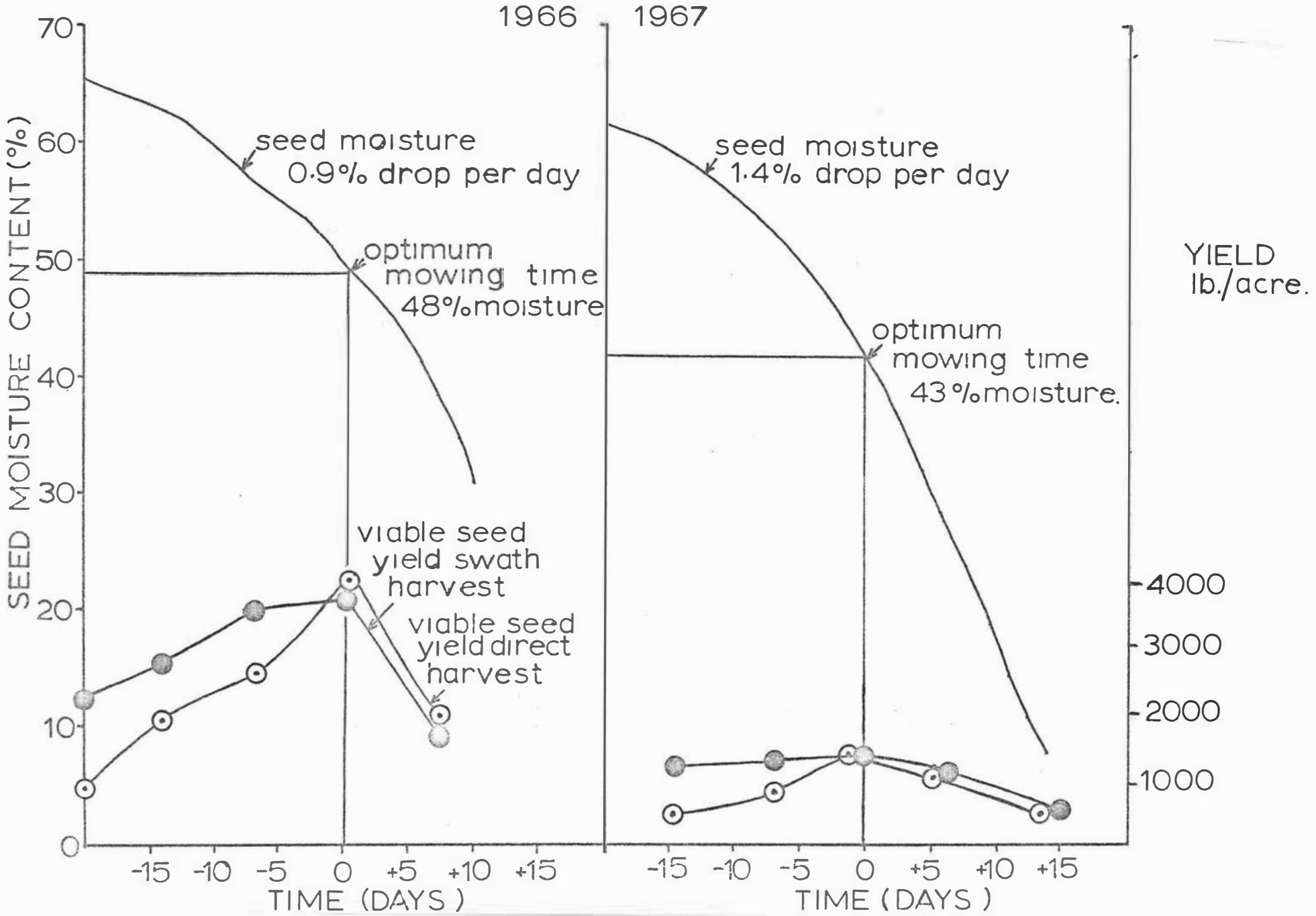


FIGURE 25 SEED DRYING CURVES. PRAIRIE GRASS.



Seed drying curves may be used to predict the correct mowing date of a seedcrop for subsequent swath-harvesting or for direct-harvesting by first measuring the seed moisture present and finding it on the curve. Then the number of days usually required for the moisture content to drop to the recommended cutting point can be determined.

In both ryegrass (Figure 23) and prairie grass (Figure 25) comparing the two harvesting methods on the basis of successive harvests, the viable seed yield obtained following swath-harvesting was superior to direct-harvesting at all harvest dates prior to peak yield and gave a higher or comparable yield at this point. This finding has also been observed in perennial ryegrass by Nellist (1967) and Nellist and Rees (1967). Irrespective of the method of harvesting the optimum time for commencement of this operation in both years was at a seed moisture level of approximately 44% (40-47%) in ryegrass and 45% (43-48%) in prairie grass. Should direct-harvesting be undertaken at this point, however, artificial drying facilities would be essential to reduce seed moisture content to a safe storage level.

The relationship between seed moisture content and viable seed yield is particularly evident in timothy (Figure 24). In this species two optimum harvest points are shown on the drying curve. The first at approximately 47% moisture content should be used when swath-harvesting methods are being employed. The second, occurring approximately 14 days later, should be used only when direct-harvesting is being considered. The rate of seed germination improvement (direct-harvest) was approximately 3% per day in both years. (Appendices 23 and 24). This rapid increase demonstrates the need to time direct-harvesting accurately and stresses the need to delay harvesting for approximately 14 days after the optimum mowing time for swath-harvesting. In 1966 unfavourable weather conditions caused slower moisture loss from the seed than in 1967. Despite this, however, seed shedding became severe in timothy plots prior to maximum yield at which point the crop was suitable for direct-threshing. These results support findings by Arnold and Lake (1966) in S48 timothy that

significantly higher seed yields could be obtained following swath-harvesting than by the use of direct-harvesting methods. Their comment that the use of swath-harvesting techniques allowed increased yields of high germination seed to be obtained while at the same time reducing shedding losses is supported by the results obtained for timothy. In addition the fact that swath-harvesting can be carried out approximately 14 days earlier than direct-harvesting, suggests that the use of the former technique may allow more flexibility in harvesting timothy seed.

The duration of a suitable crop condition for direct-harvesting in all three species was relatively brief and the risk of sudden shedding losses due to the onset of unfavourable weather conditions was high. In contrast, high quality seed could be obtained over a longer period when the crop was cut and the seed allowed to dry naturally prior to threshing. It is suggested that the improvement in quality by swath-harvesting methods results largely from increase in seed weight during maturation and ripening while on the cut straw.

It is commonly believed that the margin between under-ripeness and over-ripeness in grass seed crops is narrow. This concept is probably due to present standards of assessing seed ripeness. It is suggested that at present the use of ripeness assessment methods which emphasise seed moisture and the condition of the most advanced heads in a crop to the exclusion of later emerged smaller heads would be an advantage. This is reinforced by previous results which have stressed the important contribution of early-emerged heads in a crop to total seed yield. Since early-emerged heads contain the greatest number of seeds and the heaviest individual seeds in a crop, any delay in harvesting to enable seed in late-emerged heads to mature will result in reduced seed yield. The increased contribution of late heads will be more than offset by shedding losses from earlier-emerged heads.

Many grass seed species are considered difficult to grow because of the inconsistency in seed yield from year to year. Much of this yield variation is possibly due to uncertainty in deciding the correct harvest time. On the

other hand if the crop is harvested too early the seed is difficult to remove from the head because the abscission layer in the seed is not fully formed and sufficient dehydration has not taken place. Conversely late harvesting usually results in a loss of seed from shedding, both in the standing crop and during harvesting.

Apparently, some grower dissatisfaction exists concerning the reliability of eye-assessment characters employed for assessing crop ripeness. This is indicated by the appreciable increase in the use of portable moisture meters for seed moisture determinations in the field.

CONCLUSION

By considering seed yield results in both years, it is possible to make some general statements regarding the best management for each species to obtain high yields.

In ryegrass, while no significant treatment differences occurred in the sowing year, in the second year grazing caused a significant increase in seed yield. Nitrogen application alone did not significantly increase yield.

No treatment differences occurred in timothy in the first year. Grazing, and to a lesser extent nitrogen, were both detrimental to yield in the second year. Because neither grazing nor nitrogen promoted increased seed yields in this species in either year the best management combination was considered to be -G-N.

In prairie grass grazing depressed and nitrogen application increased yields in both years. The combination -G+N was superior to all other treatments in producing high seed yields.

In all species the results showed that similar or increased yield could be obtained by mowing the crop at a stage at, or slightly prior to, seed maturity and allowing seed development and ripening to continue on the cut straw for up to 10 days. Using this technique higher seed yields were obtained in ryegrass and timothy than when seed was direct-harvested.

In the ryegrass direct-harvesting 28 days after peak anthesis at a seed moisture of 47% gave a maximum yield of 930 lb/ac. In cases where the crop

was cut 21 days after peak anthesis and allowed to dry in the swath for 10 days yield was increased by over 300 lb/ac. In this species maximum germination was already reached at the point of highest seed yield regardless of the harvesting method employed. The advantage in yield obtained following swath-harvesting suggests this technique is more suitable for ryegrass than direct-harvesting.

In timothy, while yield maximum occurred as early as 17 days after peak anthesis neither seed germination capacity nor seed weight maximum had been reached at this point. Seed direct harvested 17 days after peak anthesis had a mean germination of only 5%. Seed from culms cut 17 days after peak anthesis and swath dried prior to threshing had a mean germination of 82%. Yield maximum occurred approximately 18 days prior to seed maturity at a moisture content of approximately 51%. However, highest yields of high germination capacity seed using swath-harvesting methods occurred following cutting 24 days after anthesis (354 lb/ac with a germination percentage of 94 in 1966). Seed moisture content at the time of cutting was 47%. In the case of direct-harvesting this operation required a delay to 38 days after peak anthesis before seed of suitable quality could be obtained (127 lb/ac, germination 95% in 1966). Seed moisture content at this point was 31% and extensive shedding had taken place. Direct-harvesting techniques appear unsuitable for timothy. Swath-harvesting resulted in an advantage of 227 lb/ac. of high germinating seed. This was caused by earlier cutting than could be used with direct-harvesting methods. At this early stage shedding losses were low.

In prairie grass the optimum point for commencement of harvesting operations was at approximately 48% seed moisture content. This occurred 31 days after peak anthesis. Similar yields were obtained whether the crop was direct-harvested at this point (4450 lb/ac) or threshed following drying in the swath for 10 days (4346 lb/ac).

The use of 'drying curves' for the prediction of correct mowing time of seedcrops is suggested for ryegrass, timothy and prairie grass. Irrespective

of the method of harvesting the optimum mowing point for ryegrass was at approximately 44% seed moisture content. Timothy crops which are swath-harvested should be mown at approximately 47% moisture content. However, crops should not be direct-harvested until seed moisture percentage has fallen to approximately 27% by which time severe yield reduction through shedding losses can occur. In prairie grass the optimum mowing point occurred at approximately 45% seed moisture content.

It is concluded that in ryegrass and timothy highest yields of high quality seed can be obtained by the use of swath-harvesting methods. In prairie grass both direct-harvesting and swath-harvesting were suitable methods.

The majority of seed producers apparently use eye assessment characteristics (particularly seed and straw colour changes and shedding losses) in the determination of correct harvest date. However, more use could be made of seed moisture content changes within the crop as a means of timing cutting and harvesting operations more accurately.

DISCUSSION OF FIELD STUDY IN RELATION TO SEED CROP MANAGEMENT

The purpose of this section is to draw together findings and conclusions reached in the foregoing sections of the field study. While generalisation is the main aim, there are obviously instances where specificity is necessary. In addition seed crop management is discussed in relation to the field study and in the light of current literature on various aspects of seed production. The section is also designed to point out areas of concord or disagreement.

Perennial grass pastures are often required to perform a dual role, providing herbage for stock as well as seed during the same farming year. Considerable attempts have been made to evolve a management system which would allow maximum utilisation of grass for grazing without impairing seed yield. Particular attention has been paid to the effects of defoliation and nitrogen application on seed production.

One of the main factors important in seedcrop management is the morphological development of the meristems of grass tillers. This includes knowledge of the time of change of the apex from the vegetative to the reproductive condition, its accessibility to stock, and the effect of the removal of these meristems on lateral meristem development or tillering. Wilson (1959), Aitken (1962) and de Booysen et al (1963) have all suggested that management of crops for grass seed production should be related to the incidence and length of the reproductive phase and of the start of the "accessible" period in the main herbage species. This has apparently been the basis for suggestions by both Cooper and Saeed (1949) and Langer (1957b) for a more morphological and physiological approach to the problems of management of grass seed crops.

A grass plant may consist of several hundred tillers of which only a proportion produce seedheads. From the point of view of seed production, it is important to know which management factors influence the total number of tillers producing seedheads, the numbers of new tillers formed at different times of the year, and which tillers contribute most to the final seed yield.

In addition, a knowledge of management practices which affect the main components of seed yield - number of seedheads, number of seeds per head and seed weight - is of great importance in maximising seed production.

A number of other workers have stressed the major influence of summer and autumn tiller production to total seedhead production (page 68). These workers have shown, as have findings in the present study, that seed yield depends primarily on the number of tillers formed before the winter, and possibly very soon after the previous harvest. The present study has also shown that new tillers formed immediately after harvest and continuing through the following autumn have a lower mortality in the vegetative condition than tillers produced following floral initiation in the spring or early summer. In converse this high mortality of spring formed tillers was a striking feature in all three species (particularly during the months of September and October in ryegrass and prairie grass and November/December in timothy). However, spring formed tillers made the major contribution to the vegetative growth of the plant over the following summer and early autumn but these tillers generally died before the following winter. Primary tillers formed following sowing also had a greater capacity for vegetative survival and subsequent reproductive development than secondary tillers. Lamp (1952) and Langer (1956) reached similar conclusions.

In temperate grasses the growing point of a tiller remains in a vegetative condition during the autumn and winter. In the spring many change their function into seedhead formation. About this time, the tissue at the base of the growing point begins to elongate, pushing the developing seedhead up within the leaf sheath. In the present study the initiation of this process varied according to the date of tiller origin. For example, floral initiation of ryegrass tillers formed in the late winter occurred approximately 3 weeks later than in those formed in the autumn. A similar effect occurred in timothy and prairie grass, a 4 week differential being recorded in each species. Floral initiation continued for approximately 9 weeks in ryegrass and prairie

grass and 12 weeks in timothy.

The majority of tillers arising in all three species during stem elongation died before or immediately following ear emergence. This is also the case in Italian ryegrass (Wilson 1959), Tama ryegrass (Davies 1969) and in cereals (Laude et al 1967). This decrease in tillering and high tiller mortality during the period of stem elongation has been explained by the effect of competition from older flowering tillers for nutrients and assimilates (Langer 1959b). As Davies (1969) has observed young tillers with many tillers preceding them on the plant are not favourably placed in this competitive "hierachy".

In the three species studied the largest number of seedheads, which also carried the heaviest and greatest number of seeds, were those emerging first. These early-emerging heads contributed over 85% of the seed yield at harvest in ryegrass and prairie grass and 55-75% in timothy. Seedheads in this category were the first to begin floral development having been formed almost exclusively from tillers originating in the immediate post-harvest period and during the autumn and early winter. In the case of autumn-sown crops, tillers formed from seed germination through until about late July in ryegrass and prairie grass and September in timothy, made the major contribution to total seed yield. Spring tillers produced fewer and later-emerged heads as previously suggested by Anslow (1963) and Ryle (1964, 1965b). The results infer that management of seedcrops to encourage tillering should begin soon after the normal autumn sowing of first year crops and immediately after the previous harvest in second year crops.

Seed yield will be determined by the number of seedheads formed in the late summer, autumn and early winter; by the number of seeds formed on each head in the spring; and by the final individual seed weight obtained at maturity in the summer. These factors of yield have implications when considering seedcrop management in relation to such factors as nitrogen application, grazing, time of closing and harvesting.

1. Nitrogen Application

The amount of literature on the effect of nitrogen on seed production is extensive. Many workers have suggested that nitrogen increases seed yields, at least in the 3 species considered here (page 112). On the other hand, some have found no significant increases in seed yield and a few suggest variable responses to nitrogen application. Only Lambert (1961, 1963a) found a significant reduction in seed yield (in S48 timothy) which he qualified by suggesting was due to dry seasonal conditions.

In the present study no significant yield increase occurred in ryegrass following nitrogen application alone in either year. Although not measured, this may have been due to the relatively high soil fertility level of the experimental site following cultivation out of grass. As with ryegrass, results in timothy generally failed to support those obtained by other workers. In timothy, nitrogen application was deleterious to yield, particularly in the second year. However, although not statistically significant, the trend in the first year was for nitrogen to slightly increase seed yields. In prairie grass nitrogen markedly increased seed yields in both years, suggesting a greater demand for nitrogen by this species and supporting the previous findings of other workers (page 112). The other important contribution of applied nitrogen was its effect in completely or partly overcoming the yield depression from grazing.

In New Zealand, most seed producers apply nitrogen to grass seed crops at closing. Although a strong visual response often occurs through a flush of new tillers these produce few heads and little seed (Hill 1970). Under these conditions, nitrogen will result in a heavy bulk of leaf. This may help reduce blind-seed disease incidence and may also cause heavy lodging. It is suggested that earlier application could have a greater effect on seed yield, since a management system which encourages tiller production in the late summer, autumn and early winter will influence seedhead number at harvest. Application at the time of floral initiation in the spring however might well influence seed number per head and later, individual seed weight. This

possibly explains the seed yield increases obtained using split applications of nitrogen - half in the autumn and half in the spring (Lambert and Thurston 1952 in cocksfoot, Lambert 1966 in timothy, Hill 1970 in ryegrass).

Nitrogen application was important in increasing total tiller numbers. However, the application of this element had little effect in increasing the percentage of tillers which became reproductive, particularly in the second year. The findings in the present study therefore are in agreement with those of Lambert (1964, 1966) with timothy but fail to support those of other workers who found that nitrogen application increased the percentage of fertile tillers (page 62).

Particularly in the second year, nitrogen application to ungrazed plots of both ryegrass and timothy resulted in a dense mass of vegetative growth which was severely frosted during the winter. This effect has also been observed by Lambert (1963a) in timothy. In addition, the ingress of weeds was a notable feature, along with severe leaf mortality and decay at the bottom of the swath. The effectiveness of prairie grass in smothering weed growth was apparent. In both ryegrass and timothy, seedhead number in the second year was markedly reduced in the ungrazed treatment to which nitrogen had been applied. In timothy the control treatment (-G-N) produced significantly more heads than all other treatments. A marked reduction in fertile tiller production occurred in the second year compared with the year of sowing.

An interesting feature in ryegrass was the striking positive interaction of nitrogen and grazing; these factors together resulting in a marked increase in fertile tiller percentage. However, in terms of conversion of vegetative to reproductive tillers nitrogen application alone actually reduced fertile tiller percentage. While other workers (Evans 1937a, Roberts 1966) have established the importance of using nitrogen to overcome the depressing effect of grazing in terms of fertile tillers in ryegrass, the current results indicate that a marked increase in fertile tiller numbers can be achieved by a combination of both grazing and nitrogen. A possible explanation may lie in the improved light regime to basal tillers following grazing and the improved stimulus to

growth from nitrogen application.

Summer and autumn formed tillers, while contributing the majority of seedheads at harvest, also produced heads which showed greater development potential than heads from tillers formed in the winter and spring. In addition to its effect in increasing tiller numbers nitrogen also affected seedhead development in terms of head length and spikelet and floret number. While it had no effect on head length in ryegrass and timothy in either year, nitrogen significantly increased head length in prairie grass. Spikelet number was increased by nitrogen in timothy and prairie grass but not in ryegrass. This stresses the value of applied nitrogen in the management of these former species for seed production. Nitrogen application also strongly influenced the number of florets on individual heads and ultimately seed number per head in all species, and again was important in partly or completely overcoming the depression in floret and seed number caused by grazing. Ryle's (1964, 1967) work with ryegrass has shown similar effects, nitrogen increasing floret number but not the total number of spikelets per head. A possible explanation of this effect could be that floret formation occurs during head development when the ear is undergoing exponential growth and therefore has a high demand for substrates. Spikelet numbers, on the other hand, are determined when the apex is small and making little growth.

While nitrogen was often beneficial to these seedhead components it is relevant to remember that total seed yield was not increased by nitrogen in ryegrass and timothy. Such an effect stresses the equal importance of fertile tiller percentage which was reduced by nitrogen, resulting in no overall increase in seed yield.

While ear emergence date influenced head length in timothy in the year of sowing, results in the second year failed to support the suggestion by Stoddart (1959), Langer (1959b), Evans (1960c), and Lewis (1961) that timothy heads could be divided into groups representing time of ear emergence purely on length, early-emerged heads being longer than late heads.

The variability in seed yields from year to year in timothy to which nitrogen had been applied indicated that other factors may modify the effect of nitrogen on seed yield in this species. Evans (1953) suggested that dry weather at ear emergence reduced seed yield by limiting nutrient transfer to the ear and Lambert (1963a) observed that rainfall in May and June seems to be essential for satisfactory seed production of timothy in the United Kingdom. The variable behaviour of timothy in its response to nitrogen, compared with other herbage grasses, may well be because it initiates and develops ears later and is therefore more liable to encounter dry conditions during ear formation. Lambert (1963a) has therefore suggested the supply of supplementary water may be an important adjunct to the efficient use of nitrogen in the management of timothy for seed.

2. Defoliation

The problems of seedcrop management relating to grazing are based on a knowledge of the rate and extent of internodal elongation and raising of the developing seedhead above ground level in the spring, and on the effect of defoliation on seedhead number and individual seedhead components.

de Booysen et al (1963) note that selective grazing by stock occurs in herbage stands. To combat this many management systems include the concept of rotational grazing involving high stocking pressures for short periods of time.

In the present study both ryegrass and prairie grass showed little internodal elongation until floral development began. During vegetative growth therefore, the growing points were below the level of defoliation and the production of new leaves and tillers could still proceed under relatively heavy grazing. In timothy, however, some internodal elongation occurred while the apices were still vegetative and the elongated shoots remained erect. The apical growing points and many of the axillary buds were thereby raised above the ground and could be removed under relatively heavy grazing. Once stem elongation occurred continued grazing could obviously result in serious detrimental effects on total head number as shown by many workers (Langer 1957b, Langer and Ryle 1959, Evans 1960a,

Roberts 1966, Hill 1971). Langer (1957b) and Roberts (1966) suggest that in ryegrass and timothy removed seedheads are not replaced. However, in some other species such as prairie grass, italian ryegrass (Griffiths et al 1967), tama ryegrass (Davies 1969) and Bromus mollis (Laude et al 1967), growing point removal by grazing stimulates tillering and results in the production of a new crop of heads which replace those previously destroyed. This effect was not considered in the present study as defoliation was discontinued prior to stem elongation. In the annual species quoted above the date at which grazing is discontinued for seed production is apparently not as critical as in ryegrass and timothy.

Total tiller numbers and new tiller production were reduced by defoliation in all species. However, as mentioned earlier, nitrogen partly or completely overcame the deterimental effects of grazing on tiller production and also on head length in all species, as well as on seedhead number in ryegrass and prairie grass.

A possible explanation of this grazing effect on total tiller numbers and new tiller production may be related to the level of so-called food reserves in the plant. Grazing or cutting herbage removes some or all of the active photosynthetic tissue. Food reserves may be transferred from storage organs, depending on the intensity of defoliation, to the remaining meristematic regions which soon produce fresh leaves and tillers. When sufficient photosynthetic tissue has been synthesised again, storage products (particularly storage carbohydrate) are replaced in the storage organs. (Milthorpe and Davidson 1965).

The reproductive cycle of the species will also influence the response of a plant to defoliation. According to Whyte et al (1959) the period of active reproduction, from elongation of the inflorescence to ripening of the seed, is critical in the life cycle, food reserves are at a lowered level, and so are the number of vegetative tillers which can form new photosynthetic tissue. The greater the number of reproductive tillers on a plant the more vulnerable is the plant to cutting or grazing. In a range of annual, biennial and perennial

strains of ryegrass Cooper and Saeed (1949) found resistance to defoliation to be closely correlated with the extent of reproductive development.

The response to cutting and grazing of a herbage species or strain depends therefore on its seasonal cycle of carbohydrate storage, on its growth habit, and also on the timing and extent of inflorescence development. In the present study grazing was discontinued at the first sign of floral initiation as determined by apical dissection. However, the timing of grazing in relation to plant growth rate and season is also important in influencing subsequent seed yield. Evans (1937a) and Roberts (1958c) have both shown that seed yield of ryegrass, timothy and cocksfoot is generally not reduced by winter grazing, except when followed by a dry period in the spring when conditions for regrowth may be unfavourable. Spring grazing reduced seed yields through the formation of smaller rather than fewer inflorescences. This latter effect has also been shown by Langer (1957b) and Langer and Ryle (1959).

A further factor in this process of grazing which warrants mention is that of treading. In a study on the effects of sheep treading on herbage and seed yield of perennial ryegrass and timothy, Brown (1968) concluded that increased seed yields were obtained under treading rates up to 12 sheep equivalents. This effect was thought to be caused by treading stimulating the formation of fertile tillers. However, nitrogen application to the trial area every 4 weeks, in all seasons except winter, may have influenced Brown's results by nullifying any deleterious effect of defoliation and treading. In addition, increased seed yields may have been due to a reduction in competition for nutrients, stock-treading reducing the number of young vegetative tillers present in the spring and early summer. As Lambert (1964) has suggested most tillers arising at these times of the year are considered to be of no value for seed production and may be considered 'parasitic' on the parent plant when crops are being grown solely for this purpose. The high mortality and short life span of spring-formed tillers observed in the present study also supports Lambert's suggestion.

Langer (1962) has suggested that in prairie grass the upright growth habit allowed a high proportion of the plant to be removed through grazing. A large part of the removed material consisted of fleshy leaf sheaths, seriously affecting recovery after repeated defoliation. Langer also noted that the tendency for prairie grass to produce flowerheads throughout the year affected its recovery from grazing. However, whatever disadvantages this species possessed it appeared to be highly palatable to stock even when mature. From this point of view heavy grazing led to loss of persistency of prairie grass in the field and as results in this study have also shown, to serious reduction in seed yield unless nitrogen was also applied.

3. Time of Closing

Because of the yearly variation in the time of onset and rate of seedhead development the common practice of closing grass seed crops on the same date each year is a haphazard way of trying to consistently maximise grass seed yields. By taking a sample of tillers from a paddock at regular frequent intervals in the spring and squeezing each tiller between the thumb and forefinger the position of the developing head within the leaf sheath can be determined. This method allows a measurement of the height of the seedhead above ground level and overcomes the need for apical dissection. Using this method, closing dates can be adjusted from year to year (Hill 1971).

Many seed growers apparently close grass seedcrops too late and/or use stock to graze the area too severely immediately prior to closing (Hill 1970). Few seed producers are criticised for closing grass seed crops too early. Apparently the lower seed yields obtained following late closing are still acceptable.

4. Anthesis

While nitrogen alone had little effect on time of onset of anthesis, a delay of up to 8 days occurred in this respect in grazed treatments with or without nitrogen. The exception was in ryegrass where nitrogen did tend to reduce this delay. Despite this delay, anthesis was generally completed in

seedheads in grazed plots more quickly than in ungrazed plots. This effect was particularly evident in the second year. Although management had some effect on anthesis, this was considered small relative to climatic conditions (e.g. anthesis continued for 74 days in timothy in 1966 under cool wet conditions, compared with only 46 days in 1967 under warm dry conditions) which appeared to be the major determinant of anthesis duration and intensity as suggested by Emecz (1961) and Lambert (1966).

5. Harvesting

Species varied in the rate of attainment of maximum seed viability following anthesis in the order prairie grass, ryegrass and timothy (12, 17 and 35 days respectively). This difference is one of the reasons for the variation in harvesting methods employed to obtain maximum viable seed yield.

As shown in the present study the use of colour to determine this time of harvest is not reliable as yearly variation in climate during seed development may make the relationship inconsistent. This agrees with the findings of Crosbie (1964). Similarly the unreliability of chlorophyll and anthocyanin degradation as measures of seed ripeness suggests that pigment changes in the floret cannot be used to accurately predict optimum harvest date. In fact the final chlorophyll and anthocyanin degradation phase was too gradual, and was not sufficiently abrupt to be useful on a field scale. However, anthocyanin content of the floret did define the point of peak anthesis in each species and could be used for determining the onset of seed development in a crop.

Relative seed yield from heads in different emergence groups was affected by seed weight. However, the reduced yield of high quality seed from late-emerged heads was due not only to lowered seed weight but also to reduced floret number per head and lower germination capacity in all species. It appears that nitrogen can increase the germination capacity of seed and in fact can overcome the reduction in germination capacity of seed from late-emerged heads in ryegrass. In contrast grazing can severely reduce seed viability in even late-emerged heads in timothy. These findings on seed quality again emphasise the importance of early-emerged heads in seed crop production and the need to

encourage and maintain their dominance in the stand.

Immature seeds removed from the plant as little as 7, 10 and 4 days after anthesis in ryegrass, timothy and prairie grass were capable of germination provided dormancy was broken. The results of germination tests carried out on seed following 3 months storage support findings by Hyde (1950) that immature seeds had only a limited storage life. Following 3 months storage maximum viability was reached in seed samples removed from plants 17, 35 and 12 days after anthesis in ryegrass, timothy and prairie grass, respectively. These results suggest that in ryegrass and prairie grass in particular maximum viability was attained some time prior to seed maturity (maximum dry weight). Consequently seed harvested at the point of maximum weight is unlikely to suffer from low germination in these species. In timothy however harvesting may have to be delayed to obtain high germination capacity seed.

The onset of the hard dough stage of seed development was not a reliable indicator of seed ripeness for harvest, occurring 24, 24 and 20 days after peak anthesis in ryegrass, timothy and prairie grass respectively. At this point 47%, 24% and 40% of heads in these species were still completely green. Following the onset of the hard dough stage seed dry weight increased a further 18% in ryegrass, 4% in timothy and 19% in prairie grass.

Maximum seed weight was influenced by different management factors in each species being attained 28, 35 and 32 days after peak anthesis in ryegrass, timothy and prairie grass respectively. For example in ryegrass, nitrogen increased seed weight, while in prairie grass grazing caused the major deleterious effect unless nitrogen was also applied. In timothy both nitrogen and grazing failed to influence final seed weight. Findings by Lambert (1956b) and Lewis (1961) that nitrogen increased seed weight and hence seed yield in timothy were not supported in the present study.

At present a consistently reliable method for determining the correct harvesting date is not available to seed producers. A more reliable indicator of mowing and harvesting time is possibly the use of seed moisture content.

Results obtained suggest a consistent and good relationship between seed moisture content and maximum viable seed yield. Seed drying curves as used in this study and previously suggested by Klein (1967) allow the point of viable seed yield maximum (designated the optimum mowing time) to be determined. This optimum mowing time can vary depending on the species and harvesting method. By measuring seed moisture changes in the standing crop a seed producer could use seed drying curves to predict the number of days normally required before the crop would be 'in condition' for harvesting the maximum yield of high quality seed. This forecasting of the correct harvesting date would be based on a seed moisture loss on the standing straw of between approximately 1% and 2.0% per day dependant on species.

Maximum viable seed yield in ryegrass was obtained following swath harvesting, the crop being cut 21 days after peak anthesis (1236-lb/ac. 1966). At this optimum mowing time seed moisture content was approximately 43%. At this point seed germination was at a maximum but final seed weight had not been reached. Delaying harvesting for a further 7 days to allow seed weight increase on the standing straw resulted in severe yield reduction through shedding (930-lb/ac. in 1966).

In timothy despite maximum yield being attained only 17 days after peak anthesis the major factor delaying harvest was the rate of attainment of full germination capacity. Highest yields of viable seed were obtained following swath-harvesting 24 days after peak anthesis, seed moisture content at the optimum mowing time being approximately 47%. (354-lb/ac. 95% germination 1966). For direct-harvesting maximum seed germination was not reached for a further 14 days. At this point seed moisture content at the optimum time for direct harvesting had fallen to approximately 31% and severe loss (227-lb/ac) of seed due to shedding had occurred. Because of this, direct heading of timothy seedcrops is not recommended.

In prairie grass the optimum mowing time was at approximately 45% seed moisture, 31 days after peak anthesis. Similar maximum yields were obtained

irrespective of whether the crop was direct harvested (4450-lb/ac. in 1966) or threshed following 10 days drying in the swath (4346-lb/ac. in 1966). This reflected the ability of prairie grass seed to attain maximum germination capacity and weight prior to the onset of severe shedding losses.

In all species the improvement in seed quality at successively later harvests up to the maximum viable seed yield point was due to an increase in both seed weight and germination capacity. Similar conclusions have been reached by Lawrence (1960) and Nellist and Rees (1967).

Maximum yields in the second year were approximately 15-70% lower than those in 1966, depending on species and harvesting method. The greatest reduction (68%) occurred in prairie grass, while direct-harvested timothy showed only a 14.8% reduction compared with 1966. One of the main reasons for this reduction in the second year was the marked decrease in fertile tiller production compared with the first year. In addition, weed growth and poor aftermath recovery may have contributed to reduced seed yields in the second year. This decline in yield in successive years has also been shown by other workers (Palmer 1937, Lambert 1963b, 1966, Griffiths et al 1967, Lewis 1967).

Because the tissues of seed are soft prior to maturity mechanical crushing and internal fracturing can occur if harvesting is carried out too early. This is particularly important since immature seed must be threshed more severely to remove it from the inflorescence. Hill and Crosbie (1966) have stated that in seedlots harvested "out-of-condition" mechanical damage is often a major cause of seed injury. This damage is often not sufficiently severe to be shown as a loss of germination in tests carried out immediately after harvest. Rather it is the subsequent breakdown in bruised tissues which brings about germination reduction in storage. Because of this, the more common practice over recent years of threshing seed prior to completion of natural drying in order to reduce the risk of weather and seed shedding losses, may have disadvantages. In addition artificial drying of seed must be employed at

additional cost to reduce seed moisture content to a level suitable for safe storage.

A detailed knowledge of the development of the plant and the use of this knowledge in the controlled management of the crop throughout the year would be a more precise and predictable method of obtaining high grass seed yields.

The results presented stress that different management systems are necessary for ryegrass, timothy and prairie grass. This is particularly important since each species differs in its tolerance and reaction to grazing and nitrogen application. The results therefore stress the hazards inherent in the use of common management techniques for different grass species grown for seed production.

THE EFFECT OF ENVIRONMENT ON ANTHESIS AND SEED DEVELOPMENT IN PERENNIAL RYEGRASS AND PRAIRIE GRASS

INTRODUCTION

The object of the present study was to investigate the effect of selected environmental variables on anthesis and seed set, and on seed development in ryegrass and prairie grass.

Throughout this investigation the individual grass floret was made the unit of observation. The effects of weather conditions on anthesis and seed set were assessed by comparing meteorological data for 24 hour periods with the behaviour of florets in bloom over the same time intervals. Observations on the sequence and duration of pollination and fertilisation were made in each species. The effect of meteorological conditions during seed development on the percentage of seeds formed at sequential harvest dates from anthesis was also examined.

MATERIALS AND METHODS

The trial was conducted outdoors at the Department of Scientific and Industrial Research, Plant Physiology Division, Palmerston North. (Lat. $40\frac{1}{2}^{\circ}$S, Long. $175^{\circ}37'$E, elevation 110', average rainfall 39.17", mean maximum temperature 61.9°F, mean minimum temperature 47°F, sunshine hours 1900 h. per annum and ground frosts 48 days per annum).

In the present study clonal material was used. This was desirable (Cooper 1951) as both ryegrass and prairie grass are totally or partly outbreeding species, where considerable genetic variation can exist within a strain. Plants of each species were propogated vegetatively from a single selected parent plant (ryegrass from a single Nucleus Stock plant and prairie grass from a single plant selection of 'Butts' strain, both made available by Grasslands Division, D.S.I.R., Palmerston North). Groups of approximately 10 tillers of the clone were propogated in pots containing vermiculite-pumice-peat mixtures (1:1:2) in the late autumn and placed in a block outside over the winter. The plants received 200 ml. of standard Hoaglands nutrient solution

on each of 5 days per week over this period. On October 1st, 1968, six ryegrass plants and five prairie grass plants were placed at random in each of seven treatments on the trial site, where they remained throughout the experiment.

The daily environmental variables recorded were:-

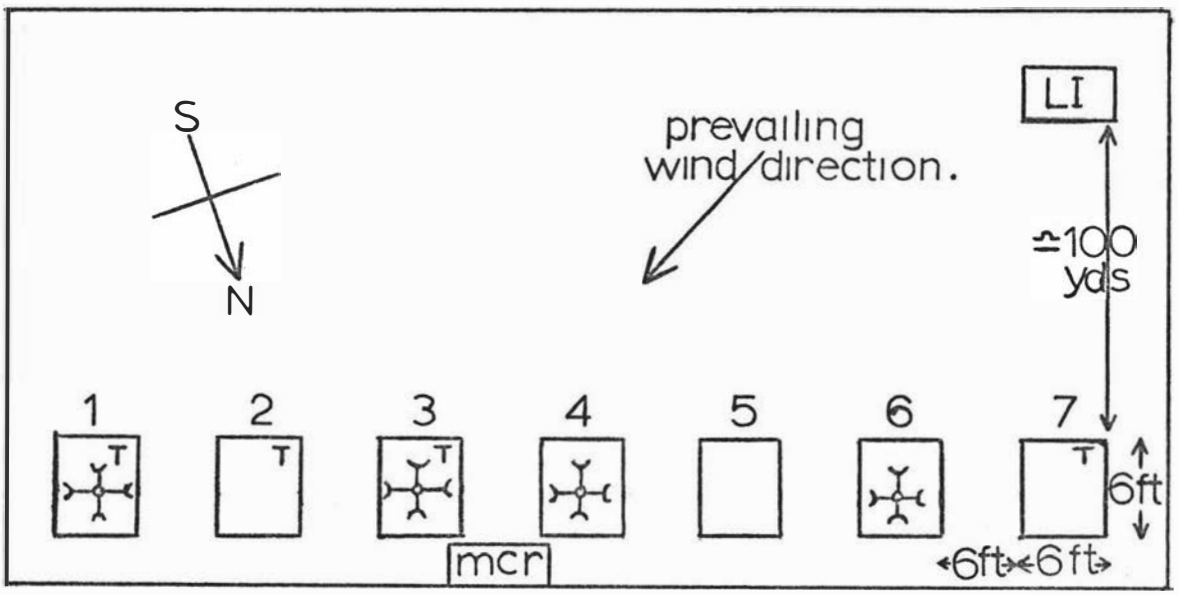
1. Temperature °F. recorded by Cu/Co thermocouples sited 36" above the ground for prairie grass and 18" for ryegrass (approximately seedhead height) and connected to a multichannel recorder.
2. Relative Humidity, recorded on a thermohygrograph sited 18" above ground level.
3. Rainfall - recorded with a Cassella rain gauge sited alongside the trial area in short pasture, with the rim of the catchment funnel 12 inches above the ground.
4. Wind Speed - measured by recording absolute wind run in a prescribed period, and the conversion of the total to average m.p.h. Wind speed records were obtained using a cup-counter anemometer sited in the centre of a treatment with the cups 18" above the soil surface.
5. Light Intensity - recorded from data obtained on an Edac light integrater (heat compensated) situated approximately 100 yards from the trial area.

The treatments were situated in a NW-SE line, each being 6' x 6' in area. Various sheltered and shaded treatments were used and some of the treatments were covered with plastic sheeting during rain and at night. The layout of the trial is shown in Figure 26.

Shelter from wind was obtained by a screen of Hessian, which gave a reduction in average windspeed of over 90% compared with open treatments (Plate 5).

The reduction of airspeed affects features of the microclimate. In general, shelter raises daytime air and soil temperatures, increases

FIGURE 26. TRIAL LAYOUT FOR ENVIRONMENTAL STUDY OF ANTHESIS AND SEED DEVELOPMENT.



℗

KEY. ℗ rain guage.
LI light integrater.
T thermohygrograph.
anemometer.
mcr multichannel recorder.

TREATMENT.
1 shelter and shade.
2 shelter. covered from rain.
3 control.
4 shade only.
5 covered from rain only.
6 shelter only.
7 shade. covered from rain.

atmospheric humidity (particularly at night) and increases dewfall (Sturrock 1969).

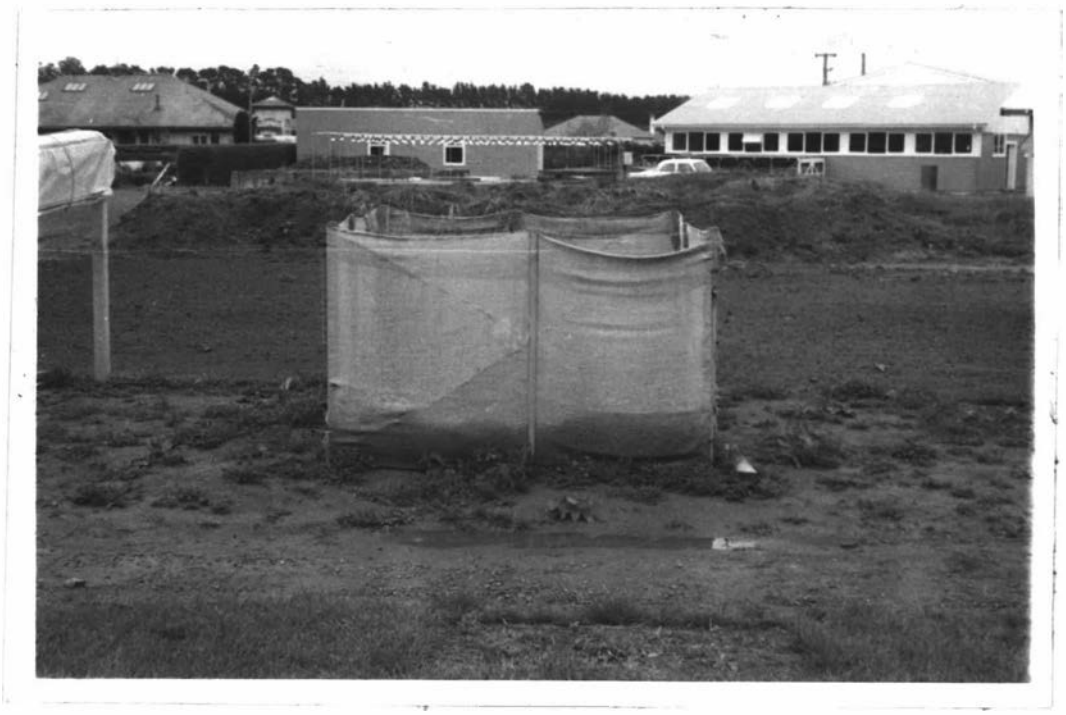


Plate 5 Sheltered Treatment Used in Environmental Study

One thickness of hessian was used to reduce incident light intensity. To overcome the possibility of impaired respiration and transpiration with this shading technique (Olugbemi 1968) an air gap of 1'6" from the ground was left to allow air circulation around plants within 'shaded' treatments (Plate 6) (over).

Light intensity reduction in each treatment varied with the construction materials used. Vertical hessian frames used as a shelter reduced daily total light intensity by approximately 25%, while the same material used to enclose the plants in shaded treatments gave a total light reduction of approximately 70%. The clear plastic covered frames used to exclude rain from some treatments reduced light intensity by approximately 40%. The light reduction compared with full light in the 7 treatments were:

TREATMENT 1	Shelter and shade	76%
TREATMENT 2	Shelter only prairie grass	15%
TREATMENT 2	Shelter only ryegrass	35%
TREATMENT 2	Shelter-covered from rain	68%
TREATMENT 3	Control	Nil
TREATMENT 4	Shaded only	70%
TREATMENT 5	Uncovered	Nil
TREATMENT 5	Covered from rain	41%
TREATMENT 6	Sheltered only prairie grass	15%
TREATMENT 6	Sheltered only ryegrass	35%
TREATMENT 7	Shaded only	70%
TREATMENT 7	Shaded and covered from rain	89%

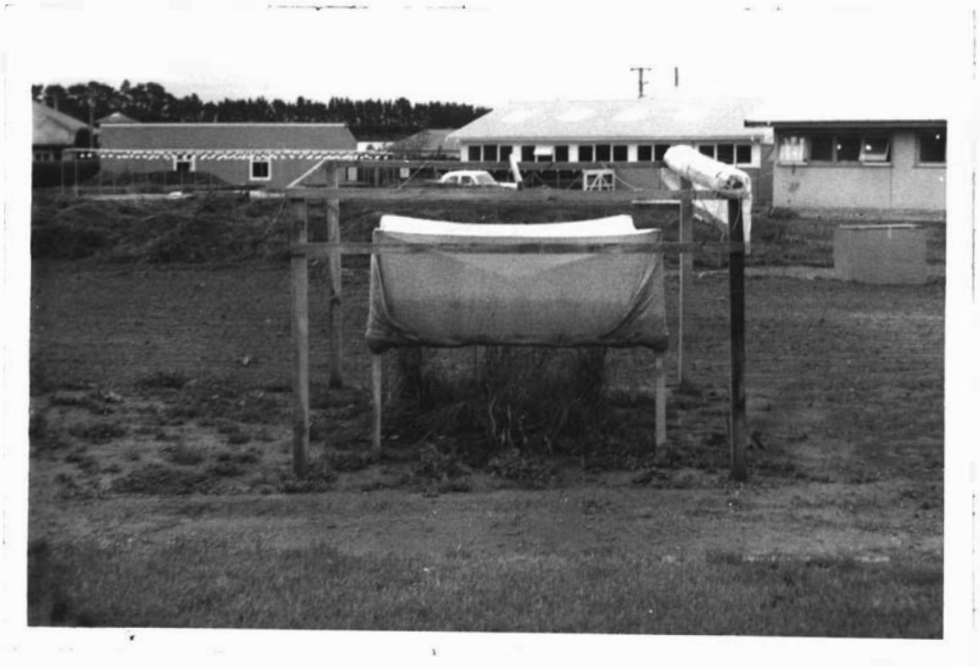


Plate 6 Shaded Treatment Used in Environmental Study

Overall light reductions imposed by different treatments were recorded using an Eppley pyranometer, voltage readings being recorded on a potentiometer.

During the period of anthesis of each species daily records were kept of the number and position of open florets on selected heads in each treatment.

Because of the acropetal pattern of anthesis within each spikelet it was necessary to proceed on an individual floret basis and to record the position of particular florets on the day of anthesis. Since individual florets are open for only a few hours, the day of anthesis was regarded as the day of pollination. The position of individual florets at anthesis was recorded

using a code for spikelet position on the seedhead and floret position within the spikelet. No tagging of individual florets was carried out, because in preliminary trials handling individual florets on a spikelet in the process of marking with coloured waterproof ink often caused more florets to open.

Daily records were made of the number of florets open in each treatment at hourly intervals. This data gave information on daily anthesis intensity and duration, the length of time individual florets remained open, the time of peak flowering, the average number of florets open per head and the total number of florets open each day.

Daily records were also made of the position on tagged heads of florets open each day. Approximately 400 open florets per species were recorded in each treatment on a particular day. On different dates from anthesis, 40 florets were harvested from each treatment (4, 7, 10, 14, 18, 21, 24, 28 and 30 days after anthesis). These were classified into three groups.

GROUP A Florets in which the ovary was shrivelled, discoloured, not enlarged and obviously had not been fertilised effectively.

GROUP B Florets containing ovaries enlarged, white, bilobed, but not showing greenness or elongation. Ovules in this group were enlarged sufficiently to suggest a growth stimulus, possibly caused by fertilisation.

GROUP C Florets containing ovaries, green, elongated, with endosperm development and seeds apparently developing normally.

Florets containing ovaries in Groups A and B were fixed in formalin : acetic acid : 70% alcohol (1:1:18) and stored for later microtome sectioning.

Florets containing ovaries in Group C were air dried and stored in envelopes for germination testing.

Preliminary investigations had shown that up to four days were required following the day of anthesis for fertilisation of the ovule to occur. For this reason florets harvested four days after anthesis were used to determine the number of florets fertilised. This allowed comparison of the number of

florets fertilised with the number of florets developing seed on successive harvest dates from anthesis.

A. EFFECT OF ENVIRONMENT ON THE PATTERN OF DAILY ANTHESIS

LITERATURE REVIEW

A number of workers have published accounts of the effect of environmental conditions on anthesis and seed development. Most of this work has been carried out on grasses, although lucerne, in particular, has received some attention.

This section is restricted to a review of research relating to those environmental factors used in the present study. viz. temperature, relative humidity, light intensity, wind speed and rainfall.

1. Temperature:

Emecz (1961) studied the influence of meteorological factors on the anthesis of 9 grass species. Temperature, measured "in the immediate vicinity of the plants at plant-base level", and light intensity had a positive effect by inducing and promoting anthesis. For S24 ryegrass a threshold value of 57°F. and 2000 foot candles light intensity for at least 2.5 hours was required before anthesis commenced. For S23 ryegrass the threshold values for temperature and light intensity were 62°F and 4400 foot candles for 1.5 hours. Thus the daily onset of flowering on a particular day varies with varieties of the same species. The duration of anthesis (either within one day or between days) and the liberation of pollen were both influenced by the factors which induced anthesis. Emecz recorded that the rate of anther exsertion was consistent for all species. Those grasses which exserted anthers relatively quickly, such as L. perenne, were affected by meteorological conditions immediately prior to anthesis. Others, (such as Dactylis glomerata and Phleum pratense) which exserted their anthers more slowly were mainly influenced by weather conditions on the previous day. Other workers have recorded essentially similar effects of temperature on anthesis in grasses (Gregor 1928, Ponomaryov 1958, Bennett 1959, Lambert 1966) and lucerne (Knowles 1943 and Doull 1967).

Hyde and Williams (1946) found that in Plantago lanceolata anther dehiscence and liberation of pollen could be delayed by high humidity, absence of wind, and temperatures below 50°F.

Anthers of grasses dehisce particularly when the weather is warming up (Faegri and Pijl 1966), irrespective of whether the increase in temperature occurs as a daily change, or belongs to more large-scale irregular changes connected with general weather development.

However, Evans (1916) in his studies on timothy, was more precise and stated that "when the minimum temperature was 65°F or more, timothy flowers continued to bloom in large numbers each day, whether the day was clear, or whether it was cloudy or raining". This result indicates that in timothy at least, temperature plays a major role in determining the time of onset, duration and intensity of daily anthesis.

Jones and Brown (1951) found that in Bromus inermis, pollen shedding was reduced by low temperatures (minimum 38°F). The optimum temperature for pollen liberation being approximately 86°F. They also suggested that poor seed set in some grasses was due to the "extreme heat-blasting (presumably this term infers heat damage and dessication) of the flowers" and dessication of the pollen.

Dotzenko (1967), on the other hand, found that low temperatures during anther exsertion retarded embryo development in Russian Wild rye (Elymus junceus Fisch) and millet (Setaria italica Beauv.) the type of injury being associated with the level of temperature. For example, anther injury and collapsed embryo sacs occurred in plants exposed to -1°C and 4°C temperatures, while style injury occurred in plants exposed to a temperature of 21°C.

Single (1966) and Olugbemi (1968) have stated that in wheat, most damage occurred at anthesis, suggesting a high degree of sensitivity of the reproductive organs to temperature stress. Olugbemi (1968) also noted that injury to the staminate floral parts in wheat was a prominent feature of frost injury. He suggested that while this was probably so for a moderate temperature stress, both male and female reproductive organs were likely to be injured with increasing intensity and duration of stress.

Olugbemi's work indicated that low temperature mainly affected the male, and high temperature mainly the female reproductive organs. It also suggested that florets of wheat at a stage from 7 days prior to anthesis, through until a few days after anthesis, were most susceptible to temperature injury. These findings are also supported by Suneson (1941) with barley, Livingston and Swinbank (1950) with wheat, and by Heslop-Harrison (1957) in a range of flowering plants.

In direct contrast, however, high night temperatures (20°C) have been shown to arrest normal anther development in Poa annua L. without damaging the pistillate organs (Hovin 1958). Similarly temperatures over 27°C during anthesis of Poa pratensis L. have resulted in reduced pollen viability in this species. (Maun et al 1969). Apparently, therefore, grass species differ in their reaction to temperature during anther maturation and anthesis.

In Italian ryegrass (Lolium multiflorum) it has been suggested that whatever the duration of light, thermoperiodism can determine the daily rhythm of flowering (Schaeverbeke 1966). In this species at least high temperature has been shown to favour floral maturation and also to have an accessory role once anthesis has been induced. Schaeverbeke stated that temperature appeared to be the essential factor in the anthesis of italian ryegrass.

It is difficult in many reports to isolate the effects of light, total radiant energy, and ambient temperature. In some research papers the words 'light' and 'radiation' appear to have become synonymous. The description of an environment with high incident radiation in terms of high temperature alone may often confuse the true explanation of observed results.

2. Relative Humidity:

The number of publications on the effect of relative humidity on grasses is small, being mainly concerned with the effects of humidity on anthesis and pollen germination.

Lambert (1966) stated that relative humidity had no effect on anthesis in a wide range of grasses. Rather it was the actual presence of rain that

hindered or even inhibited anthesis. Emecz (1961) also supported this view, but qualified his statement by noting that humidity had "no measurable effect on anthesis in grasses except when it caused altered light conditions, or when it was accompanied by precipitation".

In contrast to the above findings, other workers have suggested a direct relationship between humidity and anthesis. For example Gregor (1928) suggested that the time of onset of anthesis and the time from floret opening until anther dehiscence in perennial ryegrass may be influenced by humidity. Smith (1944) stated there was a negative correlation between humidity and seed set in grasses.

In other crops, humidity influences seed formation in the same direction as suggested by Smith (1944). Relatively dry air (less than 50% R.H.), both day and night during anthesis is considered to be one of the factors favouring seed production in lucerne (Brink and Cooper 1936, Knowles 1943 and Doull 1967) and Hyde and Williams (1946) consider that dehiscence of anthers and liberation of pollen can be delayed by high humidity in Plantago lanceolata.

In most previous work, no clear distinction is made between the effects of high humidity and rainfall on anthesis. Whether the effect of rain is a physical one with the florets reacting adversely to the presence of free water is not clear. Should this not be the case, however, one would have thought that high humidity and rainfall would have similar effects on anthesis, or at least manifest effects in the same direction.

In many records no distinction is made of the effect of humidity alone on anthesis, or on whether humidity influences anthesis by interaction with one or more other environmental variables.

3. Light Intensity:

The effect of light intensity on anthesis, as already stated, has been shown by Emecz (1961) to have positive effects in inducing and promoting anthesis in a range of grasses.

The threshold values which must be exceeded before anthesis will occur varies with species and variety. It appears that, while light intensity is not the only single environmental factor influencing the onset and intensity of anthesis, it nevertheless affects anthesis in conjunction with other variables, particularly temperature. Similar effects have been quoted by Lambert (1966).

In lucerne Knowles (1943) found the number of hours of sunshine per day to be positively correlated with seed-set, possibly through its effect on encouraging pollinating agents to the flowers rather than through any direct influence on the floral parts themselves. Hyde and Williams (1946) observed diurnal variation in grass pollen liberation to be correlated, both in frequency and duration, with the incidence of sunshine. On dull days anthesis was largely suppressed and local pollen concentration remained low. However, what particular component(s) of the environment was involved was not stated.

4. Wind Speed:

Wind pollination is the dominant type of abiotic pollination, comprising some 95 - 98% of all examples and prevailing in several families, e.g. Gramineae, Cyperaceae, and Juncaceae. Evans (1916) observed that in timothy the number of heads flowering was depressed by strong winds, and Hyde and Williams (1946) found that in Plantago lanceolata, a gentle breeze was sufficient to allow pollen to be shed within a few minutes of anther dehiscence. Dehiscence of anthers and liberation of pollen were both delayed by lack of wind.

It has been found that wind velocity is important in hindering or even inhibiting anthesis in a range of grasses. A wind velocity of 15 mph inhibited anthesis in S24 and S23 ryegrass. In timothy an 8 mph windspeed inhibited anthesis (Emecz 1961, Lambert 1966).

5. Rain:

Few workers have specifically discussed the effect of rain on anthesis in grasses. However, Faegri and Pijl (1966) noted that grass anthers generally did not open unless the weather was warm and dry and that pollen was rapidly washed out of the air by rain. Ponomaryov (1958) considered rain as an environmental factor causing "deviation from the normal pattern of daily anthesis" in grasses, while Evans (1961) stated that in different seasons the duration of anthesis of a crop could be significantly prolonged during wet weather.

RESULTS - Perennial Ryegrass

The pattern of daily anthesis (1.12.68-12.12.68) for ryegrass in relation to environmental variables (temperature, relative humidity, light, wind speed and rainfall) is presented in Figure 27 (raw data in Appendix 25). Environmental conditions caused considerable variation in the duration and intensity of daily anthesis. Conditions completely inhibited anthesis on day 2 and were responsible for greatly reduced anthesis on days 5 and 7.

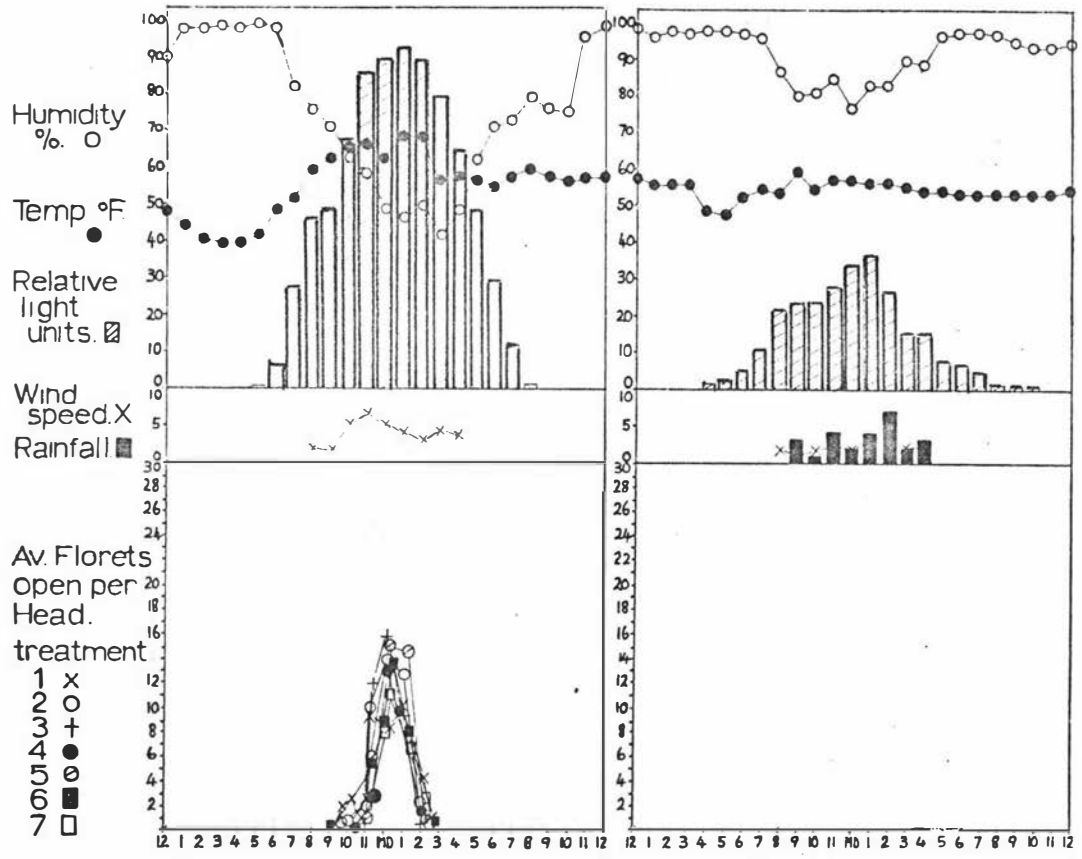
Analysis of treatment data for the components of daily anthesis is presented in Tables 17 and 18. In addition, environmental variables were subjected to correlation analysis and regression analysis in relation to daily anthesis components. The correlation matrix of this analysis is presented in Appendix 26.

Because individual environmental factors were highly intercorrelated, actual regression equations were of limited value and are therefore not quoted. However, they were used to calculate the percentage total variation of various components of anthesis which each environmental factor explained.

Individual components of daily anthesis pattern are discussed below in relation to both Tables 17 and 18 and Appendix 26.

FIG.27. PERENNIAL RYEGRASS DAY 1

PERENNIAL RYEGRASS DAY 2



PERENNIAL RYEGRASS DAY 3

PERENNIAL RYEGRASS DAY 4

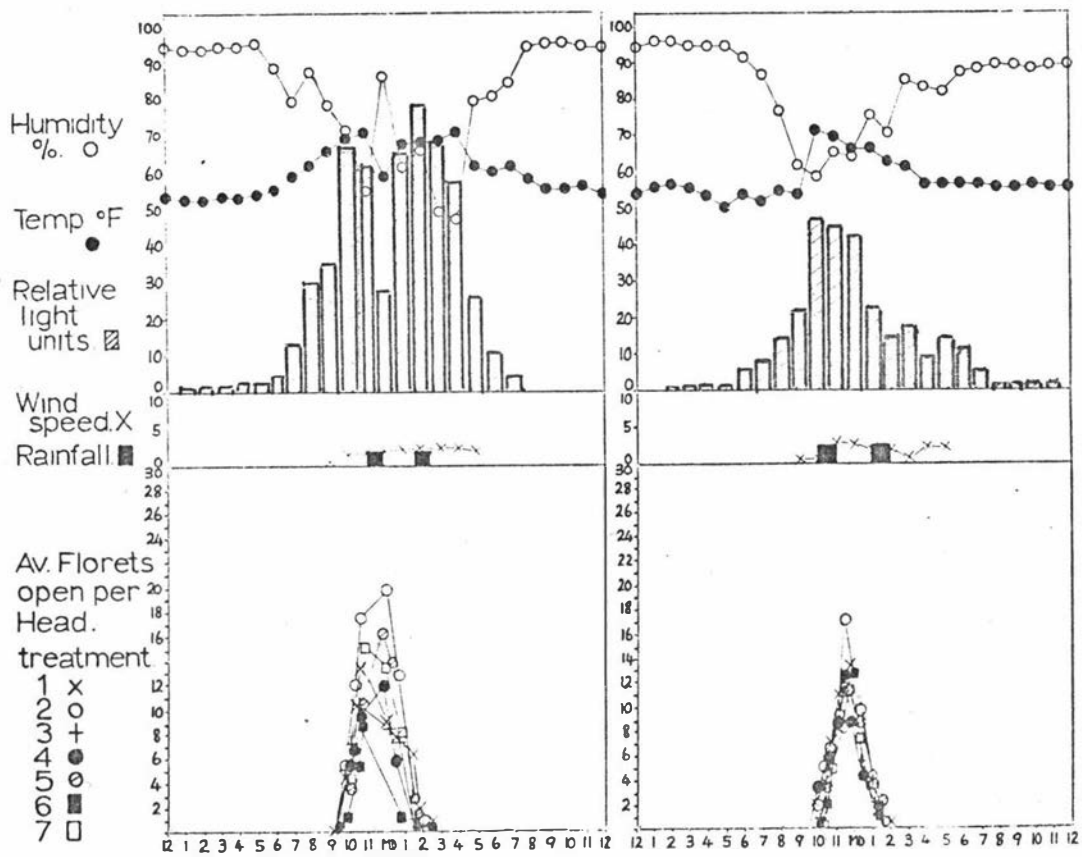


FIGURE 27 DAILY ANTHESIS PATTERN IN RELATION TO ENVIRONMENTAL CONDITIONS – PERENNIAL RYEGRASS

FIGURE 27 CONTINUED

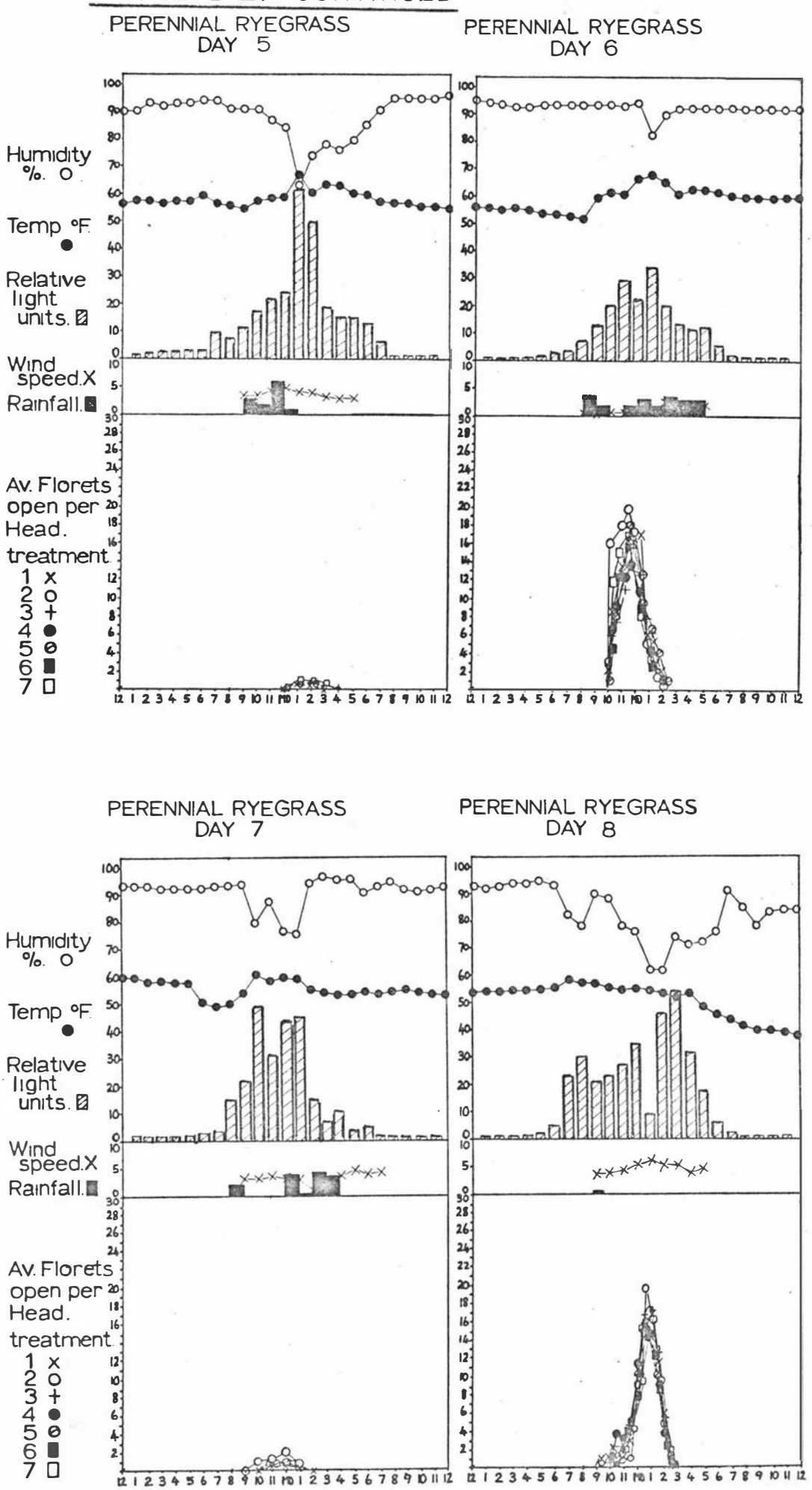
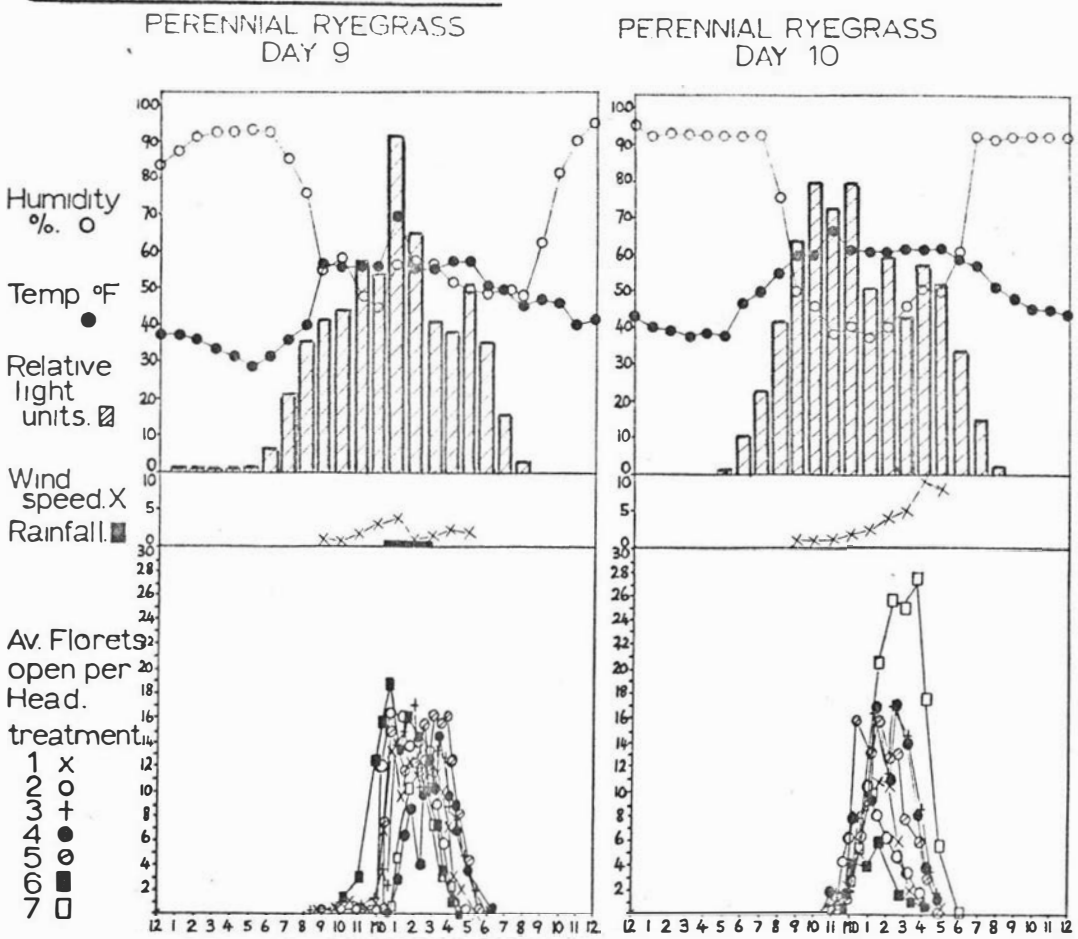


FIGURE 27 CONTINUED



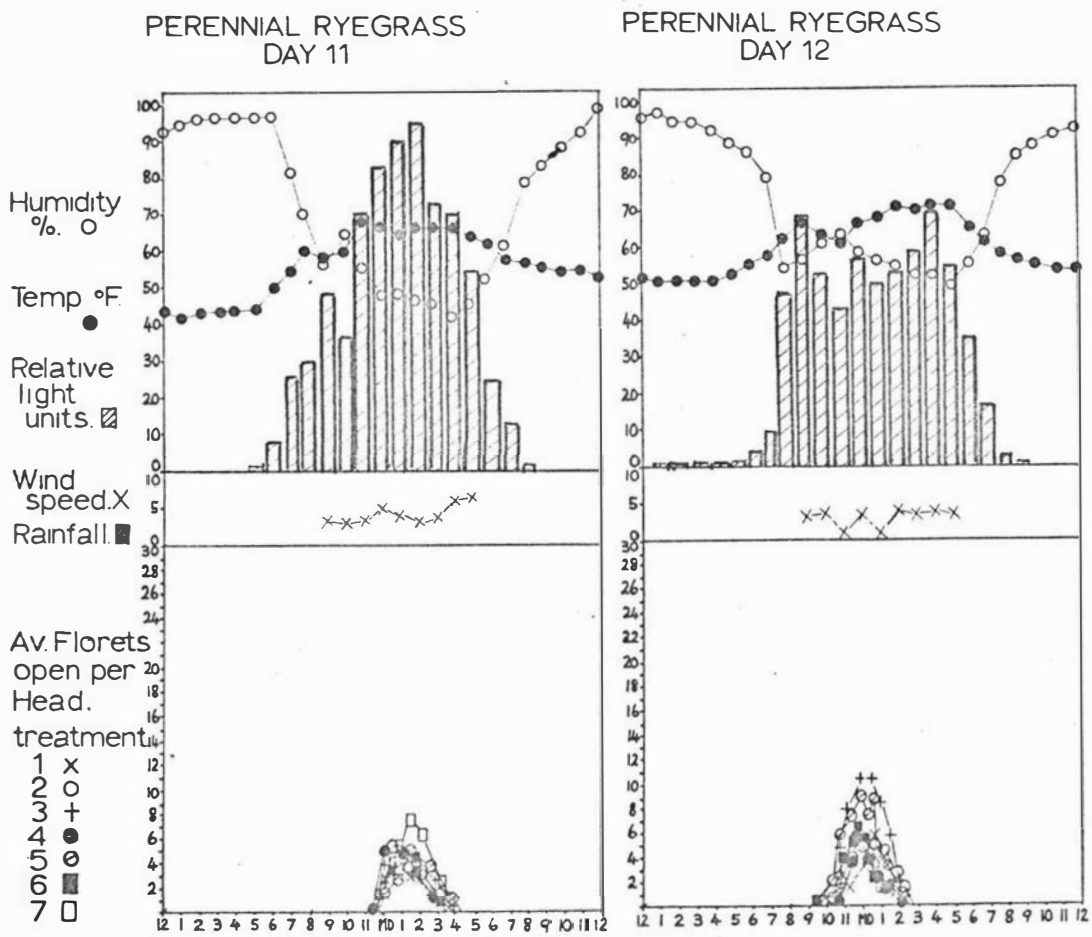


TABLE 17 Results of Analysis of Treatment Data for Components of Daily Anthesis Pattern in Ryegrass

Treatment	Time of Onset (mean hrs)	Time of Peak Anthesis (mean hrs)	% Total Florets Open at Peak Anthesis (mean %)
1. Shelter and Shade	0942 ABb	1136 a	54 a
2. Shelter and Covered	0924 Bb	1048 a	52 a
3. Control	0954 ABab	1242 a	53 a
4. Shade only	1024 Aa	1312 a	55 a
5. Covered only	1000 ABab	1400 a	52 a
6. Shelter only	0936 ABb	0924 a	53 a
7. Shade and Covered	1000 ABab	1448 a	53 a
C.V.%	6.0	6.0	9.5
L.S.D.	0.7(0042)	7.7(0742)	6

Time of Onset of Daily Anthesis

Daily anthesis commenced between 9.20 and 10.20 a.m. The time of onset was the only aspect of daily anthesis pattern significantly influenced by the treatments imposed. As shown in Table 17 the shelter/covered treatment significantly advanced the time of onset compared with the shade treatment. The correlation matrix shows that a large number of climatic measurements were significantly correlated with the time of onset of daily anthesis. However, many of these correlations were low. The main effects came from temperature and humidity variations which accounted for 51% and 67% of the total variance respectively.

The major significant correlations are presented below.

Temperature minimum previous night -0.38**

Temperature minimum on night 36 hours prior to day of anthesis -0.54**

Humidity minimum and mean previous night -0.33** and -0.27*

Humidity minimum and mean on day of anthesis -0.34** and -0.47**

Humidity maximum, minimum, mean previous day -0.44**, -0.49** and -0.53**

Humidity mean on night 36 hours prior to day of anthesis -0.73**

Wind speed maximum on day of anthesis +0.44**

Light minimum on previous day +0.39**

It appears that low night temperatures and humidity levels prior to anthesis advanced the time of onset of daily anthesis. Low light intensity

on the previous day and high wind speeds on the day of anthesis also delayed time of anthesis onset. Low humidity on the day of anthesis and humidity levels on the previous day caused earlier daily anthesis. In addition the time of onset of anthesis was significantly correlated with the number of florets open on the previous day (+0.44**).

Time of Peak Anthesis

Peak anthesis occurred generally between 11 a.m. and noon, but was delayed until early afternoon if the time of onset of anthesis was also delayed. The time of peak anthesis (Table 17), while not influenced by the treatments imposed, was strongly affected by both temperature and humidity. Almost all temperature and humidity variables were significant and negative, in particular, the minimum and mean temperatures for the previous night (-0.71** and -0.75**). All temperatures together explained 70% of the variation, but mean night temperature alone explained 56%. All humidities explained 68% of the total variation. Rainfall was negatively correlated with the time of peak anthesis (-0.29*) and wind speed maximum was also shown to have a small positive effect (+0.36**). While rainfall tended to hasten the time of peak anthesis, strong winds apparently delayed the time of peak anthesis.

The time of peak anthesis on a particular day was influenced significantly and positively by the duration of anthesis, the length of time individual florets remained open and the intensity of anthesis on the previous day.

% Total Florets Open at Peak

Approximately 50% of the total florets open on a particular day were open at peak anthesis. The percentage of total florets open at peak anthesis (Table 17) was unaffected by treatment and showed little variation due to environmental conditions. In fact the few correlations that did show statistical significance accounted for very little of the total variance (approximately 17%).

Minimum night temperature prior to the day of anthesis was negatively and significantly related to the percentage of florets open at peak anthesis

(-0.25*). In addition, the intensity of anthesis on the previous day (+0.34**) the time of onset (+0.27*) and the duration of time individual florets remained open on the day of anthesis (+0.34**) were all related to the percentage of florets open at peak flowering.

TABLE 18 Results of Analysis of Treatment Data for Components of Daily Anthesis Pattern in Ryegrass

Treatment	No. Florets Open at Peak Anthesis (mean)	Length of Time Florets Open (mean mins)	Duration of Anthesis (hours)
1. Shelter and Shade	118 a	156 a	5.47 a
2. Shelter and Covered	144 a	149 a	5.50 a
3. Control	141 a	147 a	5.04 a
4. Shade only	126 a	142 a	4.70 a
5. Covered only	143 a	146 a	5.09 a
6. Shelter only	118 a	131 a	4.97 a
7. Shade and Covered	143 a	145 a	5.29 a
C.V.%	23.0	16.0	15.0
L.S.D.	40	26	0.85

Number of Florets Open at Peak Anthesis

Although there was no significant treatment effect, (Table 18) temperature, humidity and light were significantly correlated with the number of flowers open at peak anthesis (Appendix 26). Temperature explained 63% and humidity 69% of the total variation. Minimum and mean temperatures both on the day of anthesis (-0.47** and -0.38**), and on the previous day (-0.38** and -0.42**) were negatively correlated with the number of florets open at peak anthesis. Minimum and mean temperature (+0.30** and +0.32**) and minimum and mean humidity (+0.57** and +0.37**) on the night 36 hours prior to the day of anthesis were significantly correlated with floret numbers open at peak anthesis.

Length of Time Florets Open

Individual florets remained open for approximately 2.5 hours. No treatment effect was evident (Table 18). Temperature on the day of anthesis had little effect on the time individual florets remained open (Appendix 25). However, night and day temperatures for the 36 hour period prior to the day of anthesis showed significant negative correlations (between -0.3 and -0.5), and explained 64% of the total variation. Humidity on the day of anthesis, showed a significant negative correlation. This factor exerted the major day

of anthesis effect on the length of time individual florets remained open.

The length of time a floret remained open was significantly correlated (+0.37**) with the time of peak anthesis. Under conditions where florets remained open longer the time of peak anthesis was delayed.

Duration of Daily Anthesis

Total daily anthesis duration varied from 4 to 9 hours with an average duration of approximately 5 hours.

No treatment effect was evident (Table 18). A number of temperature correlations were significant. These included minimum and mean temperature on the day of anthesis (-0.58** and -0.42**) maximum, minimum and mean temperatures during the previous night (-0.54**, -0.54** and -0.57**) and maximum, minimum and mean temperatures on the previous day (-0.42**, -0.57** and -0.55**). While humidity did not appear to be highly correlated with the duration of daily anthesis, humidities explained 66% of the total variation and temperatures only 59%. Minimum temperatures were most significant, minimum temperature on the day of anthesis (-0.58**) and minimum temperature on the previous day (-0.57**) together explaining 50% of the variation.

The duration of daily anthesis was directly related to the length of time individual florets remained open (+0.42**) and with time of peak anthesis (+0.38**).

RESULTS - Prairie Grass

The pattern of daily anthesis for six days (commencing 11.11.68) in prairie grass in relation to environmental variables (temperature, relative humidity, light, wind speed and rainfall) is presented in Figure 28 and Appendix 27. These results show that considerable variation can occur in the time of onset, intensity and duration of daily anthesis in prairie grass as measured by the average percentage of florets open.

Analysis of treatment data for the components of daily anthesis is presented in Tables 19 and 20. In addition environmental variables were subjected to correlation and regression analysis in relation to daily anthesis components. The correlation matrix of this analysis is presented in Appendix 28.

FIG.28.

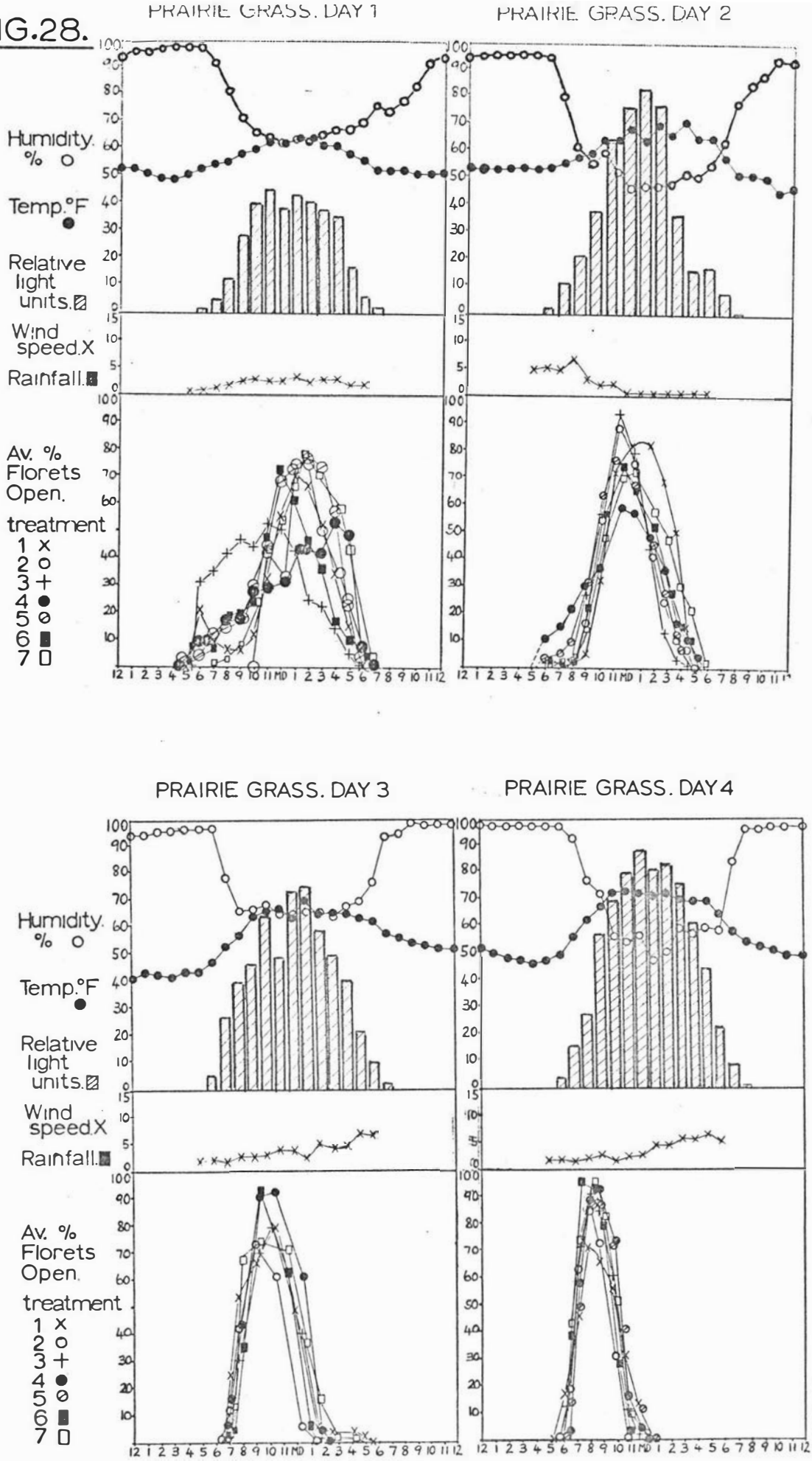
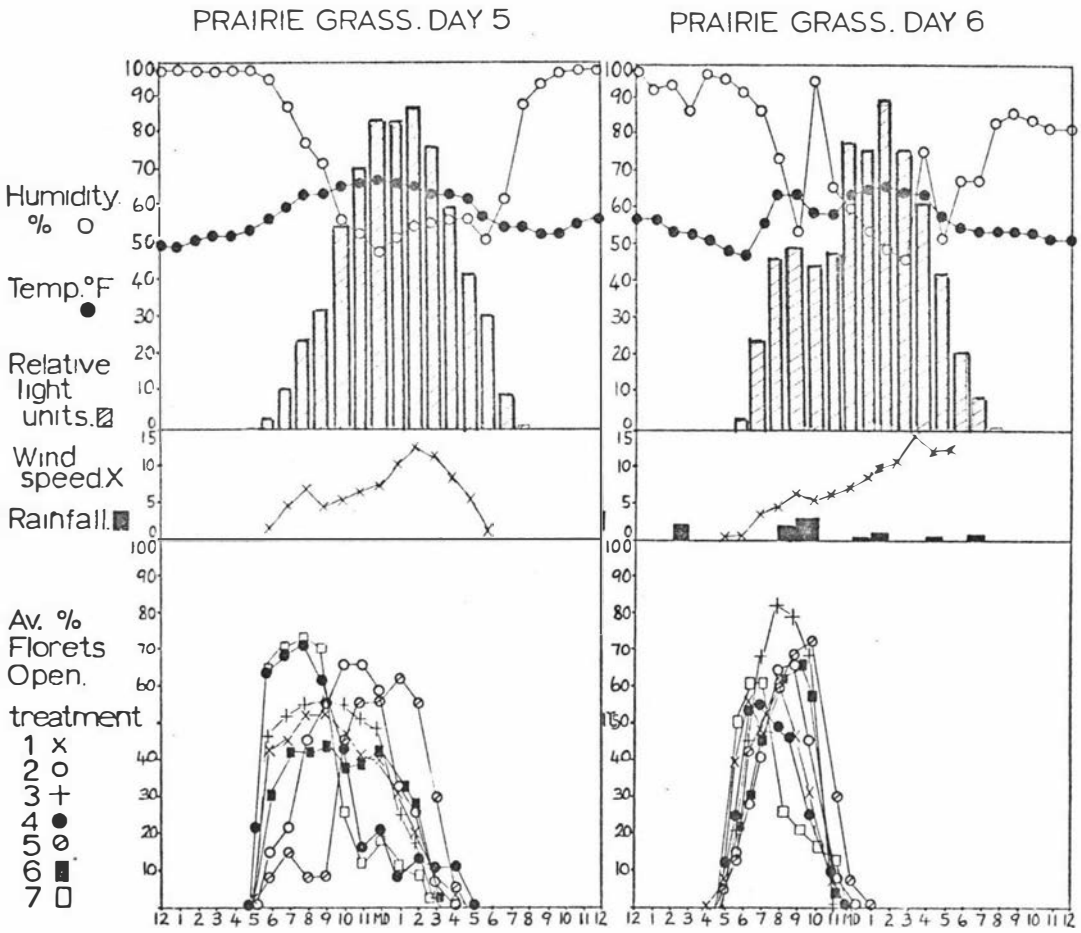


FIGURE 28 DAILY ANTHESIS PATTERN IN RELATION TO ENVIRONMENTAL CONDITIONS - PRAIRIE GRASS

FIGURE 28 CONTINUED



The significant correlations quoted are for each individual variable.

As the individual environmental factors were highly intercorrelated, actual regression equations were of limited value and are therefore not quoted. However, they were used to calculate the percentage total variation of various components of anthesis which each environmental factor explained.

TABLE 19 Results of Analysis of Treatment Data for Components of Daily Anthesis Pattern in Prairie Grass (Mean of 6 days)

Treatment	Time of Onset (mean hrs)	Time of Peak Anthesis (mean hrs)	% Total Florets Open at Peak Anthesis (mean %)
1. Shelter and Shade	0542 a	0954 ab	71 b
2. Shelter and Covered	0618 a	0842 b	77 ab
3. Control	0506 a	0930 ab	76 ab
4. Shade only	0500 a	1012 ab	71 b
5. Covered only	0524 a	1112 a	79 a
6. Shelter only	0500 a	0948 ab	76 ab
7. Shade and covered	0536 a	1112 a	77 ab
C.V.%	18.4	17.0	13.8
L.S.D.	1.3(0118)	2.3(0218)	7

Time of Onset of Anthesis

Anthesis generally commenced between 5.00 and 6.00 a.m. The results in Table 19 show that no treatment differences occurred. Regression analysis showed that overall temperature and humidity explained only 33% and 37% of the total variation. Significant negative correlations were obtained between time of onset and maximum temperature and humidity two nights prior to the day of anthesis (-0.37*, -0.37* respectively). Apart from this it appears that the climatic factors studied had little effect on the time of daily onset of anthesis.

Time of Peak Anthesis

Peak anthesis generally occurred between 9 a.m. and 11 a.m. but could be delayed until the early afternoon if total anthesis duration was protracted (Figure 28). The treatment means presented in Table 19 show that covered and shade/covered significantly delayed the time of peak anthesis compared with the shelter/covered treatment. However, an examination of the correlation matrix (Appendix 28) suggested that the major environmental factors involved were temperature and humidity which together accounted for 70% of the

variation obtained. For example maximum night temperatures, both on the night immediately prior to the day of anthesis (-0.68**) and during the night 36 hours prior to the day of anthesis (-0.63**) were both negatively correlated with time of peak anthesis. A positive relationship was shown by low day temperatures on the day of anthesis (+0.44**) and a negative correlation with high temperatures the previous day (-0.39**). Minimum humidity during the day of anthesis and during the previous night were positively correlated with the time of peak anthesis (+0.41** and +0.52** respectively).

Percentage Total Florets Open at Peak Anthesis

Approximately 75% of total florets flowering were open at peak anthesis. An examination of the results in Table 19 indicates that shade was the major factor reducing the percentage of florets open at peak anthesis. Temperature and humidity conditions together explained 55% of the variation recorded. As shown in the correlation matrix the most significant conditions and times were the minimum temperature and minimum humidity levels on the day of anthesis (-0.43** and +0.42**) and the mean temperature and mean humidity levels two nights prior to the day of anthesis (-0.35* and -0.54**).

TABLE 20 Results of Analysis of Treatment Data for Components of Daily Anthesis Pattern in Prairie Grass

	Number of Florets Open at Peak Anthesis (mean)	Length of Time Floret Open (mean mins)	Duration of Anthesis (hrs)
1. Shelter and Shade	54 ABab	195 a	10.4 a
2. Shelter and Covered	30 Bb	171 a	8.1 a
3. Control	57 ABab	205 a	9.6 a
4. Shade only	44 ABab	198 a	11.1 a
5. Covered only	66 ABa	202 a	10.4 a
6. Shelter only	53 ABab	152 a	9.8 a
7. Shade and Covered	72 Aa	170 a	10.5 a
C.V.%	36.0	20.0	11.6
L.S.D.	29	53	4.6

Number of Florets Open at Peak Daily Anthesis

The results presented in Table 20 show that the treatment 'shelter and covered' had significantly fewer florets open at peak anthesis than the treatments 'covered only' and 'shade and covered'.

No significant treatment/day interaction occurred in the number of florets open at peak anthesis or in the length of time individual florets remained open. Because of this mean values for these components of daily anthesis were used in Table 20.

In terms of the regression analyses both temperature and humidity were equally important and accounted for 52% of the variation in number of florets open. The number of florets open at peak anthesis on a particular day was significantly correlated with minimum day temperature (-0.44**) with minimum temperature on the previous day (+0.37*), and with both maximum and minimum night temperature 36 hours prior to day of flowering (-0.38* and +0.47** respectively). Apparently night temperature immediately prior to the day of flowering did not significantly influence floret numbers open at peak anthesis, the major night temperature effect being determined two nights prior to the day of anthesis.

Maximum relative humidity on the day of anthesis was negatively correlated with the number of florets open at peak anthesis (-0.42**) as were maximum and mean humidities the previous night (-0.49** and -0.51** respectively). The only other significant correlation was minimum light on the day of anthesis (+0.36*).

The number of florets open on a particular day was significantly correlated with the number of florets which were open on the previous day (+0.40**).

Length of Time Individual Florets Open

There was no evidence of a significant treatment effect (Table 20) and once again temperature and humidity were the major components of the environment affecting the length of time florets remained open (together accounting for 60% of the variation). In terms of the particular conditions significant

correlations were recorded for minimum day temperature (+0.46**) and maximum temperatures during each of the two nights prior to the day of anthesis (-0.38* and -0.41** respectively). Minimum and mean humidity two nights prior to anthesis were also significantly correlated with duration of anthesis of individual florets (+0.50** and +0.34* respectively).

From a detailed examination of these florets subsequently (results presented in Appendix 29) it appeared that the length of time individual florets remained open in a particular treatment or on a given day was fairly constant irrespective of whether a seed was ultimately formed or not.

Duration of Daily Anthesis (Hours)

Daily anthesis continued for 8 to 11 hours. No significant treatment differences occurred (Table 20). The fact that temperature explained 77% and humidity 76% of the variation indicates that these two variables were highly correlated. The main significant correlations were:

Temperature minimum day of anthesis +0.72**

Temperature maximum and minimum previous night -0.53** and +0.48**

Temperature maximum 36 hours prior to anthesis -0.42**

Humidity minimum and mean 36 hours prior to anthesis +0.64** and +0.54**

Light maximum, minimum and mean on day of anthesis -0.36*, -0.39* and -0.35*

The correlations indicate that low night temperature prior to, and low temperature on the day of, anthesis extended the duration of daily anthesis. Similar effects also occur with high humidity prior to, and low light intensity on, the day of anthesis. The correlations between light and duration of daily anthesis are of particular interest as they represent the only significant light effect obtained in prairie grass other than the effect of minimum light on the day of anthesis (+0.36*) on the number of florets open at peak anthesis as previously mentioned (page 159).

DISCUSSION

Interpretation of results from experiments in which individual environmental variables are not controlled is difficult since climatic factors are often highly inter-correlated. A high mean temperature probably infers there may be high maximum and minimum temperatures and possibly even lower humidities and high light radiation. An effect caused by a high maximum temperature, therefore, may be correlated not just with maximum temperature but also with those other effects which influence it.

Throughout the experiment it was apparent that the intensity of flowering on the previous day had a considerable influence on the time of onset, the duration of anthesis and the time of peak anthesis on the succeeding day. Despite this, however, temperature and humidity exerted the major effect on daily anthesis, minimum night and day temperature levels generally being most consistent in influencing the time of onset and intensity of anthesis on a particular day.

In both ryegrass and prairie grass anthesis proceeded in a more or less regular manner from the tip of the head downwards. Within the individual spikelet the basal floret reached maturity first, anthesis continuing regularly from the basal to the terminal floret.

Anther dehiscence occurred generally within a few minutes of exsertion but appeared to be delayed under conditions of low temperature and high humidity. No anthers were observed to have liberated pollen prior to extension of the stigma branches. In ryegrass the shortest time between the opening of a floret and anther dehiscence was 3 minutes and the longest approximately 85 minutes. In prairie grass the corresponding time intervals were 4 minutes and approximately 95 minutes respectively. The times for ryegrass correspond to the relative duration of 2 minutes and 77 minutes quoted for this species by Gregor (1928).

No instances of a floret fully opening and closing twice during the same day or on successive days were observed in either species in the present study. This is contrary to findings in Italian ryegrass by Gregor (1928).

The mean length of time individual florets remained open was 167 minutes for ryegrass and 185 minutes for prairie grass. In neither species was there any apparent relationship between the duration of floret opening and closing and subsequent seed set.

The daily period of anthesis in each species varied to some extent. Prairie grass commenced anthesis between 4 a.m. and 6 a.m. and continued for from 8 hours (days 4 and 6) to 14.0 hours (day 1). The mean duration over the six days studied was 11.0 hours. Ryegrass on the other hand began daily anthesis later in the morning (9-11 a.m.) and continued for approximately 6 hours. Atmospheric conditions, particularly temperature and humidity, appeared to regulate the onset of daily anthesis in both species.

Each anther dehisced by a longitudinal slit. The two sacs of the anther dehisced, if not simultaneously, within a very few minutes of each other. Given a gentle breeze the great bulk of the pollen was shed within a few minutes of anther dehiscence.

In both species the importance of night temperatures on the pattern of daily anthesis was marked. High night temperatures (approximately $10^{o}C$ or higher) generally resulted in earlier onset, contracted duration and earlier peak anthesis and also reduced the length of time individual florets remained open in both ryegrass and prairie grass. Low night temperatures generally had an opposite effect. This promotion of daily flowering intensity as a result of exposure to high night temperatures could be considered in relation to the findings of other workers (Suneson 1941, Livingston and Swinbank 1950, Heslop-Harrison 1957, and Olugbemi 1968) who as previously stated have suggested that anther development and pollen maturation are encouraged by high night temperatures.

This would result in anthers maturing and containing ripe pollen in a condition for dehiscence. As a result an intensive and contracted anthesis pattern could occur provided daily environmental conditions were favourable. With low night temperatures the rate of anther and pollen development could

be retarded, with the result that anthesis would be delayed until temperatures suitable for the completion of these processes occurred.

In ryegrass high temperatures (above approximately 10°C) during the two nights prior to the day of anthesis also resulted in a greater number of florets open at the time of peak anthesis. Low night temperatures (approximately 0-5°C) had an opposite effect. These findings support the suggestion by Evans (1916) that in timothy daily anthesis pattern "seems to depend to some extent on the climatic conditions during the preceding days".

The results for both species do not generally support the suggestion by Hovin (1958) and Maun et al (1969) that high night temperatures arrest normal anther development. However, the results cannot be considered to be a direct contradiction of findings by these workers as maximum night temperatures of the order of 20°C as used in their previously described experiments with Poa spp. were not reached in the present study.

In both species daily anthesis pattern was strongly influenced by day temperature. Low temperatures (below approximately 14°C in ryegrass and 16°C in prairie grass) during the day either inhibited anthesis (particularly in ryegrass) or, when anthesis occurred, affected the number of florets open at peak anthesis and increased the duration of daily anthesis in both species. In addition, under such conditions low temperatures caused a delay in the time to peak anthesis in ryegrass. In prairie grass individual florets remained open for longer and the percentage of florets open at peak anthesis was reduced.

Low relative humidity (below approximately 50%) during the day of anthesis generally advanced the time of peak flowering in prairie grass, but the percentage of florets open at this point was often high (over 75%). In both species low humidity reduced the number of florets open at peak anthesis. Daily humidity levels apparently exerted little effect on the duration of anthesis or on the length of time individual florets remained open in prairie grass. However, in ryegrass low humidity generally resulted in an earlier

onset of anthesis and reduced the time individual florets remained open.

Light apparently played little part in influencing daily flowering pattern in ryegrass although low light intensity delayed the onset of anthesis. This relatively minor effect of light on flowering was unexpected as Emecz (1961) and Lambert (1966) had both stressed the importance of light intensity on daily anthesis pattern in S23 and S24 ryegrass and in S48 timothy.

The influence of light intensity on duration of daily anthesis in prairie grass was not clear when this factor was considered as an independent variable. During day 1 reduced light intensity apparently interacted with temperature and humidity resulting in protracted duration of anthesis. Although extended duration of flowering also occurred on days 2 and 5 light intensity alone did not appear to be the sole contributing cause. The only other significant light effect in prairie grass was that of low light intensity reducing the number of florets open at the time of daily peak anthesis.

Although it was often difficult to interpret some of the significant treatment effects shown in the present study shading appeared to delay the time of peak anthesis and to reduce the percentage of florets open at peak anthesis in prairie grass.

The maximum light values obtained in this study were 1902 units for ryegrass (day 11) and 1778 units for prairie grass (day 6). These figures represent maximum light levels of approximately 10,500 and 9,800 foot candles per hour respectively. The former figure is approximately 2 and 5 times higher than the level quoted as influencing anthesis in S23 and S24 perennial ryegrass by Emecz (1961).

While it is important that grass anthers be fully exposed to the environment during anthesis it appears that air movement is necessary to carry pollen away. Faegri and Pijl (1966) have suggested that the opening of grass anthers causes some arrest of the pollen, which will soon block the exit unless movement of the stamens removes the first pollen. This is probably the reason why even low wind speeds influenced the rate of anther dehiscence and pollen liberation.

Wind speeds over approximately 10 m.p.h. delayed both the time of onset and time of peak anthesis in ryegrass, and caused closing of open florets and cessation of floret opening in both species. Conversely low wind speeds of approximately 3-5 m.p.h. apparently advanced anthesis onset and extended the duration of daily flowering.

In ryegrass, looking at treatment effects generally, it appeared that shelter led to earlier onset of daily anthesis. Plants in sheltered treatments generally commenced anthesis earlier in the day than plants in treatments exposed to the wind.

In the present study (in ryegrass in particular) it was observed that the presence of heavy dew retarded or even inhibited the onset of anthesis, until moisture on the florets had evaporated.

In both species the effect of rain on anthesis was not well defined. If rain occurred after florets had started to bloom on a particular day, and the temperature was warm (over approximately 15^{o}C), there appeared to be little apparent inhibiting effect of rain, in that florets continued to bloom. However, under these conditions rain generally hastened the closing of florets in which anther dehiscence had already occurred and retarded the opening of further florets. This resulted in earlier peak anthesis, particularly in ryegrass. Under low temperature conditions anthesis intensity was reduced or no further florets were observed to open when it was raining.

The major effect of rainfall in both species was to advance the time of peak anthesis and to curtail or inhibit anthesis under low temperature and high humidity conditions.

The effect of rainfall was apparently not a predominantly physical one, open florets not necessarily closing due to the presence of free water on the exposed floral organs. This was particularly evident in ryegrass (days 3, 6 and 9) where anthesis continued during light rain.

The effect of rain on anthesis was more marked in ryegrass than in prairie grass. This suggests that the latter species was more tolerant to environmental conditions which could affect daily anthesis pattern. This is further supported by the fact that far fewer significant environmental correlations were detected in prairie grass than in ryegrass throughout this study.

One of the factors which had a major bearing on the pattern and intensity of daily anthesis in both species, was the number of florets open on the previous day. In general, intensive anthesis on one day was followed by later onset and by reduced numbers of florets open during anthesis on the succeeding day. This was particularly the case when the intervening night temperature was low (below approximately $6^{o}C$) and was also dependent upon the minimum night temperature prevailing two nights prior to the day of anthesis.

In this study it was often difficult to explain some of the significant effects which occurred between treatments. In prairie grass little effect due to shelter and covered treatment combinations was observed. In ryegrass shade and covered treatments showed little effect on anthesis. This was attributed to the fact that temperature, and to a lesser extent humidity, were the factors exerting the main influence on daily anthesis. Unfortunately the variation in levels of these two environmental components between treatments was not as great as expected. In both cases only a mean variation of approximately $\pm$ $1.5^{o}C$ occurred between all treatments used in the present study.

B. POLLINATION, FERTILISATION AND SEED 'SET'

INTRODUCTION

Observations of anthesis alone give little or no information on the ability or otherwise of pollination to ultimately result in seed development (Beddows 1931).

While attempts have been made to determine some of the environmental factors which affect anthesis, itwas also important that information be obtained about the processes of pollination and fertilisation. For this reason observations were made of the pollination, fertilisation and seed setting of ryegrass and to a lesser extent prairie grass.

LITERATURE REVIEW

The term 'pollination' is used to describe processes occurring from the time of anther dehiscence until the pollen tube reaches the embryo sac in the ovary. The term 'fertilisation' infers the actual fusion of the male nucleus with the ovum. 'Seed set' is used to describe the early growth of the embryo and endosperm of a successfully fertilised ovary.

Anslow (1963) quotes Visser's work on the retention of viability of pollen, which states that the life of pollen grains of the Gramineae is short, especially under conditions of low humidity. Anslow therefore suggests that, since anther exsertion in ryegrass is most profuse under conditions of low relative humidity, pollen life should be shortest at times of the day when most pollen is shed. Also, Jones and Brown (1951) suggested "that the poor seed-set observed in some grass species may be due to the susceptibility of the stigmas to damage under high temperatures and to dessication of the pollen".

Watanabe (1955) has described the morphological changes undergone by pollen grains in contact with the stigmas of a range of Gramineae, and also noted that when the progress of pollen germination is disturbed pollen grains tend to shrink or burst at any stage. He also observed (1958) that withering of the stigmas of grasses begins a few hours after pollination possibly due to an increase in cell permeability of the pollinated stigma cells. This 'stigma reaction' was defined by Kato and Watanabe (1957)as the change taking

place in the stigma cells following the attachment of pollen grains to them. Self incompatability, the inability of a plant with functional gametes to produce selfed seeds, occurs widely (Brewbaker and Majumder 1959), and is probably the most important outbreeding mechanism in many flowering plants (Lundqvist 1959). Incompatability results from the inhibition of pollen tube growth, occurring either on the stigma or in the pistillar tissue.

In the Gramineae the inhibition of self-pollen is confined to the tips of the stigmatic hairs (Brewbaker and Majumder 1959). Gregor (1928) noted that in self pollinated ryegrass plants many pollen grains germinated on the stigma. However, growth was retarded after pollen tubes had travelled a short distance in the stigma branches and no tubes were observed to enter the central column. Self sterility in this species occurs because the male gametes fail to reach the ovules.

Characteristics of the pollen grains of grasses, including ryegrass and prairie grass have been described by Wodehouse (1965).

On the stigma, grass pollen shows about 60-80% germination under natural as well as artificial pollination conditions, the percentage of germination increasing with greater pollen and stigma maturity. (Watanabe 1961).

Several other workers have given detailed descriptions of the pollination and fertilisation processes in specific members of the Gramineae. (Pope 1946 in barley; Brown and Shands 1957 in oats; and Hoshikawa 1959, 1960 in wheat). These descriptions closely follow the general sequence outlined by James and Clapham (1935).

Brewbaker and Majumder (1959) observed that pollen grains have a mutually stimulating effect on pollen germination, so that at low concentrations, their germination is low. Thus Anslow (1963) suggested that the possibility of an ovule being fertilised was likely to be reduced with fewer pollen grains falling on the stigma.

In his studies on pollen tube growth and fertilisation in barley, Pope (1946) suggested that, since no evidence was seen of digestion of cells to

allow passage of the pollen tube, it was probable that pectinase, secreted by the pollen tube, dissolved the middle lamellae, thereby permitting the passage of the tube between the cells of the conducting tissue. However, more recent histological studies of pollen and pollen tubes by Poddubnaya-Arnoldi et al (1959) have shown that the most active area of the pollen tube was in the tip, where high peroxidase activity and intensive phosphatase secretion provide the pollen tube with nutritive substances and soften surrounding tissues by dissolving them, facilitating the entry of the pollen tube into the ovary.

Pollen Germination on Artificial Media

The pollen of many types of plants has been tested for viability under a wide range of cultural conditions. Emerging from a complex assortment of findings is one general conclusion - that certain pollen species are exceedingly difficult to germinate in vitro. Pollen of members of the Gramineae are notorious in this respect.

In most instances, poor pollen tube development indicated that, although the culture media used by different workers were adequate for pollen germination, they lacked some of the ingredients present in the style. Eshel (1968) suggested there were possibly several constituents released by metabolic processes when the pollen penetrated the stigmatic surface and grew between the stylar cells.

Anthony and Harlan (1920) obtained inconsistent results in attempts to germinate barley pollen artificially. The outstanding feature of their experiments was the extreme delicacy of the water adjustment of the grain. Exposed to dry air for as little as 2 minutes, the walls of the grain collapsed through water loss. If grains were placed in a saturated atmosphere they imbibed water so fast that they also burst. Bair and Loomis (1941) suggested that apparently a near isotonic relationship between the nutrient medium and the cytoplasm was required to prevent bursting.

At best however, a germination percentage obtained by placing pollen on artificial media can be expected to give only an indication that at least some pollen is viable, and is not a reliable pre-pollination estimate of its potency

in the field (King 1955).

Methods for Detecting Pollen Tube Growth

Many investigators have attempted to detect the presence of pollen tubes in the styles of flowering plants. Chandler (1931) devised a technique in which acetocarmine, aniline blue and magenta were used to stain pollen tubes of small flowers, and Nebel (1931) similarly applied a lacmoid-martius yellow stain on a range of species. Wilson and Brown (1957) used lacmoid to trace the pattern of pollen tube growth in the stylar tissue of prairie grass, oats and cocksfoot, and Adams (1953) employed potassium permanganate, oxalic acid, and lactophenol in work on maize. Studies on pollen tube development in barley using potassium iodide - iodine solution have been carried out by Pope (1946). Bolton and Fryer (1937) microtome-sectioned lucerne styles. A lactophenol-cotton blue stain was used by Gregor (1928) to detect pollen tubes in the stylar tissue of a range of species, including four grasses, and Dionne and Spicer (1958) used safranin and aniline blue to stain pollen tubes in dissected styles and stigmas. Datta and Naug (1967) also used Gregor's (1928) technique with success in studies of pollen tube development in ryegrass.

Despite all of these methods, which have been used with apparent success, the Biological Stain Commission (1962) recommended the techniques described by Chandler (1931) and Nebel (1931) as the most suitable and effective methods for detecting the presence of pollen tubes in stylar tissue of a wide range of plants.

Seed Set

The term 'seed-set' has been widely used in discussions on seed production. In many cases the precise meaning of the term is unclear.

Many workers have used the number of fully developed seeds on a seedhead as the criterion for measuring 'seed set' (Stoddart 1959, Anslow 1963, 1964, Kahre 1964) while others seem to equate this process with successful fertilisation, (Anthony and Harlan 1920, Gregor 1928, Beddows 1931, Jones and Brown 1951, Crocker and Barton 1953, Griffiths and Lewis 1967) or seed

development (Jenkin 1931, Knowles 1943, Smith 1944, Butler 1948, Barnard 1955b, Rytova 1968, Campbell, McBean and Green 1969, Campbell and Ferguson 1969).

'Seed-set' as shown by early embryogenesis appears to be simply an increase in the number of cells in the ovary; 'set' being indicated by the presence of cell division following successful fertilisation. Unless this cell division occurs the ovules eventually shrivel and die, even though pollination has taken place.

MATERIALS AND METHODS

In the present study difficulty was experienced in the detection of the path of pollen tube development within the stigmatic hairs and stylar tissue. Various methods of mounting and staining stigmas were tried. Unfortunately a suitable method was only obtained late in the investigation. The technique finally adopted was as described by Chandler (1931), using aceto-carmine, aniline blue and magenta followed by destaining in absolute alcohol. The cytoplasm of the pollen tubes stained blue and the surrounding tissue pink to red. Thin hand-cut sections were found to be suitable for the purpose as they allowed relatively long portions of pollen tubes to be detected.

RESULTS AND DISCUSSION

Attempts to germinate pollen artificially in sucrose solutions or on the surface of agar media containing sucrose were unsuccessful. The addition of boron as advocated by O'Kelley (1959) also proved ineffective. However, on the basis of reaction of pollen grains in 1% tetrazolium chloride solution both ryegrass and prairie grass were observed to produce a high percentage of viable pollen. Almost invariably at least 80% of the grains in each species showed intense staining when placed in tetrazolium solution for 30 minutes. A small percentage of grains were either devoid of contents or stained only slightly. These were considered to be non-viable. These findings infer that low viable pollen potential is probably not an important factor influencing pollination effectiveness.

Grains adhering to the stigmatic hairs soon germinate in the sugary solution secreted by the papillae of a mature stigma. (James and Clapham 1935),

producing a single pollen tube through the germ pore. The tube nucleus moved to the tip of the tube which passed between the stigmatic papillae. A diagrammatic representation of pollination and the path of pollen tube development in ryegrass is shown in Figure 29.

The factor which causes pollen tubes to grow down the style towards the ovule, thus bringing about fertilisation in a wide range of plants has been shown to be an increasing calcium gradient (Mascarenhas and Machlis (1964) and Van Overbeek (1966)).

The pollen tubes did not travel in one plane within the stylar tissue. Frequently only short lengths of pollen tubes were observed in sectioned material. The pollen tube continued growth down the outer wall of the ovary and eventually entered the micropyle.

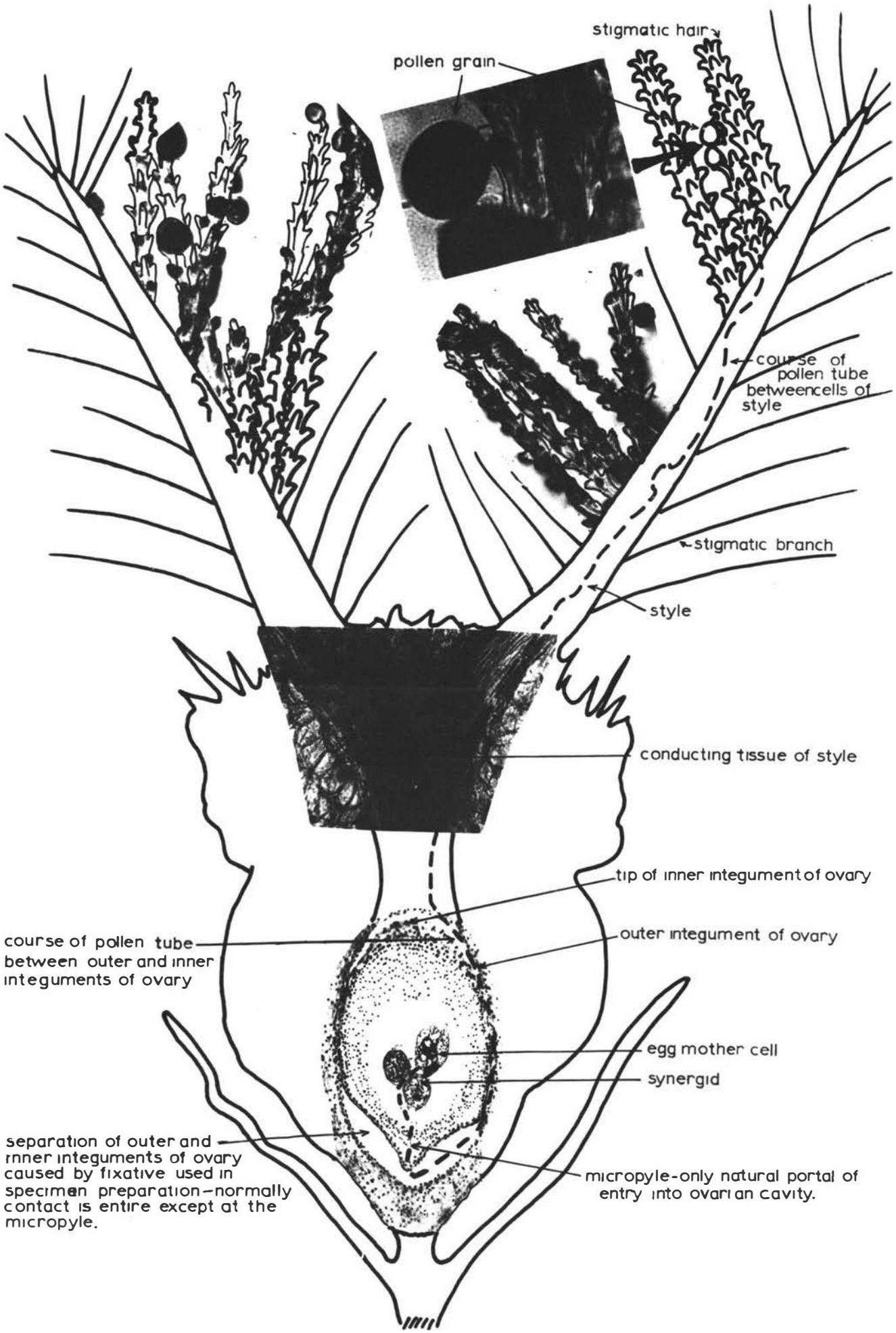
Prior to fertilisation the fully developed ovule was in an apparently resting state, there being no evidence of cell division in any of its parts (Plate 7).

Following micropyle entry the generative nucleus of the pollen tube divided into two male nuclei. When the tube reached the embryo sac its tip perforated the wall of the sac, pushed between the two synergidae and opened to liberate the male nuclei (Plate 8).

The fate of the tube nucleus was not determined, although it appeared to remain intact until or slightly after the point of male nucleus discharge. James and Clapham (1935) have stated that in the process of fertilisation one male nucleus from the pollen tube fused with the egg nucleus while the other fused with the central nuclei. The first fusion, of male nucleus and ovum, and the further development of the fertilised egg gave rise to the embryo. The second fusion, of male nucleus and central nuclei underwent rapid cell division, and eventually developed into the endosperm.

Unless this process occurred the ovule eventually shrivelled and died, even though pollination had taken place (James and Clapham 1935). Thus although pollination was an essential preliminary, it was effective fertilisation which was the essential process in seed production. Once cell division of the egg

FIGURE 29



DIAGRAMMATIC REPRESENTATION OF POLLINATION AND THE PATH OF POLLEN TUBE DEVELOPMENT IN PERENNIAL RYEGRASS.

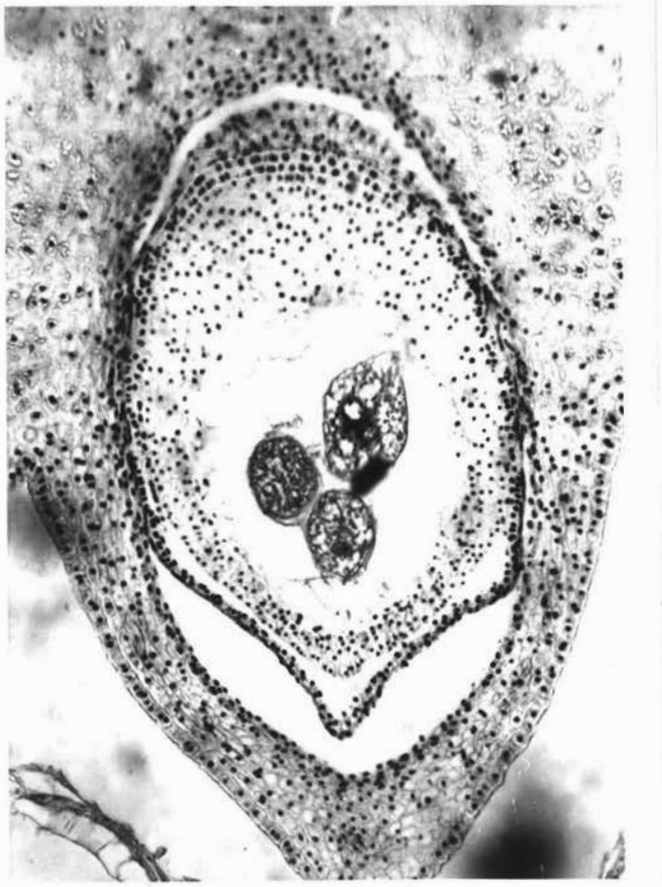


Plate 7: Ovary prior to fertilisation - perennial ryegrass

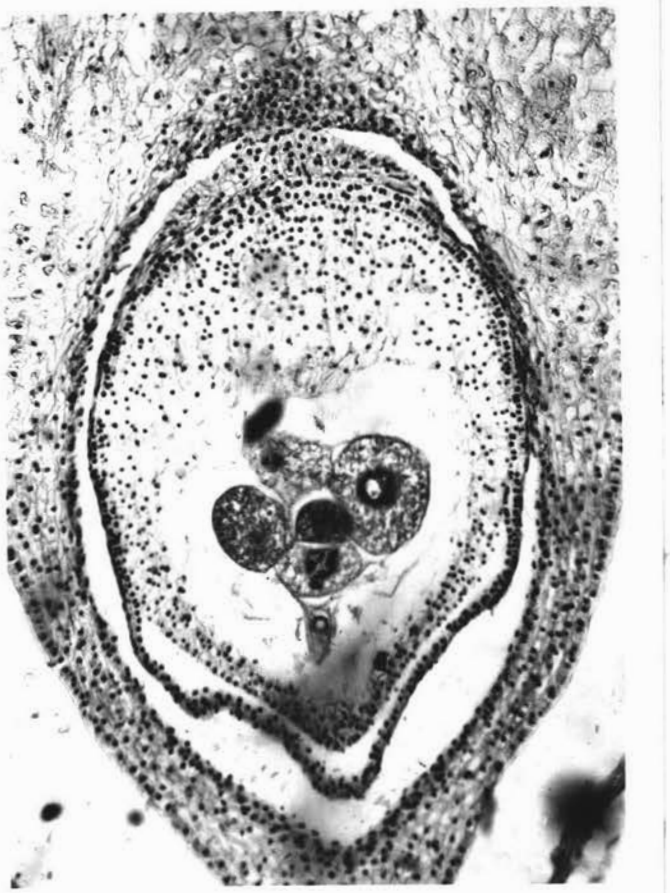


Plate 8: Pollen tube tip pushing between the two synergidae immediately prior to discharge of male nuclei - perennial ryegrass

all x120

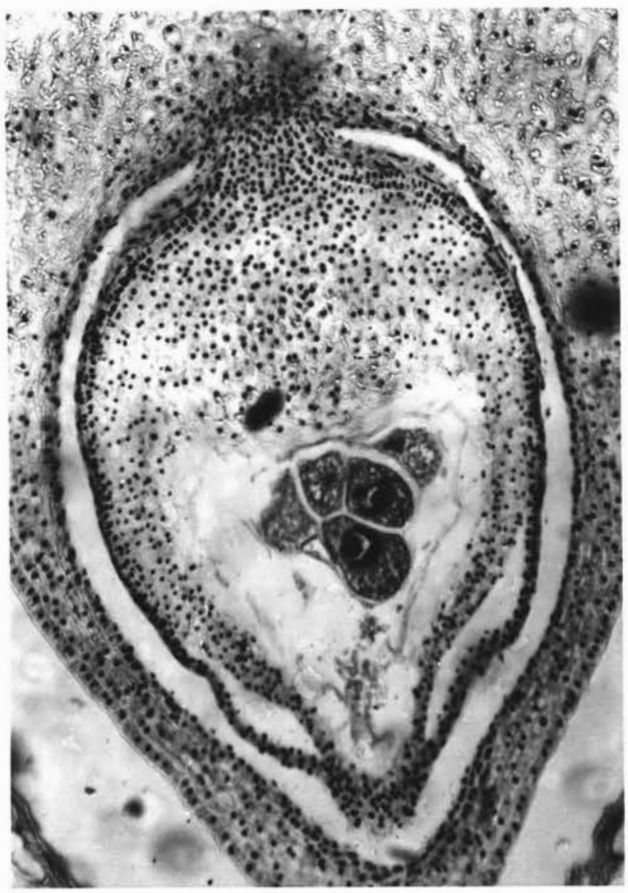


Plate 9: First division of egg mother cell - perennial ryegrass

apparatus had been observed by microtome sectioning a seed was considered to have 'set'(Plate 9). In both species studied this stage was observed to occur within 4 days after anthesis. Seed-set determinations were therefore made at this time interval following anthesis.

Immediately after fertilisation the fusion nuclei divided repeatedly. James and Clapham (1935) state that generally the fertilised egg divides in a characteristic way, forming a chain of cells of which the one at the micropylar end becomes enlarged. This cell and all the others except the one at the far end constitute the suspensor. The embryo is formed principally from the end cell remote from the micropyle. In the present study however despite the large number of microtome sections cut, no evidence of suspensor formation was observed.

If no suspensor is formed this could be considered to be an evolutionary adaptation allowing rapid seed development. This is particularly significant since both ryegrass and prairie grass have been previously shown to develop viable seed as little as 7 days and 4 days after anthesis respectively (Page 100). The elimination of a suspensor stage could allow cell division to occur rapidly and would eliminate one stage in the process of seed development following fertilisation. This would also reduce the number of organisational stages at which failure of development could occur.

A necessary condition for the development of the seed is that fertilisation of the egg within the ovule occurs. A histological study of the ovary during the period immediately following completion of pollen tube growth permitted a measurement of the frequency with which fertilisation occurred. Failure of fertilisation could thus be distinguished from subsequent failure to develop seed.

Previous work on a range of plant species has shown that temperature exerts a strong influence on the rate of germ tube growth following pollen germination (Smith and Cochran (1935) in tomatoes, Sexsmith and Fryer (1943a, 1943b) in lucerne, and Pope (1946) and Brown and Shands (1957) in barley. The results in Table 21 show that the time interval from pollination to seed

'set' in ryegrass and prairie grass is also influenced by temperature.

TABLE 21 Mean Time Intervals Required for Completion of Various Stages of Pollination, Fertilisation and Seed 'Set'.

Stage	Ryegrass		Prairie Grass	
	Incubation temperature and time (hours)		Incubation temperature and time (hours)	
	20°C	30°C	20°C	30°C
Pollen germination after pollination	0.32 (19 mins)	0.2 (12 mins)	0.13 (8 mins)	0.12 (7 mins)
Pollen tube growth in stigma branches	0.7	0.6	0.5	0.5
Pollen tube in central column	1.3	1.2	1.3	0.9
Pollen tube reached ovary	4.6	3.7	3.4	3.0
Tube entry through micropyle	7.9	6.8	5.4	4.7
First division of fertilised egg (seed 'set')	Approx. 74	Approx. 68	Approx. 27	Approx. 22

The major difference between the species is in the time required for the first division of the fertilised egg - approximately 24 hours for prairie grass versus 72 hours for ryegrass. This infers a much shorter 'rest' period prior to zygote division in the former species. It is possible that the length of this 'rest' period may have a bearing on the subsequent ability or failure of seed development. In prairie grass ovule abortion was not common. In ryegrass, however, it is possible that the 60-65 hour delay following tube entry through the micropyle before zygote division may have influenced the number of fertilised ovules eventually developing into seeds.

Despite the large number of sections cut, no evidence of the presence of either central or polar nuclei was observed. Apparently if these are present they disintegrate or disappear some time prior to fertilisation. Coincident with fertilisation, active cell division occurred. Fertilised ovules could be

distinguished from those that had not been fertilised by the increased size of the ovary 96 hours after pollination. If effective fertilisation did not occur there was no further ovule development, the embryo sac collapsed and eventually the entire ovule. In this case only a vestige of the ovary remained at a later date (Plate 10).

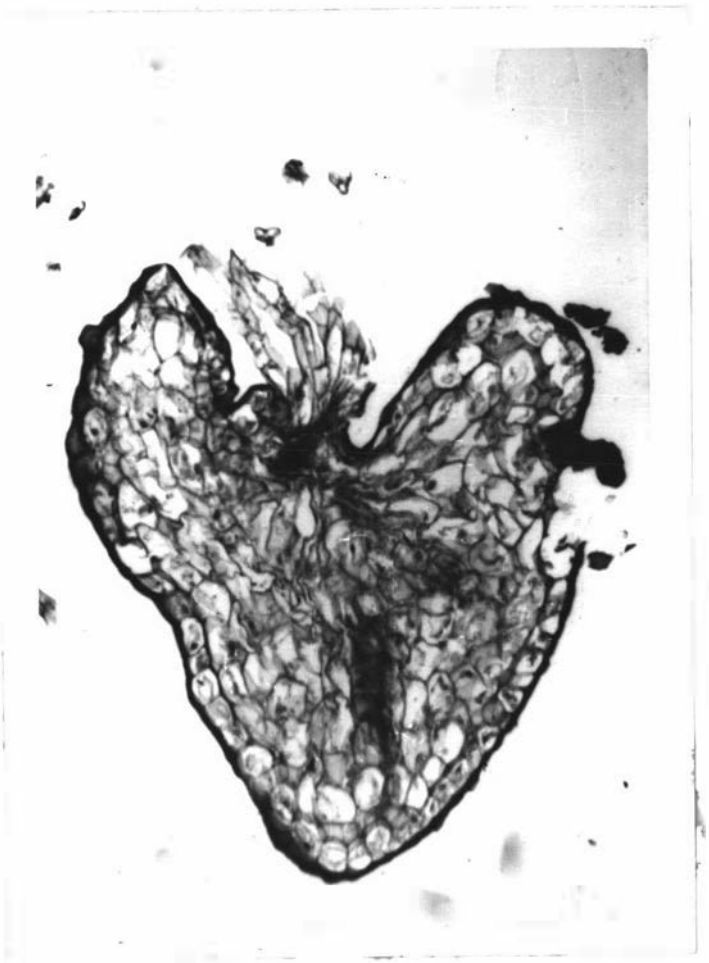


Plate 10 Microtome Section of Ryegrass Seed 7 Days After Pollination Showing Ovule Collapse Following Ineffective Fertilisation x36

Within 72 hours after pollination, pollen tubes had degenerated and could no longer be found within the ovary. At this point, the fertilisation process was considered to have ended. For this reason a valid estimate of the frequency with which the process of 'seed set' occurred (as measured by the frequency of effective fertilisation) could be made 4 days after anthesis.

At a point 96 hours after pollination the average number of cells in the ovary of prairie grass was about 50, (Plate 11) and in ryegrass approximately 10.

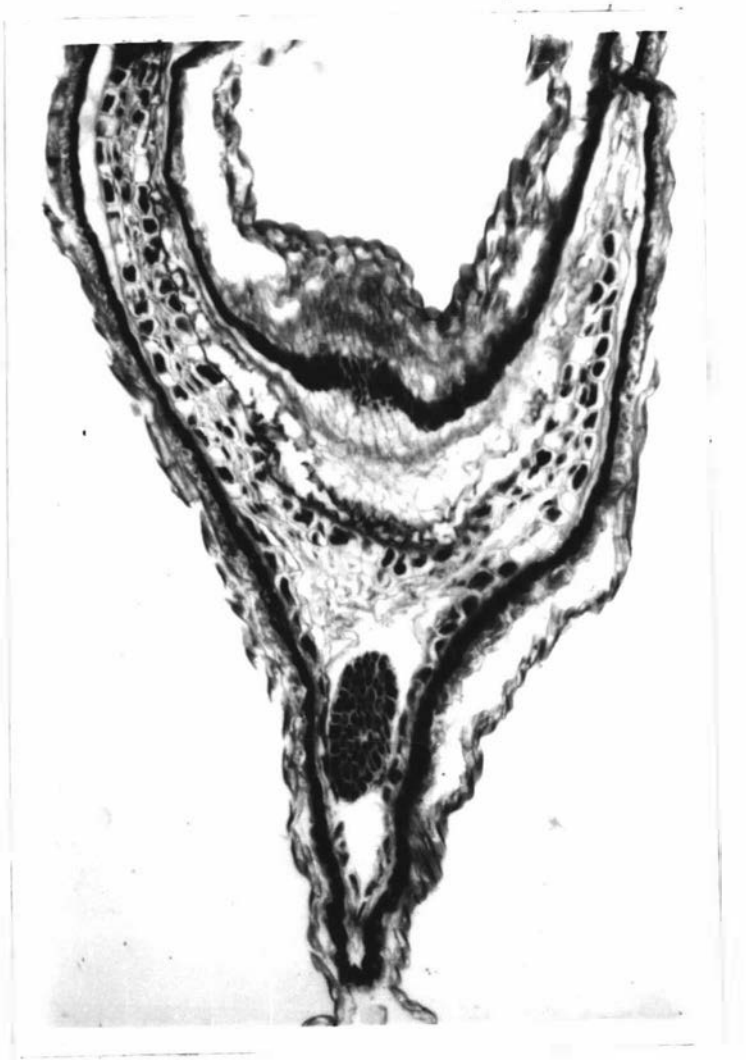


Plate 11 Microtome Section of Developing Prairie Grass Seed Four Days after Pollination x45

One of the most important aspects was that not all ovules which were fertilised continued development into seeds. In a number of cases ovule collapse occurred in ovaries in which cell division had commenced. Similar findings have been recorded by Cooper and Brink (1940) in lucerne (Medicago sativa L).

The mean percentage of florets setting seed in the present study was 38 for ryegrass and 79 for prairie grass. The former figure is much lower than the 62% quoted by Griffiths and Lewis (1967) in studies on S24 ryegrass

and the 92.9% quoted by Jenkin (1931) on a range of ryegrass plants. The figure for seed set in prairie grass compares favourably with the mean value of about 83% of seeds developed in this species given by Beddows (1931) but is less than the 97% quoted by Smith (1944). It should be noted, however, that in Smith's experiments the plants studied were considered to be highly or completely self-fertile.

The number of seeds formed was less in many cases than might be expected. Even in a cleistogamous species such as prairie grass where absolute fertility might be anticipated, a varying number of florets remain unfertilised.

SEED DEVELOPMENT

INTRODUCTION

The development of the embryo does not continue indefinitely. Cell division gradually decreases in frequency and ultimately ceases. Concurrent with this cessation of cell division, a progressive loss of water takes place and the outer coat hardens. At completion of this process the seed is ripe. At this stage the endosperm cells contain starch grains and protein. The moisture content of a ripe seed is low and the food reserves consist chiefly of insoluble substances, little sugar or amino acid being detectable. (Crocker and Barton 1953, Stoddart 1964a, 1964b, 1964c, 1965, 1966, and Ojima and Isawa 1968). At this stage the endosperm has become solid and granular in appearance.

The object of this aspect of the study was to determine whether the number of seeds present at full development was determined solely by the number of seeds effectively fertilised, or whether collapse or abortion of seeds occurred during development.

LITERATURE REVIEW

Knowles and Baenziger (1962) suggest that, while a proportion of the infertility in bromegrass (Bromus inermis) and wheatgrass (Agropyron spp) is genetic in origin, the environment influences the proportion of florets which set seed. Similarly Johnston (1960) has demonstrated up to 10% morphological sterility in cocksfoot florets. Anslow (1964) has shown that the position of a floret on a ryegrass head influences not only its chance of developing a large seed, but also affects its chance of developing a seed at all. No information seems to be available on these relationships in multi-branched panicles (Ryle 1965b).

Coincidental with fertilisation, active nuclear and cell division is stimulated, causing a considerable increase in the size of the ovule in a short period of time. In lucerne, Cooper and Brink (1940), observed that fertilised ovules could be distinguished from those which had not been fertilised by increases in ovule size, as little as 48 hours after pollination.

They also noted that of the ovules which became fertile, 34.4% containing inbred embryos and endosperms collapsed within 6 days of pollination, compared with only 7.1% containing hybrid embryos and endosperms.

While they supported the contention that wheat was most susceptible to temperature stress at anthesis, Livingston and Swinbank (1950) also recorded injury to seeds in which the fertilised embryo had begun to develop. They reported a significant reduction in average grain weight produced on wheat plants frozen very soon after fertilisation. Similar results have recorded in wheat plants heat stressed on consecutive days from fertilisation through to seed maturity (Paquet 1968).

Butler (1948) found that wheat grains in the milky stage of development were more susceptible to frost damage than at a later stage of development, although apparently some germination injury could occur when an appreciable amount of seed moisture was present.

Atlas barley and White Wonder Millet were heat-stressed at stages of maturation during the 5 weeks following heading by Laude (1967). A single exposure to a maximum temperature of 49 or 54°C was used, and resulted in reduced germination percentage in both species.

In studies on the influence of temperature on the development of the endosperm in wheat grains Hoshikawa (1960) observed that division of the endosperm cells (i.e. increase in cell number) was independent of temperature. However, at high temperatures (30°C constant) the rate of cell growth was retarded, cells being smaller and fewer in number than those formed in the endosperm of grains held at 20°C. Temperature also influenced seed maturation rate, high temperatures (30°C) shortening the time of ripening of the seed. Seeds ripened at 30°C were also thin and light.

Olugbemi's (1968) study on the effect of temperature stress on wheat plants at different stages of development, suggested that complete floret sterility on a head was rarely a feature of temperature injury. He indicated that each floret reacted independently to temperature stress, that florets on the same ear were rarely all susceptible to injury at the same time, and that

the period for which an individual floret was susceptible to temperature injury was rather short. Under low temperature conditions where frost occurred, damage to plants was not due to the formation of frost in itself, but to the effect of low temperatures on the water in plant cells. Hewett (1968) showed that water present between the cells froze first with ice formation, more water was drawn through the cell walls, the structure of cell proteins was disrupted, and the cell died. He stated that, in general, the formation of ice in plant tissue for more than half an hour resulted in cell death.

MATERIALS AND METHODS

The development of seed of both ryegrass and prairie grass was followed by sequential harvesting from 4 days to 30 days after anthesis as described previously (Page 145).

RESULTS AND DISCUSSION

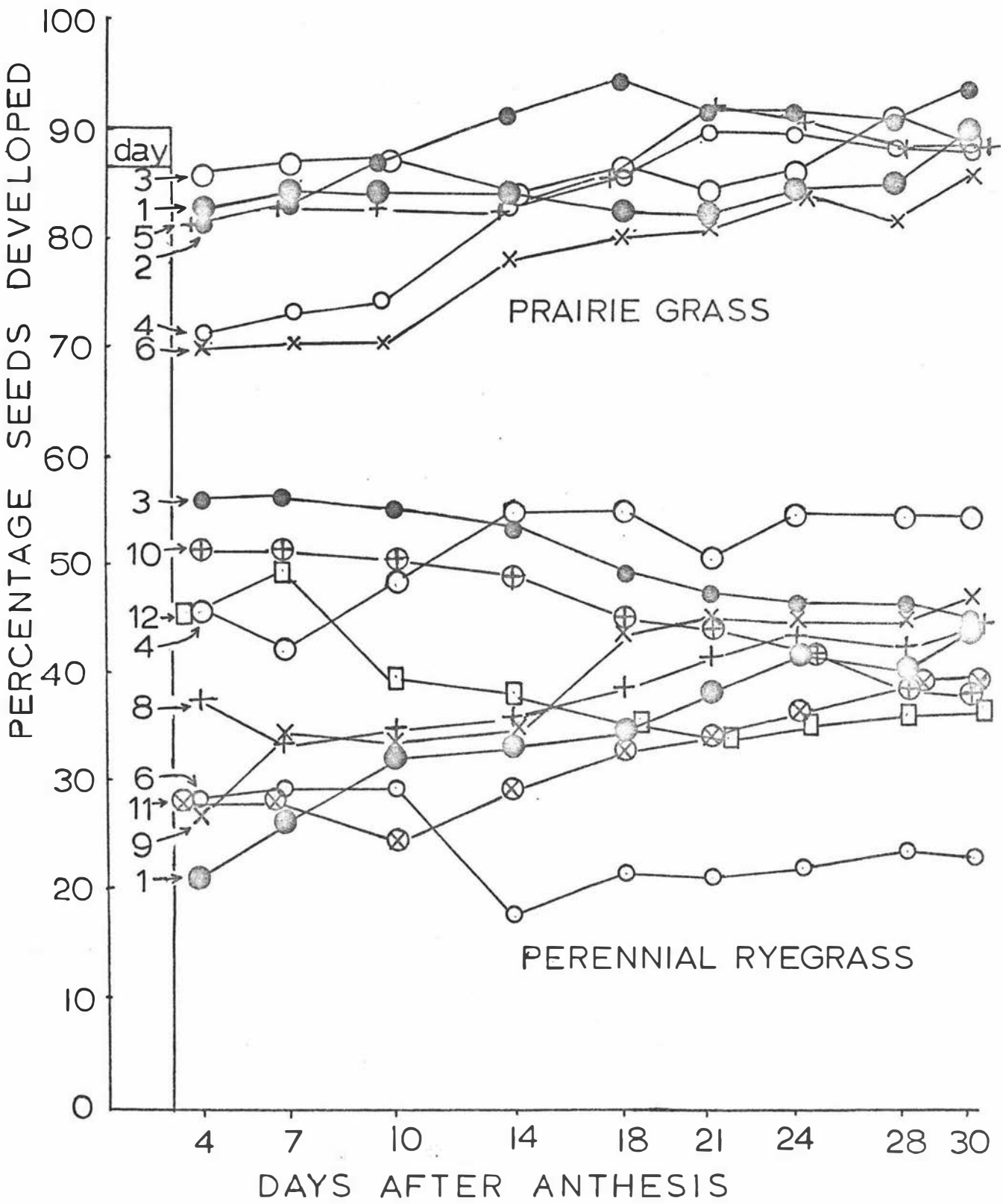
The results of the percentage of seeds that developed from florets open on different days and harvested at intervals up to 30 days after anthesis are presented in Appendix 30 with mean results shown graphically in Figure 30.

These results show that in ryegrass in particular, considerable increase or decrease in the number of seeds present 30 days after anthesis occurred when compared with the original percentage of seeds 'set' 4 days after anthesis. There appeared to be wide variations in the direction and extent of such changes, particularly in ryegrass, which did not consistently relate to either conditions of daily anthesis or to specific treatments.

Considering the percentage of seeds present on different sampling dates in relation to individual days of anthesis, wide variation occurred.

In ryegrass, initial seed set 4 days after anthesis ranged from 21% for florets open on day 1 up to 57% for florets open on day 3. Final seed number present 30 days after anthesis ranged from 23% (for florets undergoing anthesis on day 6) to 54% (for florets open on day 4). Wide differences between the percentage of seeds present 4 days and 30 days after anthesis on a particular day occurred. An increase in the percentage of seeds present occurred with progressively later sampling dates for florets open on days 1,4,8,9 and 11.

FIGURE 30 PERCENTAGE OF SEEDS FORMED AT DIFFERENT INTERVALS AFTER ANTHESIS.



Conversely, a fall in the percentage of seeds present occurred in florets open on days 3,6,10 and 12. Nil or insufficient anthesis occurred on days 2,5 and 7 for comparisons to be made.

In prairie grass mean seed 'set' on day 4 ranged from 70% for florets open on day 6 to 86% for florets open on day 3. Final seed number 30 days after anthesis ranged from 86% (day 6) to 94% (day 2). An increase in the percentage of seeds developed at successively later sampling dates from anthesis was evident. The maximum increase occurred for seeds developed from florets open on days 4 and 6 (16.4% and 16.1% respectively). The mean increase in seed number over all 6 days determined by comparing the results 4 and 30 days after anthesis, was 10.2%.

In the process of individual floret dissection for assessment of seed development, ovules were classified into three groups (A= apparently not fertilised, B= swollen, and C= developing) as described earlier (Page 145). The ovules classed in group B showed a bilobal swelling of the exterior of the ovule as shown in Plate 12(B). Ovules in this category were readily distinguished from those in the other two groups (Plate 12, A&C).

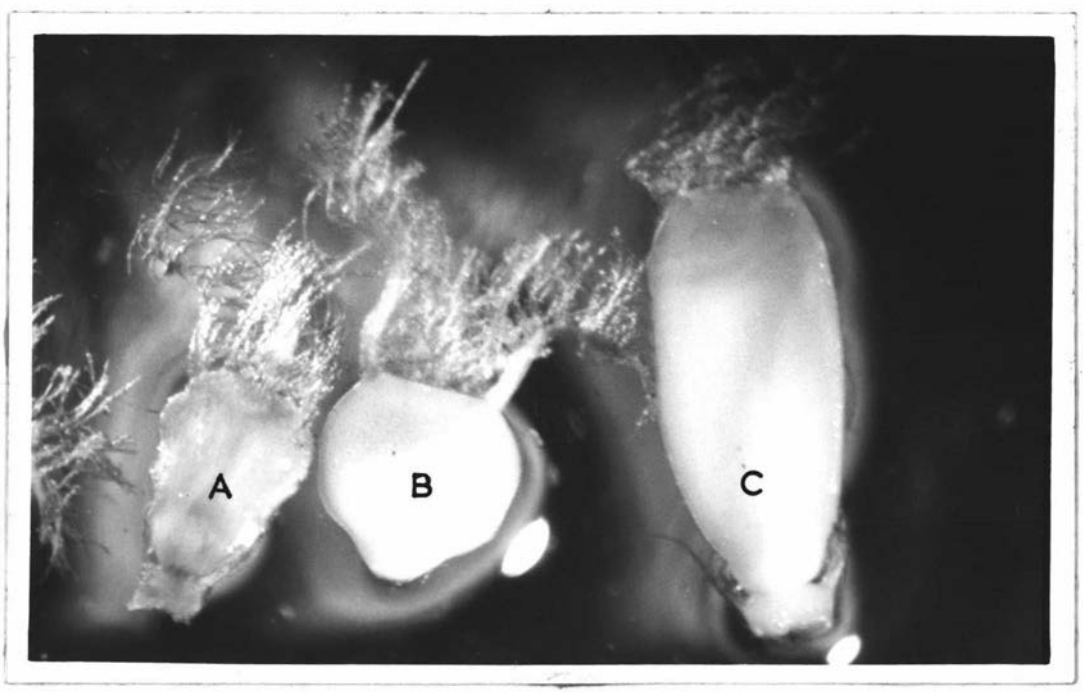


Plate 12: Ovule classification groups following floret dissection x17

Following microtome sectioning it was observed that ovules in group B, while apparently setting seed normally contained ovaries which were in the form of an inverted T initially (Plate 13). This was in contrast to those observed in groups A and C which were approximately spherical in shape.

Plate 13 Ovule showing inverted T ovary shape (group B). x 74

The frequency of ovules in this condition varied within and between treatments and was apparently not restricted to any particular part of individual seedheads. In some cases up to 50% of ovules examined were classed in this group(B). Generally these ovules remained apparently quiescent for varying periods up to 21 days after anthesis. In response to conditions which were not determined ovaries in this group eventually recommenced apparently normal development or collapsed. The fate of ovaries in this group was

responsible for the increase or decrease in the percentage of seeds found in samples taken at intervals from anthesis. This suggests that the number of ovaries effectively fertilised, while important in determining potential seed number, is not the only factor influencing the final number of seeds developed. The ability of some ovaries to apparently curtail normal development following seed set for a period up to 3 weeks after anthesis and then continue or terminate further development is of particular interest and would be worthy of more intensive study. The suggestion that such a situation could occur in grasses has been previously observed by Johnston (1960) in studies on cocksfoot (Dactylis glomerata L).

The collapse of ovules of a wide range of plants following fertilisation has been previously recorded by a number of workers. This phenomenon has been shown to occur in a range of stonefruits (Bradbury 1929, Harrold 1935); in peanuts (Arachis hypogea)by Reed (1924); and in lucerne (Medicago sativa) by Brink and Cooper (1936), Cooper, Brink and Albrecht (1937) Sayers and Murphy (1966). However, this phenomenon has apparently not been previously described in either ryegrass or prairie grass.

Cooper and Brink (1940) suggested that in lucerne the collapse of fertilised ovules may be a "manifestation of self-incompatibility per se or it may be an inbreeding effect". However, Sayers and Murphy (1966) subsequently showed that in lucerne, abortion was not necessarily an effect of inbreeding, since a high degree of abortion also occurred in plants following crossing. Neither the frequency of fertilisation nor the incidence of ovule abortion in lucerne was affected by the pollen parents used in such crosses. They therefore suggested that ovule abortion in lucerne was controlled by the genotype of the female parent. (Sayers and Murphy 1966).

The results of analysis of the percentage of seeds formed in each treatment are shown in Table 22.

In ryegrass a two degree frost (-2.2^{o}C) occurred during the first 4 days of seed development. This apparently influenced seed 'set', particularly in the control treatment. From 7 days after anthesis until the final sampling

TABLE 22 STATISTICAL ANALYSIS OF PERCENTAGE OF SEEDS FORMED AT VARYING TIMES FROM DATE OF ANTHESIS

RYEGRASS

TREATMENTS	Days after Anthesis 4	7	10	14	18
Shelter and Shade	35 AB P	36 A	39 A	38 A	38 A
Shelter and Cover	51 A P	46 A	41 A	42 A	45 A
Control	19 B P	24 A	26 A	28 A	31 A
Shade Only	39 AB P	42 A	41 A	43 A	44 A
Cover Only	39 AB P	41 A	38 A	34 A	31 A
Shelter Only	41 AB P	42 A	40 A	39 A	42 A
Shade and Cover	41 AB P	44 A	47 A	47 A	44 A
MN SG. Diff		25	23	24	25
C.V. %	65.9	58.7	54.0	58.4	57.9

TREATMENTS	Days after Anthesis 21	24	28	30	Mean
Shelter and Shade	40 A	37 A	39 A	38 A	33 A
Shelter and Cover	41 A	41 A	42 A	45 A	43 A
Control	32 A	37 A	39 A	39 A	31 A
Shade Only	45 A	48 A	49 A	49 A	44 A
Cover only	32 A	34 A	36 A	38 A	36 A
Shelter	44 A	47 A	47 A	48 A	43 A
Shade and Cover	43 A	45 A	45 A	45 A	45 A
MN SG. Diff.	25	26	27	28	21
C.V. %	57.3	57.1	59.2	58.8	47.2

PRAIRIE GRASS

TREATMENTS	Days after Anthesis 4	7	10	14	18
Shelter and Shade	69 B P	74 A	73 A	73 A	82 A
Shelter and Cover	76 AB P	80 A	77 A	80 A	85 A
Control	86 AB P	88 A	86 A	85 A	87 A
Shade Only	81 AB P	85 A	85 A	90 A	88 A
Cover Only	89 A P	89 A	90 A	88 A	86 A
Shelter Only	73 AB P	80 A	75 A	83 A	84 A
Shade and Cover	77 AB P	83 A	81 A	85 A	88 A
MN SG. Diff.		18	18	20	13
C.V. %	17.3	17.0	17.0	17.4	11.1

TREATMENTS	Days after Anthesis 21	24	28	30	Mean
Shelter and Shade	87 A	81 B P	76 B Q	81 C Q	78 B P
Shelter and Cover	87 A	87 AB P	87 AB PQ	84 C PQ	83 AB P
Control	92 A	93 A P	94 A P	94 A P	90 A P
Shade Only	85 A	89 AB P	85 AB PQ	92 AB P	87 AB P
Cover Only	85 A	88 AB P	91 A PQ	93 A P	89 A P
Shelter Only	84 A	84 AB P	85 AB PQ	85 BC PQ	82 AB P
Shade and Cover	85 A	92 A P	92 A PQ	92 AB P	87 AB P
MN SG. Diff.	10				
C.V. %	8.5	7.9	10.6	7.0	8.9

date 30 days after anthesis however no further treatment effect was detected.

In prairie grass overall mean figures show that the combination of shelter and shade in treatment 1 had a deleterious effect on the percentage of seeds developed compared with the covered treatment. This was attributed to the lowered initial seed 'set' value obtained 4 days after anthesis in treatment 1. During the 20 days following seed 'set' assessments 4 days after anthesis, the prevailing treatments failed to cause significant variation in seed development. The sudden variation occurring 24 days after anthesis is difficult to explain. A two degree frost (-2.2°C) at this time was the only outstanding environmental feature. It seems unlikely however that at this late stage of development low temperature could have exerted such an effect. This was reinforced by the fact that no shrivelled or decayed seeds which were fully developed were observed 30 days after anthesis. The cause of the variation in results is unexplained.

The relative increase in seed size in prairie grass at 4,7,14 and 21 days after anthesis is shown in photographs of sectioned material (Plates 14, 15, 16 and 17).

Seeds from each sampling date were air-dried and tested for germination. The results, presented in Appendix 31, show that full seed viability was attained in ryegrass approximately 24 days after anthesis, and in prairie grass approximately 18 days after anthesis. The first viable seeds were obtained in prairie grass as little as 4 days after anthesis and in ryegrass after a further 3-6 days. This difference in the onset of viability is similar to that found in the field trial results presented earlier (Page 101). In the previous section (Page 175) it was shown that there was a much shorter 'rest' period prior to the division of the zygote in the ovary of prairie grass than ryegrass (approximately 24 hours versus approximately 72 hours respectively). This was apparently one of the factors influencing the length of time required before viable seeds were formed.

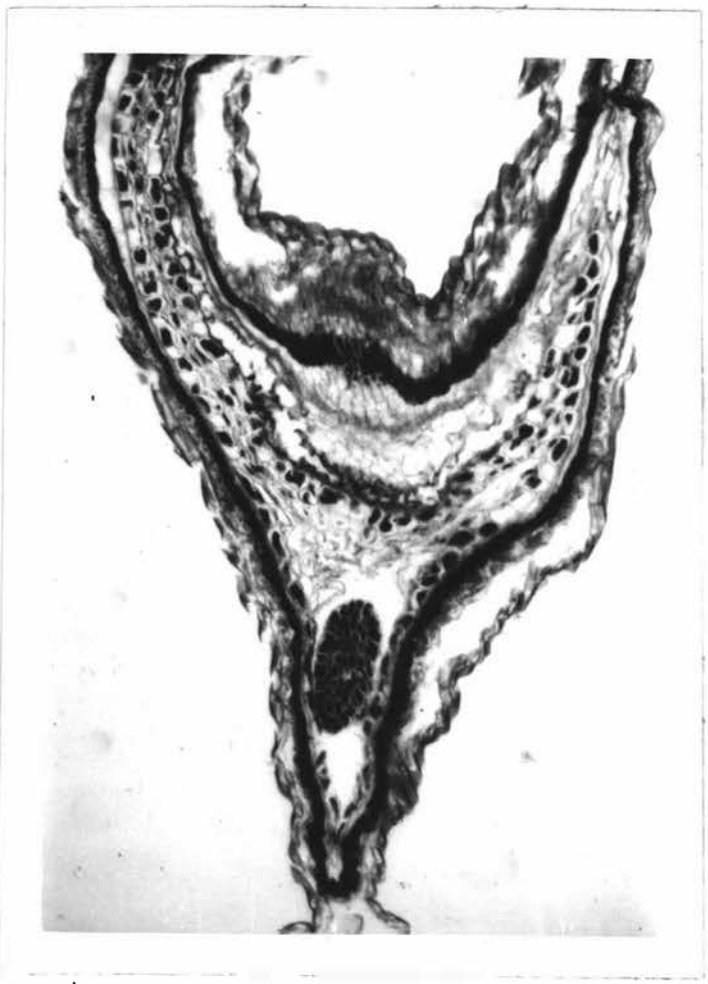


Plate 14: Developing prairie grass seed
4 days after pollination

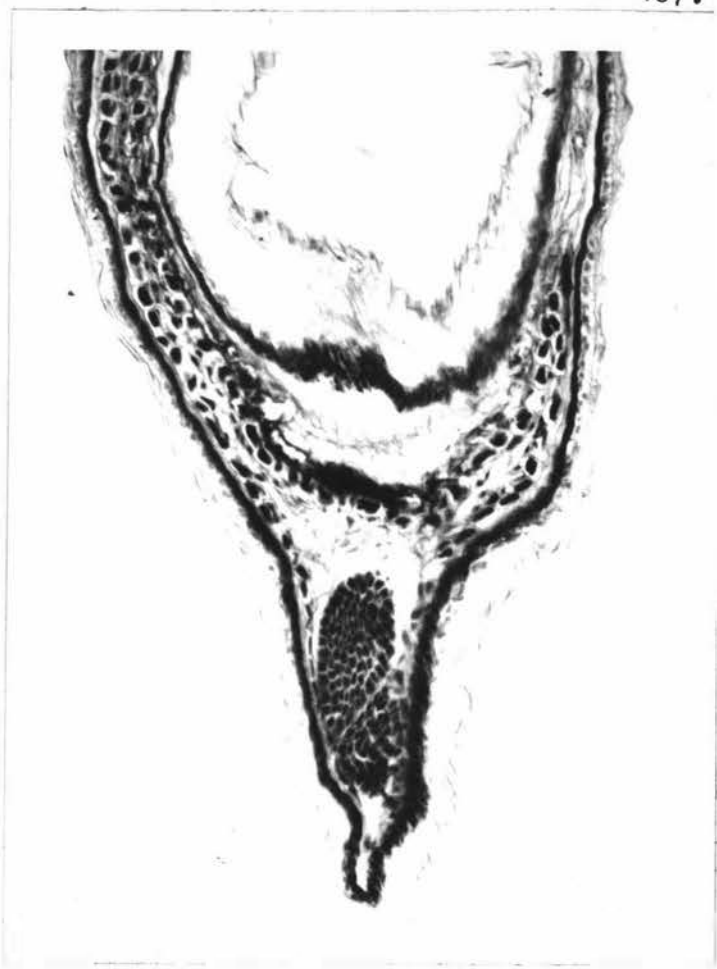


Plate 15: Developing prairie grass seed
7 days after pollination

all x45

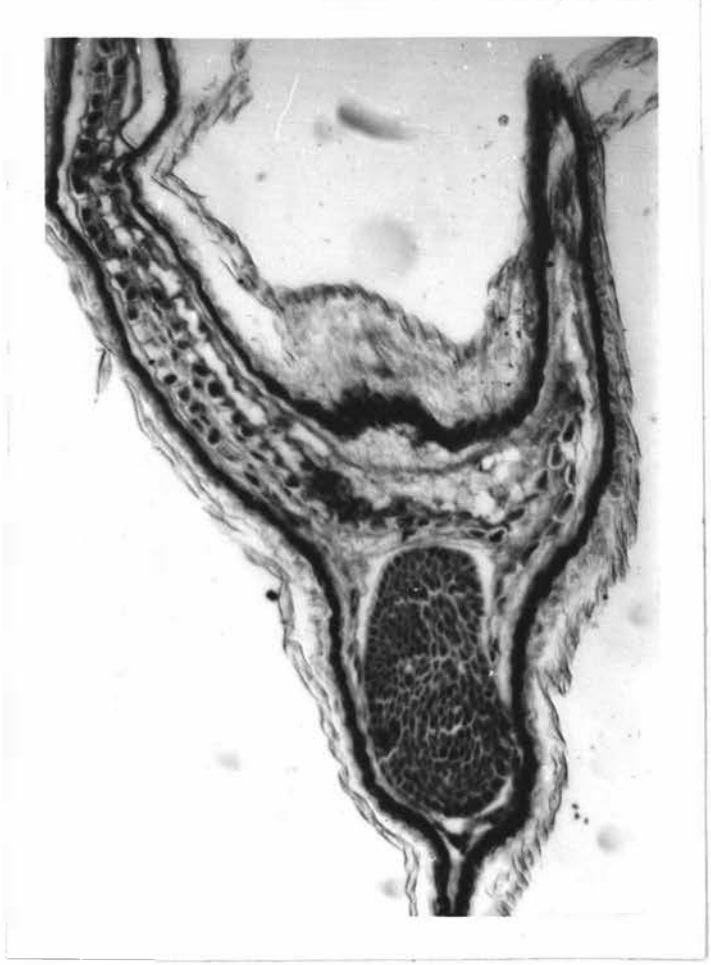


Plate 16: Developing prairie grass seed
14 days after pollination

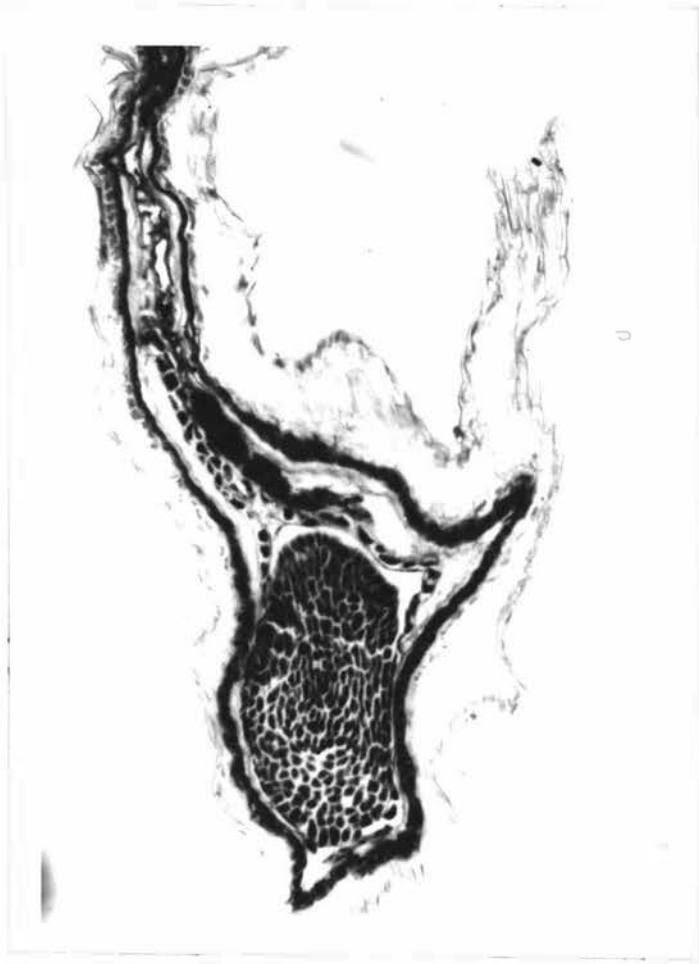


Plate 17: Developing prairie grass seed
21 days after pollination.

CONCLUSION

Studies on the effect of selected environmental variables on anthesis showed that the environment played a significant part in controlling daily anthesis pattern in both ryegrass and prairie grass.

Little effect due to shelter, shade and covered treatment combinations was observed. In ryegrass however, plants in sheltered treatments generally commenced daily anthesis earlier than plants in treatments exposed to the wind. Shading delayed the time of onset of anthesis in prairie grass and reduced the percentage of florets open at the peak of daily flowering.

Within each species the onset of anthesis occurred at approximately the same time each day. Although the time of peak anthesis varied between days this variation was not significant, the percentage of florets open at the point of peak anthesis being reasonably constant. The length of time individual florets remained open was similar, irrespective of whether subsequent seed set occurred or not. Duration of daily anthesis was approximately 6 hours in ryegrass and 11 hours in prairie grass.

Anther dehiscence occurred 3-4 minutes after exsertion in both species under warm, dry conditions. Under conditions of low temperature and high humidity dehiscence was delayed up to 85-95 minutes after exsertion.

Temperature, and to a lesser extent relative humidity appeared to exert the major influence on daily anthesis pattern in both species. As well as a day temperature effect, a strong correlation was evident between daily flowering pattern and temperature on one or both of the two nights prior to the day of anthesis.

Day temperatures below approximately $14^{o}C$ generally increased the duration and in some cases completely inhibited anthesis. On most days anthesis did not commence until air temperatures had reached approximately $18^{o}C$.

In both species high night temperatures (over approximately $10^{o}C$) caused earlier onset, contracted duration, and earlier peak anthesis and also reduced the length of time individual florets remained open. Low night temperatures

(below approximately 10°C) decreased flowering intensity and also reduced the number of florets open at peak anthesis.

Low humidity on the day of anthesis generally delayed the time of peak anthesis in prairie grass and caused earlier onset of anthesis as well as reducing the length of time individual florets remained open in ryegrass.

Light intensity alone appeared to exert only a minor effect on daily anthesis pattern. Low light intensity delayed the onset of anthesis in ryegrass. Shading appeared to delay the time of peak anthesis and to reduce the percentage of florets open at peak anthesis in prairie grass.

Some air movement appeared to be necessary for anthesis (3-5 m.p.h.). Reduction in anthesis occurred at wind speeds over approximately 10 m.p.h.

Rainfall itself did not greatly affect anthesis once daily flowering had commenced. However, in ryegrass in particular, rain resulted in earlier peak anthesis and reduced the duration of daily anthesis. Anthesis was inhibited during rain accompanied by low day temperatures.

A regression of means of all environmental variables (temperature, humidity, light, wind speed and rainfall) together explained approximately 80% of the variation in daily anthesis pattern and duration. This suggests that the five environmental variables considered in this study, while accounting for a high percentage of the variation in daily anthesis, were not the only factors regulating daily anthesis in ryegrass and prairie grass.

Studies on the path of pollen tube development following germination showed that pollen tube growth from the stigmatic hair to the ovary occurred down the stylar conducting tissue, between the inner and outer integuments of the ovary and into the ovarian cavity through the micropyle. Following fertilisation of the egg mother-cell, cell division occurred. Once this division was observed fertilisation and seed 'set' were considered to have been successfully completed.

No evidence of suspensor formation was observed in either species. The time for completion of the various stages of pollination, fertilisation and seed 'set' in both species was temperature dependant, the entire process being

more rapid at 30°C than at 20°C. The major difference between species was the time required for the first division of the fertilised egg, being approximately 72 hours for ryegrass and 24 hours for prairie grass.

In ryegrass ovule abortion was more common than in prairie grass.

Microtome sections cut 4 days after anthesis, showed that the proportion of florets 'setting' seed was approximately 80% in prairie grass but only 40% in ryegrass.

Most investigations into the causes of failure of seeds to develop have been concerned with the factors influencing pollination. Often effective pollination and fertilisation are considered sufficient to guarantee seed formation. In the present study it was shown that in ryegrass and to a lesser extent in prairie grass ovule mortality could occur during seed development. Mortality occurred following seed 'set' and continued up to approximately 21 days after anthesis. This process was first evident in the arrested development of the embryo very soon after fertilisation and appeared to involve disruption of cell division, giving the ovary a misshapen appearance. At a later stage cell division and seed development often resumed apparently normally. Conversely in some cases cell disintegration occurred, until only a few of the cells of the embryo could be detected. In such cases the entire ovule collapsed.

Wide variation occurred in the percentage of ovules aborting. This effect apparently occurred irrespective of the variation in environmental conditions imposed by the majority of treatments used in the present study. In prairie grass however a significantly lower seed 'set' figure 4 days after anthesis was recorded in the shelter/shade combination treatment compared with the **covered** treatment.

Marked variation between the percentage of seeds 'set' 4 days and 30 days after anthesis on a particular day occurred.

The results suggest that while anthesis, pollination and seed 'set' are essential preliminaries to seed production, considerable alteration in the number of seeds present at harvest can occur during the process of seed development.

As Ryle (1965b) has pointed out, there still remains much to be done before the physiological processes underlying seed production are thoroughly understood. However, it seems that studies on the environmental control of anthesis, and the processes of pollination, fertilisation, seed 'set' and development have been somewhat neglected in ryegrass and prairie grass compared with studies on vegetative and inflorescence development. The formation of a large number of seedheads is not the only requirement for maximisation of seed yield. A high percentage of florets must be effectively fertilised and develop seed of maximum weight and germination capacity to realise the full yield potential of the crop.

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