SEED PRODUCTION STUDIES WITH WEEPING LOVEGRASS

ERAGROSTIS CURVULA (SCHRAD.) NEES

by

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DECLARATION

I hereby declare that the research work in this thesis is my own original work but that assistance was received for routine field work and for statistical analyses of the data.

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CHAPTER I

INTRODUCTION

In South Africa the present concept of grassland agriculture calls for greater use of cultivated or improved pasture. Areas established in cultivated pasture must be increased if the demand for greater production from agricultural lands is to be satisfied. The rate of increase of land planted in cultivated pasture is dependent almost entirely on the supply of seed.

In addition production from areas already established in cultivated pasture can be increased by changes in cultural and management practices and by increasing the quality of forage produced. Any increase in pasture quality is largely dependent on the quality of sown seed. Therefore the provision of good quality seed is a major factor promoting pasture production.

Weeping lovegrass, Eragrostis curvula (Schrad.) Nees, is an improved pasture grass which has become extremely important in South Africa, worthy of being grown on the best soil and managed as extensively and as efficiently as possible. Its most desirable quality of high potential forage production, particularly in semi-arid regions, in association with its ideal hay-making qualities especially in the more humid summer rainfall regions, has made it the most popular forage crop for hay production in South Africa. The species is also noted for its ability to commence growth earlier in spring than other improved subtropical herbage species. This attribute when combined with efficient management and correct fertilisation and stocking techniques, allows E. curvula to compare most favourably with other summer producing perennial grasses in a grazing proposition. Research in the United States (Dalrymple, 1969) has shown that weeping lovegrass can increase the carrying capacity and production of many livestock units and should

be included in most forage systems in its main region of use.

Seedling vigour, ease of establishment, competitiveness with weeds, lack of disease or pest problems and response to management are other desirable qualities which have created a continued interest in the species. An added attraction is that weeping lovegrass produces reasonable quantities of good quality seed under normal growing conditions.

To date seed production in this grass has received little attention in South Africa. When compared with other subtropical species E. curvula is a relatively good seed producer and this may account for the lack of research. In addition demand for seed over the past thirty years has been satisfied by the importation of seed, supplemented by a small quantity of locally produced seed so that an increase in local production has been considered unnecessary. However, in present-day agriculture seed supplies have become unreliable and not adequate to meet consumer demand either on the local market where greater areas are being sown to E. curvula (Rethman, 1973) or on the international market. This situation can be attributed to three important factors. Firstly, seed yields are now considered low. This is due almost entirely to the lack of firm crop recommendations available to seed producers. Secondly, seed for most of the land planted to E. curvula is produced from multipurpose stands which are usually grazed and utilised for hay production but may be managed and harvested for seed when prices are favourable. Consequently supplies to the consumer have become unreliable. And thirdly, the majority of seed is produced under dryland conditions so that yields are unpredictable and irregular from year to year because of variable climatic conditions.

Seed production must be improved by increasing and stabilising not only yields but also the area of stands grown for seed. Unfortunately the stability and growth of a weeping lovegrass seed production enter-

prise in South Africa, as elsewhere in the world, will never be truly feasible until consumers demand certified seed of improved strains.

Of these three factors influencing seed supply in South Africa the first is considered the most important and consequently demands the greatest attention. Therefore in 1972 a programme of research was initiated at the University of Natal, Pietermaritzburg, in association with the Department of Agricultural Technical Services to study seed production in E. curvula.

A study of the literature pertaining to research on reproductive growth and development in E. curvula has revealed that research into this field is exceedingly limited (Chapter II). A detailed knowledge of the physiological processes involved in seed production is essential in any agronomic study of herbage seed production for these processes are closely associated with the complex relationships of environmental factors, cultural conditions and genetic factors to crop yield. A high seed yield of any grass crop can be achieved only when a proper combination of environment, variety and agronomic practices is obtained. A knowledge of plant growth and development will help therefore to determine the optimum combination of these three factors and could suggest more precise and predictable methods of obtaining increased seed yields in a given environment.

Consequently a series of experiments were carried out under both glasshouse and field conditions to investigate not only tiller growth and development within the plant but also seed formation and maturity within the inflorescence. Although most physiological processes are studied best in single plants in a controlled environment, crop production occurs not only in a community in which plants may differ in many ways from single plants but also under a highly variable environment. With this in mind field trials were designed to study growth and development under various cultural conditions.

Emphasis was placed on the relationship of cultural conditions to

crop yield, particularly the effect of nitrogen nutrition, as environmental and genetic factors were not considered to be of greater priority in the seed producing areas of South Africa. Nitrogen fertilisation is used extensively throughout the world to promote growth and production of crop plants, and is one of the most important elements required by higher plants for growth (Viets, 1965).

In addition to the nitrogen effect the response of the seed crop to forage removal, either by mowing or controlled burning, was studied. This work was designed to examine the concept of the multipurpose weeping lovegrass stand to determine if both forage and seed production can be successfully integrated within the one system. A knowledge of the effects of nitrogen nutrition and forage removal should contribute greatly to improved management techniques resulting in increased yields of high quality seed.

CHAPTER II

REVIEW OF LITERATURE ON THE SPECIES *Eragrostis curvula*

1. DESCRIPTION

a) Taxonomy

One of the most widely distributed graminaceous genera in the world is the genus *Eragrostis*, composed of approximately 280 species (Streetman, 1970) which are commonly referred to as 'the lovegrasses'. The genus belongs to the tribe *Eragrosteae* (Chippendall, 1955) which is distinguished from other tribes of the Gramineae by possessing glumes that are shorter than the spikelet, and lemmas that may be awned or awnless. If an awn is present it is neither bent nor twisted. The inflorescence of the *Eragrosteae* may be a panicle or it may consist of two or more spikes or spike-like racemes. Vegetatively the ligule is usually a fringe or rim of hairs but in some cases may be a membrane usually fringed with hairs.

According to Chippendall (1955) the genus *Eragrostis* may be distinguished from other genera of *Eragrosteae* in that it possesses an awnless, but sometimes accuminate, entire lemma. The inflorescence is a panicle which can be lax and open or very dense and contracted (de Winter, 1955). Leaf blades are usually expanded or rolled and the ligule consists of a short fringe of hairs in most species (de Winter, 1955).

Eragrostis curvula is the most variable species in the *Eragrostis* genus and contains many different forms or types (de Winter, 1955). Material previously recognised as *E. chloromelas* Steud. and *E. robusta* Stent has been included in the species (de Winter, 1955; Leigh, 1961a). However by recognising that there are many intermediate forms, which make it difficult to demarcate species, Streetman (1970) considered that any taxonomic revision of these species has been premature.

Several other species including E. planiculmis Nees, E. lehmanniana Nees and E. barbinodis Hack are also closely related to E. curvula (de Winter, 1955).

For pasture purposes Leigh (1960a, 1961a) proposed that strains of E. curvula be grouped into five types: curvula, robusta blue, robusta green, robusta intermedia and chloromelas. This classification was based primarily on leaf colour, texture and size, the type of inflorescence and the growth habit.

This range of types has led to some confusion when research data of various workers are compared. Leigh (1961a, 1967) reported no apparent differences in growth habit with strains of the curvula type. However more recent work by Voigt, Kneebone, McIlvain, Shoop and Webster (1970) has demonstrated clearly significant differences within the curvula type.

b) Cytology

The chromosome compliments of the five morphological types of Eragrostis curvula proposed by Leigh (1960a, 1961a) range from the tetraploid (2n = 40) to the octoploid (2n = 80) level (Streetman, 1970). The chromosome numbers associated with four of the five morphological types are as follows: curvula (2n = 40), robusta green (2n = 60), robusta blue (2n = 70) and chloromelas (2n = 40, 80). Streetman (1970) found no evidence of diploid (2n = 20) plants in the strains studied. However four strains with diploid pollen have since been discovered (Voigt, 1971a). One of these, E. curvula var. conferta (2n = 20), has been extensively studied.

Cytological data indicate that the E. curvula complex reproduces apomictically. Streetman (1970) found meiotic behaviour of 2n = 60, 70 and 80 chromosome plants to be highly irregular and this, in association with morphological uniformity and constant chromosome numbers of plants, supported the apomictic concept of reproduction. This concept was supported further when megaspores readily detected in

the sexual species E. superba were found to be absent in ovule development of E. curvula (Streetman, 1970).

The diploid type, E. curvula var conferta, is a highly cross-pollinated sexual strain. This conclusion was reached by Voigt (1971a) after studying seed set in self-pollinated plants and all progeny performance data. Further research (Voigt and Bashaw, 1972) confirmed this finding when the presence of meiosis and tetrad megaspores were observed in plants of this sexual strain.

It appears that the mode of reproduction of E. curvula parallels that found in Paspalum notatum Flugge (Burton, 1955). In both species the diploids which were examined were sexual and the natural polyploids obligate apomicts. Frequently when polyploid strains of a species are apomictic, diploids will be sexual (Brown and Emery, 1958).

2. DISTRIBUTION

Species of Eragrostis are widespread throughout the tropical and subtropical regions of the world (de Winter, 1955). On the African continent they are characteristically prevalent in the medium (750 mm) to low (250 mm) rainfall areas particularly south of latitude 16^{o} S (Rattray, 1960). The genus is an important component of indigenous grasslands in the drier regions of Southern Africa (Rattray, 1960) including South West Africa and Botswana (de Winter, 1955). According to Lightfoot (1970) sixty-two species are found in the natural grasslands of Rhodesia. Approximately seventy-three species are indigenous to Southern Africa (de Winter, 1955).

About forty species of Eragrostis occur naturally in the United States (Hoover, Hein, Dayton and Erlanson, 1948). The genus is also widespread in Australia (Leigh and Mulham, 1965; Tothill and Hacker, 1973). It comprises the largest of the grass genera in Central Australia with seventeen species (Lazarides, 1970). A few species have been found in India (Hoover et al., 1948) and in other parts of

Asia (Bor, 1960).

Generally, species of the genus Eragrostis are of secondary agricultural importance and only a few have been recognised as being of agricultural value (Hoover et al., 1948). In Southern Africa species are classified as either weeds with no forage value and almost entirely unpalatable, or grasses of average to good forage value (Lightfoot, 1970; Roberts, 1973). In the sheep growing areas of Australia some species are regarded as useful, producing good forage of reasonable palatability (Leigh and Mulham, 1965). However the majority of indigenous species in Australia are virtually worthless as pasture grasses (Lazarides, 1970). Species of agricultural importance include Eragrostis lehmanniana Nees, E. tef (Zucc.) Trotter, E. superba Peyr and E. curvula (Schrad.) Nees.

Eragrostis curvula is indigenous to east and southern Africa (Rattray, 1960). It is widespread in South Africa (de Winter, 1955) and the eastern districts of Rhodesia (Lightfoot, 1970). In eastern tropical Africa it is present but only in isolated areas (de Winter, 1955).

In South Africa typical indigenous grassland which includes E. curvula as a component occurs at altitudes mainly below 1 200 metres with a rainfall of between 130 mm and 260 mm annually (Rattray, 1960). The species is also associated with Themeda types of grassland particularly in areas ranging in altitude from 1 400 to 2 000 metres in an annual rainfall zone of between 460 mm and 760 mm (Rattray, 1960). In association with other Eragrostis spp, E. curvula is particularly prevalent in areas of disturbed grassland where it tends to replace Themeda triandra and other climax species (Bayer, 1955). E. curvula is an aggressive grass in the intermediate stages of secondary succession which may occur in cultivated areas left fallow (Davidson, 1964; Altona, 1972).

3. ORIGIN AND DEVELOPMENT OF IMPROVED STRAINS

Eragrostis curvula was initially recognised and studied as a conservation and forage grass in the United States. It was introduced to that country in 1928 from a plant collection made in Tanzania (then Tanganyika) in 1928 (Hoover et al., 1948). In 1934 three promising species of the genus Eragrostis, including E. curvula, were introduced to the United States from both East and South Africa (Crider, 1945). It was first planted in Oklahoma in 1936 and became widely used for erosion control in south-west and south-central United States (Dalrymple, 1969). After six years of observation it received serious attention as a valuable conservation (Gamble, 1970) and pasture grass (Staten, 1949). However, during the next 15-20 years interest in the species waned and its value was questioned because of alleged low palatability, which is now known to result from incorrect and inefficient management (Dalrymple, 1969). With improved management and cultural techniques weeping lovegrass is now recognised as a top-quality forage and conservation grass and has become a tremendous asset to grassland agriculture in the United States (Dalrymple, 1969).

In 1943 a vigorous strain of E. curvula was discovered in the Ermelo district of Transvaal (Leigh, 1967). Seed of this strain was collected and sown at the Rietvlei Agricultural Research Station, near Pretoria. Eventually seed was supplied to other research stations in South Africa and successful trials with this Ermelo strain were carried out (Botha and Hamburger, 1953; Davidson, 1965). Since 1950 the Ermelo strain has become the most widely used of the E. curvula types in Southern Africa (Rethman, 1973).

For the past twenty years the primary goal of researchers has been to increase the palatability of weeping lovegrass forage. This has been accomplished by improved management (Dalrymple, 1969) and also by selecting for palatability. In 1970 'Morpa' weeping lovegrass was released in the United States (Voigt, 1970). This strain was selected

from an introduction collected from the Rietvlei Research Station in 1953 and first grown in Oklahoma in 1955 (Voigt, 1971b).

Morpa was subsequently selected for its greater palatability relative to other strains of E. curvula while maintaining the desirable characters associated with the species (Voigt, 1970, 1971b). Of importance, too, is that for the first time it provides growers and seedsmen with a strain of E. curvula of proven type and potential.

4. ADAPTATION

Eragrostis curvula is one of the most widely adapted perennial grasses in Southern Africa although several research workers (Rethman, 1973) have noted that this grass can be grown most successfully wherever the annual rainfall exceeds 600 mm. A survey conducted in south eastern Transvaal in 1970 indicated that approximately 10 per cent of all soil under cultivation was planted to E. curvula. Rethman (1973) calculated that in 1972 between 40 000 and 50 000 hectare had been sown to this crop in this area.

In South Africa weeping lovegrass is used primarily for hay production. However it is often grazed (Davidson, 1965) and has a definite role as a ley crop. Several studies (Rethman, 1973) have demonstrated its beneficial use in rotation with maize crops. Dense stands of weeping lovegrass can be used to control soil nematodes. Koen and Grobbelaar (1965) found that this crop markedly decreased the Meloidogyne javinica population in soils. A drastic reduction in the concentration of free CO_2 in the soil was considered to be the cause of death of larvae of this nematode. In the tobacco-producing areas of Rhodesia also, E. curvula is used extensively for control of soil nematodes (Barnes, 1968; Lightfoot, 1970). The crop can be used also for the effective control of certain weeds in cultivated lands (Edwards, 1970).

E. curvula is particularly well-adapted to both soils and climate of the Southern Great Plains of Oklahoma and Texas in the United States (Hoover et al., 1948) and is used extensively as a forage crop for grazing (Staten, 1949; Dalrymple, 1969). The grass is also grown on a limited scale in Arizona and New Mexico (Shoop and McIlvain, 1970a), and throughout the humid south-eastern United States where its use is restricted primarily to conservation areas (Dalrymple, 1969). In soil conservation and erosion control programmes it is subjected to a wide variety of growing conditions (Tabor, 1962; Vogel and Berg, 1968; Gamble, 1970; Vogel, 1970).

The species is well-adapted to the semi-arid Pampean region of the Argentine where the annual rainfall varies between 450 mm and 650 mm. Covas (1960) reported that E. curvula was not only ideal for stabilising soils and sand dunes but also far superior to any other cultivated grass species as a 'soil builder' in this region.

Weeping lovegrass has an aggressive fibrous root system ideal for binding and holding soils in place and so reducing the risk of erosion in areas subjected to erosion hazards. Also, the organic material provided by the root system contributes to the physical improvement of the soil. According to Gamble (1970) this factor is important in soil conservation programmes in intensive cropping areas. Increased infiltration, more efficient use of fertiliser and better crop yields have been attributed to the use of E. curvula as a ley crop.

Weeping lovegrass will establish and produce well on most well-drained soil types although it is better adapted to sandy loam soils. Performance is best on fertile soils although the grass will grow and produce comparatively well on low fertility soils (Dalrymple, 1969). Regardless of the inherent fertility of the soil, forage produced by the grass is nutritious and palatable when fertilised and managed properly.

Soil pH within the range encountered in agricultural soils has

little influence on the growth and adaptation of E. curvula (Dalrymple, 1969). It grows well on very acid soils with pH 4 (Vogel and Berg, 1968) but is not tolerant of alkaline soils with pH above 8 (Dalrymple, 1969), especially when the cause of basicity is sodium. In laboratory tests Dalrymple (1969) has reported that growth at pH 5 was better than at pH 4,5 or pH 6.

According to Dalrymple (1969) E. curvula requires an annual rainfall of at least 375-500 mm to become permanently established under dryland conditions. However crop performance is far superior where the rainfall exceeds 700 mm each year. The grass responds well to precipitation and is also resistant to drought conditions.

E. curvula has withstood temperature extremes of -29° C and 40° C (Dalrymple, 1969). High temperatures can induce semi-dormancy but this is rapidly broken by cooler temperatures and precipitation. Winter dormancy is induced mainly by low temperatures (Leigh, 1960a, 1960b).

The species is not tolerant of prolonged waterlogging (Rethman, 1973) and will succumb after only 3-5 days of flooding (Dalrymple, 1969).

5. VEGETATIVE GROWTH AND DEVELOPMENT

Most studies of morphology, physiology and biochemistry of plant growth have been associated with temperate grasses (Barnard, 1964; Evans, Wardlaw and Williams, 1964; Jewiss, 1966). Investigations on the climatic responses of herbage grasses to light and temperature have also been restricted largely to the temperates (Langer, 1963; Evans et al., 1964; Anslow, 1966). However the increasing importance of tropical and subtropical grassland production has necessitated that similar information on forage species adapted to these regions also be available.

The growth and development of some subtropical grasses indigenous to South Africa has received some attention (Booysen, Tainton and Scott,

1963; Bridgens, 1968) and Cooper and Tainton (1968) have compared the basic growth requirements of tropical and temperate grasses. In spite of a considerable amount of research carried out on the management of Eragrostis curvula in the sward both in South Africa (Rethman, 1973) and overseas (Dalrymple, 1969), comprehensive published information on growth and development of this plant is limited (Rabie, 1954; 1963; 1964; Leigh, 1960a; 1960b; 1961c; 1967; Tainton, 1967; 1968).

a) Germination and Early Seedling Growth

Under favourable field conditions germination and emergence of the seedling takes between 1 and 2 weeks. Germination of viable seed of Eragrostis curvula can exceed 90 per cent in four to five days, but if conditions are unfavourable it may continue for several weeks (Dalrymple, 1969). Rabie (1954) studied germination and early seedling growth in E. curvula and found that both the coleoptile and coleorhiza emerged from the caryopsis almost simultaneously, only two days after inbibition began. After seven days the first leaf had appeared and the first node, origin of the first adventitious or nodal roots, had formed immediately below the soil surface. The first of the seminal roots was well developed at this stage. After two weeks three leaves had emerged on the main stem and during the third week the first adventitious roots were formed. This coincided with initial tiller development although the first primary tiller only emerged during the sixth week, after the establishment of the nodal root system. The seminal root system had usually completed its function three to four weeks after initial growth had begun (Dalrymple, 1969). After eight weeks of growth, the young E. curvula plant assumed the characteristic tufted appearance (Rabie, 1954).

i. Factors affecting germination. Alternating temperatures from a minimum of 20°- 25° C to a maximum of 32°- 40° C appear to be optimum for germination of E. curvula seed. Under these conditions Dalrymple, (1969) reported a germination count of 94 per cent. When germinating

seed was exposed to constant temperatures of between 10° C and 25° C a maximum of only 73 per cent was obtained.

Dry seed of weeping lovegrass can withstand nine hours exposure to temperature extremes of -17° C and 68° C (Leigh, 1960b). In addition Leigh (1960b) found that low temperature exposure increased not only the capacity of seed to germinate but also the rate of germination as compared with seed held at normal temperatures. However Dalrymple (1969) reported that low temperature pretreatment was only of benefit to 'fresh' seed; in older seed prechilling was not beneficial.

Dormancy can be induced if seed is exposed to unfavourable conditions during the germination process. Voigt (1973) found that inbibition of E. curvula seed for 29 days in complete darkness at a temperature of 10° C induced dormancy in 79, 36 and 14 per cent of one, two and three-year-old seed respectively. In similar conditions, but using continuous light, only 32 per cent of the one-year-old seed became dormant. Voigt (1973) suggested that temperature-induced dormancy may be a cause of poor establishment following winter or early-spring sowing in the field.

Photoperiod has a marked effect on the germination of E. curvula seed. Tainton (1967) reported that germination was significantly more rapid in a 16-hour photoperiod compared with an 8-hour photoperiod. Four days after sowing the first leaf had already appeared from the coleoptile in 47 per cent of seedlings germinated in long days. In short days only 23 per cent of the seedlings had produced the first leaf. According to Tainton (1967) there existed the possibility of an association between the nature of E. curvula seed and its reaction to photoperiod during germination. Weeping lovegrass seed dispersed on the surface of the soil will remain there under natural conditions. It will not move into the soil because the seed is awnless. Consequently the influence of photoperiod during the germination process could be strong, and act as one of the factors inhibiting germination

during the winter in the natural environment.

Germination of weeping lovegrass seed is little affected by pH. Stubbendieck (1974) found that seed germinated well in the range pH 4,0 to pH 11,5 and Leigh (1960a) obtained maximum germination between pH 3 and pH 5 in a buffered solution. The wide range of tolerance to pH is an important factor in the adaptation of this grass to a wide range of growing conditions.

ii. Early seedling growth. The greater rate of extension of the first leaf in seedlings growing in long days resulted in higher leaf area and leaf mass ratios than in those seedlings growing in short days (Tainton, 1967). The initial advantage of a higher leaf area ratio in the 16 hour photoperiod was associated with a higher specific leaf area and a significantly greater relative growth rate. However, after nine weeks of growth Tainton (1967) found that differences in relative growth rate between plants growing in the two photoperiods were small and not significant. Relative growth rate was independent of photoperiod by the time plants were nine weeks of age.

The relative growth rate of plants growing in a 16-hour photoperiod, and with alternating 25° C day and 10° C night temperatures, reached a maximum value before the seedlings were two days old (Tainton, 1967). The rate then declined steadily to reach minimum values between 20 and 24 days of age. However, with increasing plant age the relative growth rate gradually recovered and after 36 days of growth had a value approximately half that of the early maximum rate.

Rabie (1954) reported a similar decline in growth rate of E. curvula seedlings growing outdoors. The decline coincided with the initial development of the nodal root system and an associated decrease in efficiency of the seminal roots. Accordingly the recovery in growth rate occured with the establishment of nodal roots. This relationship between growth rate and development of the nodal root system would appear to be extremely important in terms of seedling

establishment and growth.

The optimum temperature for seedling growth lies between 30° and 35° C. At these temperatures Tainton (1967) found that seedlings had produced twice the number of leaves as those growing at 20° C - as early as eleven days after seedling emergence.

Seedlings of E. curvula are able to survive extremely low temperatures. With constant growing conditions Leigh (1960b) found that 12-day old seedlings survived a temperature of 1,7° C for 24 hours; seedlings exposed to lower temperatures died.

b) The Shoot Apex

The centre and control of growth and form of the grass plant is the shoot apex. A knowledge of the organisation and development of the shoot apex is therefore necessary in order to appreciate the characteristics of plant growth and development of the species. Shoot apex morphogenesis and development in the Gramineae have received considerable attention (Evans and Grover, 1940; Sharman, 1945; 1947; Cutter, 1965). The development of the shoot apex in several sub-tropical grasses indigenous to South Africa has been investigated (Booysen et al., 1963; Tainton and Booysen, 1963; Tainton, 1964) and Rabie (1954) has studied the developmental morphology of the shoot apex in Eragrostis curvula.

Morphologically the shoot apex in E. curvula is similar to that in Agropyron repens (Sharman, 1945), consisting typically of the distal apical dome and a subapical region, which is characterised by alternately arranged leaf primordia. With an average of only three leaf primordia (Rabie, 1954), shoot apices of E. curvula are relatively short structures when compared with other herbage species (Sharman, 1947; Jewiss, 1966).

As in A. repens (Sharman, 1945) the outer tissues of the apical dome in E. curvula are arranged in three definite layers, the dermatogen and hypodermis, which are associated with leaf initiation, and

and the inner subhypodermis, meristematic activity of which gives rise the axillary buds.

The alternately arranged leaf primordia arise in acropetal succession as protuberances formed by periclinal divisions in the hypodermis and adjacent dermatogen. Early in the development of the leaf the subhypodermal tissue begins to divide both periclinally and anticlinally. This activity gives rise to the formation of the axillary bud, a replica of the parent structure. Rabie (1954) found that the formation and mode of growth of both leaf primordia and axillary buds were the same as Sharman (1945) described for A. repens.

The vegetative shoot apex in E. curvula plants always remains at or below the soil surface. The internodes formed during the vegetative phase of growth are very compact since no active internodal elongation occurs in E. curvula while the shoot apices are vegetative. Rabie (1954) obtained a definite correlation between internodal elongation and the onset of the reproductive phase.

c) Leaf Growth

Some factors controlling the growth of leaves in grasses are well-known (Anslow, 1966; Silsbury, 1970) but comparatively little research has been done on those factors influencing the rate of leaf initiation on the shoot apex or the growth of leaves prior to their emergence from the enclosing leaf sheaths. The knowledge of leaf growth and production in tropical and subtropical grasses is limited (Cooper and Tainton, 1968). Tainton (1967) investigated the influence of light and temperature on leaf growth and production in E. curvula and his findings are presented in this section.

i. Rate of leaf appearance. Tainton (1967) found the optimum temperature for leaf production in E. curvula to be 30°- 35° C. Production on the main stem was reduced from 0,35 to 0,28 leaves per day when the temperature regime was changed from a constant 25° C to an alternating 25° C day and 10° C night. The rate of leaf appearance

was negligible when plants were subjected to a constant 10° C.

Changes in light energy input also affect rate of leaf appearance. Tainton (1967) noted that leaves appeared more rapidly as total energy input was increased, although this was only significant at high temperatures. An increase in light energy from 74 to 148 cals/cm^2/day almost doubled the rate of leaf appearance on the main stem from 0,25 to 0,44 leaves per day, when plants were grown at 35° C.

Distinct from total light energy input, the effect of photoperiod on the production of leaves in established plants was not significant (Tainton, 1967). Cooper and Tainton (1968) reported that photoperiod appeared to have only a minor effect on the rate of leaf appearance in both temperate and tropical species, although conflicting results have been obtained (Anslow, 1966).

No published data showing the effect of the level of nutrition on leaf production in E. curvula are available. However results obtained with other herbage species have suggested that nitrogen has little effect (Anslow, 1966).

ii. Leaf size. The area of each leaf, an important component of the photosynthetic surface, is influenced by environmental conditions. Tainton (1967) found that an increase in photoperiod resulted in a longer and wider leaf, although the photoperiodic effect was largely implemented by its effect on leaf length. Photoperiod appeared to have little effect on the relative leaf growth rate in E. curvula but an increase in light energy input resulted in a marked increase in the leaf growth rate (Tainton, 1967).

Leaves grew most rapidly at 30° C and Tainton (1967) noted that a decrease in temperature to 20° C caused a significant decline in the relative leaf growth rate. Temperatures below 10°- 15° C often caused chlorosis in the leaves and this was followed by the death of the plant.

While leaf size has a direct effect on the size of the photosynthetic system, both the leaf area and leaf mass ratios express a

relationship between the size of the photosynthetically active system and the size of the whole plant. Both ratios are greatly affected by light and temperature in E. curvula.

The optimum temperature for both leaf area and leaf mass ratios was 35° C; as temperature decreased so did the value of both ratios. The leaf area ratio for plants receiving 148 cals/cm^2/day was significantly less than that for plants receiving only 74 cals/cm^2/day. In the high light energy regime leaf thickness and the density of leaf tissue were greater than in leaves of plants exposed to the low light energy level. This resulted in a decrease in specific leaf area as light energy input was increased.

As in other subtropical grasses Tainton (1967) found little response to a change from an eight to sixteen-hour photoperiod in leaf area ratio, leaf mass ratio, or specific leaf area.

The net photosynthetic activity of the individual leaf in E. curvula was greatest at 30° C, a lower optimum temperature than for the leaf area ratio (Tainton, 1967). At temperatures below 20° C the actual net assimilation rate was less than that obtained for temperate grasses (Cooper and Tainton, 1968).

Whether based on unit of leaf area or leaf mass (Tainton, 1967) the net assimilation rate increased as light energy input was increased, except at temperatures below 10° C. The net assimilation rate increased with light intensity and showed no signs of levelling off at intensities in the order of 6 000 foot candles (Tainton, 1967). E. curvula has been reported to utilise the C-4 carbon pathway in photosynthesis (Cooper and Tainton, 1968; Wynne et al., 1973), although recent evidence suggests that it may also use the C-3 pathway at certain times (Creswell, pers. comm.)*

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d) Tillering

According to Jewiss (1972) tillers have two important functions in the life of the plant. Tillering in the young seedling aids establishment and is also essential for the regeneration or perennation of the sward. Results have shown that, in swards, a progressive decline in plant numbers with time is associated with an increase in the number of tillers per plant so maintaining tiller numbers per unit area and prolonging the longevity of the sward as a productive unit (Langer, Ryle and Jewiss, 1964). The annual replacement of tillers, either following flowering as in a seed crop or following the removal of fertile tillers as in a cut for conservation, is an important feature of perennation (Jewiss, 1972).

Comparatively little is known about the physiological mechanisms controlling lateral bud development in the Gramineae (Jewiss, 1972). In contrast much is known about the life history of tillers and also factors affecting tillering, particularly in temperate species (Langer, 1963). Studies of tillering in subtropical species indigenous to South Africa are limited to the work of Rethman (1965), Tainton and Booysen (1965a; 1965b) and Rethman and Booysen (1967; 1968). The knowledge of tillering in improved strains of E. curvula is limited primarily to the studies of Rabie (1954; 1964) and Tainton (1967).

i. The life history of tillers. E. curvula is a tuft-forming or bunch grass. Tillers are characteristically intravaginal for they grow upwards within the leaf sheath and are closely associated with the axis of the parent tiller (Langer, 1963).

The life history and longevity of tillers will vary considerably with time of origin and environment. According to Bridgens (1968) the work of Rabie (1954; 1964) suggested that spring-initiated tillers of E. curvula could complete their life cycle within a seasonal year. This implies that tillers possess an annual growth habit and certainly exhibit less perennial characteristics than tillers of Themeda triandra

(Tainton and Booysen, 1963), Heteropogon contortus, Apochaete hispida and Cymbogon excavatus (Rethman, 1965). However, to date no published information dealing specifically with the life history of tillers of E. curvula either in the sward or single plant is available.

ii. Factors affecting tillering. The rate of tiller production in any grass is basically dependent on the rate of leaf appearance although there is an obvious difference in magnitude. Under constant growing conditions leaves appear on a tiller axis at a linear rate while the rate of tillering tends to be exponential as long as the plant remains vegetative (Langer, 1963).

Tillering in weeping lovegrass has shown a response to temperature similar to that recorded for leaf production. An increase from 10° to 35° C increased the number of tillers appearing per day in single plants of E. curvula from 0,6 to 8,8 (Tainton, 1967). The optimum temperature for tillering was 35° C. Compared with a constant 25° C the rate of tiller production was reduced by almost 60 per cent when the temperature was reduced from 25° to 10° C for 12 hours during a 16-hour photoperiod. A similar temperature reduction during the dark period had little effect on the rate of tillering (Tainton, 1967).

Neither light energy input nor photoperiod had any great influence on tillering in established plants of E. curvula (Tainton, 1967). However, an increase in either photoperiod or light energy input had a slight depressing effect on tillering particularly at high temperatures. In the subtropical Andropogon scoparius (Larsen, 1947) and Paspalum dilatatum (Knight, 1955) an increase in photoperiod also depressed the tillering rate, regardless of any effect of flowering. A similar effect has been reported in temperate grasses (Cooper and Tainton, 1968).

The effects of nutrient supply, moisture and flowering on tillering in E. curvula have apparently not been investigated. Despite the extensive use of this grass in forage producing systems in South Africa, no published work could be found in which the effect of defoliation on

tillering or leaf growth and production had been studied.

In Argentina Vera and Gorgano (1972) found that an increase in intensity of cutting caused a significant decline in tiller numbers in the sward.

e) Plant and Crop Growth

i. Relative growth rate. The optimum temperature for growth in Eragrostis curvula is 30° C. At this temperature Tainton (1967) obtained a maximum relative growth rate of 1,67 g/g/week when plants were growing in a 16-hour photoperiod; in 20° C and 10° C temperature regimes, recorded growth rates were 1,14 and 0,22 g/g/week respectively. At these lower temperatures Lolium multiflorum grew relatively more rapidly than E. curvula (Tainton, 1967). The response of other subtropical grasses to temperature is similar to that of E. curvula (Evans et al., 1964; Tainton, 1967). All subtropical grasses appear to be extremely sensitive to low temperatures (Cooper and Tainton, 1968). The relative growth rate, net assimilation rate and leaf area ratio are all minimal for these grasses at temperatures below 10° C and, in addition, rates of leaf production and tillering are extremely slow.

Changes in relative growth rate with changing temperature are the result of additive changes in leaf area ratio and net assimilation rate. Tainton (1967) found that the influence of temperature was highly positively correlated with these two latter growth parameters.

Plants were significantly heavier when growing in a 16-hour rather than an 8-hour photoperiod, even though Tainton (1967) reported that photoperiod had little effect on the rate of growth in established plants of E. curvula. Differences in plant mass were due to the initial significant effect of photoperiod on relative growth rate in those seedlings growing in the 16-hour photoperiod.

Total light energy input had a marked effect on the growth of E. curvula. Tainton (1967) found that relative growth rate increased

with increasing light intensity and reached a value of 8,7 g/g/week when at 6 000 foot candles. This was the highest level of intensity tested and the growth rate showed no signs of levelling off as found in temperate species (Cooper and Tainton, 1968).

In E. curvula the response of plant growth to defoliation has been studied by Steinke and Booysen (1968) and Bartholomew and Booysen (1969). Steinke and Booysen (1968) found that the regrowth of tops, as measured by dry matter yield, was progressively less with increasing frequency of defoliation. In addition, during the first three weeks of the regrowth period the highest average relative growth rates of tops were obtained from plants defoliated less frequently during the preceding treatment period. There was a significant correlation between average growth rate and the total available carbohydrate status of the plant. The results indicated that the plants drew on their carbohydrate reserves for at least a short period during regrowth.

ii. Growth distribution index. This function, used by Tainton (1967; 1968) to investigate the effect of climatic factors on the distribution of growth, provides a record of the changes in mass of a component of the plant relative to changes in the mass of the whole plant.

As the temperature in which E. curvula plants were growing was increased, Tainton (1967) observed an increase in growth of leaf blades relative to the growth of the remainder of the plant. The relative increase in leaf blade growth was associated with a decline in the distribution of growth in the root fraction of the plant. At high temperatures therefore, the growth distribution index of the leaf blades was greater than that for the root component.

In absolute terms root growth response to temperature was similar to that of leaf growth. The optimum temperature for both these components was 30° C. As a result Tainton (1967) concluded that temperature had no direct effect on the growth potential of leaf blade,

sheath or root. The actual effect was the result of a temperature effect on the ability of the various plant components to compete for those energy substrates required for growth. Therefore, at high temperatures leaf blades possessed a greater competitive ability than roots in E. curvula.

While an increase in temperature increased the growth distribution index of the leaf blades and decreased that of roots, an increase in light energy favoured the growth of roots at the expense of the leaf sheath component, but only at high temperatures, for when temperatures were low the high energy regime favoured the growth of leaf blade and sheath.

Similarly, the effect of photoperiod interacted with temperature effects. In the temperature range 30^{o} - 35^{o} C the growth distribution index of the leaf sheath component increased and that of the leaf blades decreased when the photoperiod was increased from 8 to 16 hours. At these high temperatures, photoperiod had no effect on root growth. However, when the temperature was reduced to 10^{o} C, the growth of roots was favoured at the expense of the leaf sheaths in the 16-hour photoperiod.

E. curvula possesses a wide range of tolerance to temperature and Tainton (1968) suggested that the ability of the grass to vary the mass ratio of its component parts may account for this phenomenon. Tainton (1968) reasoned that 'the ability of a plant to survive under a wide range of conditions is partly dependent on the extent to which it can adjust its morphological form to that appropriate to the conditions'.

iii. Crop growth. The typical growth curve of E. curvula is characterised by early spring growth, rapid growth in early summer, a mid-summer 'semi-dormant' period, and winter dormancy.

The stand's ability to commence growth earlier in spring than most other subtropical herbage grasses has encouraged its use for spring

grazing, particularly in the United States (Dalrymple, 1969). Early production in spring is encouraged by an early spring controlled burn and adequate nitrogen fertilisation (Dalrymple, 1969).

During early summer, research in the United States (Dalrymple, 1969) has shown that the rate of regrowth of an E. curvula stand may be as high as 5,0 cm/day, compared with much slower rates of between 1,2 cm and 1,8 cm/day obtained in the autumn. In South Africa Leigh (1960a) found that growth of E. curvula was 'rapid' until mid-December, declined until mid-January, increased again in February and then declined gradually as temperature declined in the autumn. The onset of the reproductive phase must be partially responsible for the rapid growth obtained in the early summer.

Moisture (Leigh, 1960a), temperature and fertility status of the soil (Nash and Tainton, 1975) were all found to be more than adequate for growth when forage production declined in mid-summer. The cause of the reduction in growth has been attributed to the dormancy or only very slow growth of lateral tiller initials at this time (Nash and Tainton, 1975). In temperate herbage species Jewiss (1972) suggested that this restriction of tillering occurred during reproductive development, when growth regulating substances were derived from meristematic centres in either the elongating stem or the terminal meristem. These substances indirectly suppressed the metabolic activity of the lateral buds, thus restricting tiller growth and development and limiting the immediate potenital for regrowth. Jewiss (1972) also intimated that environmental conditions, particularly high light intensity, may indirectly induce lateral bud suppression in mid-summer.

Leigh (1960a, 1960b) studied winter dormancy in E. curvula and concluded that temperature was the most important factor inducing dormancy. Soil moisture was of secondary importance and light had no effect over an 11 to 18 hour photoperiod range.

However, winter injury could not be attributed to low temperature

alone. Soil moisture, humidity, plant age and the degree of dormancy of the plant all contributed to the susceptibility of E. curvula to winter kill (Leigh, 1961c). Injury is often associated with a rapid temperature drop in autumn when the grass is still actively growing (Dalrymple, 1969). E. curvula is also susceptible to cold dry periods in late autumn or early winter particularly if the stand is encouraged to remain green at this time (Leigh, 1961c). Dalrymple (1969) reported that autumn growth prolonged by irrigation and/or fertilisation appeared to increase susceptibility to winter injury. Late autumn grazing or cutting also increased the chances of more severe winter injury in stands.

6. REPRODUCTIVE GROWTH AND DEVELOPMENT

The transition from the vegetative to the reproductive phase of growth marks a profound ontogenic change in herbage grasses. The onset of the reproductive phase is associated with a number of histological, morphological and physiological changes in the shoot apex (Barnard, 1964), which induce changes in the pattern of growth and distribution of assimilates (Ryle, 1970). The changes that occur are almost always permanent and irreversible (Cutter, 1965). Consequently this stage in the life cycle of the grass crop is of considerable biological and economic significance. It necessitates a change from the continued production of vegetative matter to the ultimate production of seed.

a) Development of the Inflorescence

i. Floral induction and initiation. Eragrostis curvula is independent of low temperature and short photoperiod requirements for flowering (Gardner and Loomis, 1953) and therefore has no vernalisation requirement (Cooper, 1960; Evans, 1964). In fact it is unlikely that such a requirement would have evolved among any of the tropical grass species (Cooper, 1960).

Most grasses pass through an obligate vegetative phase before

flowering can take place (Calder, 1966). Rabie (1954) found that tillers of E. curvula each tended to form a specific number of leaves prior to inflorescence initiation. Each tiller produced 7-8 leaves before the onset of flowering could occur, although Rabie (1954) did not indicate if this included primordial leaves on the shoot apex. Tainton (1967) also found that plants of E. curvula flowered only after they had produced a certain number of leaves, irrespective of the day-length conditions in which the plants were grown.

Calder (1966) could not support the concept of minimum leaf number as a direct measure of the achievement of the ripe-to-flower condition, but conceded that plants of a given species could produce a relatively small constant number of leaves prior to inflorescence initiation when grown under optimum flowering conditions. This 'minimum leaf number' concept can be accepted as a measure of the length of the vegetative phase for any given environmental conditions.

Leigh (1960b) proposed that E. curvula was completely indifferent to daylength for initiation of floral primordia. However Tainton (1967) found that a 16-hour rather than an 8-hour photoperiod was more conducive to flowering particularly when temperatures were low. Rumi (1971) grew E. curvula plants in 8, 13 and 16-hour photoperiods at temperatures of 17°, 21° and 27° C, and found that optimum conditions for flowering included a 13-hour photoperiod with a temperature of 21° C. Flowering in E. curvula did not occur in continuous light which prompted Tainton (1967) to suggest that the species had a short day response but with a high threshold value. Although the actual control mechanism of inflorescence initiation in E. curvula is not well understood, daylength as well as temperature appear to have some influence.

ii. Ontogeny of the inflorescence. At the onset of the reproductive phase in E. curvula, the shoot apex remains at ground level. Rabie (1964) observed little movement of the culm internodes even when the inflorescence had reached a marked degree of development. When

internodal elongation did occur Bridgens (1968) suggested that the elevation of the developing inflorescence was due to the elongation of the intermediate or distal culm internodes of the stem rather than the proximal internodes. The distal culm internodes were also concerned with the elevation of the shoot apex in Themeda triandra (Tainton, 1964; Bridgens, 1968).

The initial signs of inflorescence initiation in tillers of E. curvula are extremely difficult to trace due to the rapidity of the transformation. Rabie (1963) could only recognise initial changes in the shoot apex by a slight increase in length and diameter of the shoot apex. The characteristic double-ridge phase which is taken as a definite indication that the reproductive process has begun in temperate grasses (Barnard, 1964) is not noticeable in E. curvula.

The first definite outward sign of the inception of floral development in E. curvula was, according to Rabie (1963), the formation of protuberances, which appeared to rise in basifugal succession from the externally undifferentiated shoot apex. Rabie (1963) described these protuberances as representing spikelet primordia, but as the inflorescence of E. curvula is a panicle, they develop into the primary branches of the inflorescence (Barnard, 1964). This is followed in identical manner by the formation of secondary branches on all of which spikelet primordia appear.

According to Rabie (1963) the bud primordia originated in a polystichous manner around the shoot apex and not distichously as in Agropyron repens (Sharman, 1947) and other temperate grasses (Evans and Grover, 1940). Although Barnard (1964) suggested that when branches appear to be arranged polystichously they in fact arise distichously, Rabie (1963) observed that the early meristematic activity associated with the bud primordia occurred in positions wholly outside the plane of the leaves. As a result the branching pattern in the inflorescence of E. curvula was not the same as in the

vegetative body, as it is in those inflorescences in which the branches are arranged distichously (Barnard, 1964).

iii. Morphology of the inflorescence. According to de Winter (1955) the panicle can be lax or contracted and between 6 cm and 30 cm long. The primary branches are either appressed or spreading and arranged on the central axis either singly or in pairs where they are at almost the same level on opposing sides of the axis.

The spikelets are usually pedicelled and appressed to the secondary branches, although in some E. curvula types they may be spreading in habit. The secondary branches are normally arranged on the primary branch singly and are characteristically spreading.

The number of florets in each spikelet can range from 3 to 18 (de Winter, 1955) and the subtending glumes are almost but not quite equal in length. Incomplete disarticulation occurs in the spikelet when mature although de Winter (1955) reported that the rachilla did not easily disarticulate between the florets at this time.

The lemmas are normally 2,0-2,5 mm long, obtuse and membranous and are characterised by distinct lateral nerves (de Winter, 1955). The grain has been described (de Winter, 1955) as being subellipsoidal in shape and approximately 1 mm long. The embryo occupies approximately half the length of the grain.

b) Seed Formation

As Eragrostis curvula reproduces apomictically (Streetman, 1970) seeds are produced without fertilisation so that the resulting embryo is usually identical with its maternal parent in chromosome number and genotype (McWilliam, 1964). Pollination appears to be necessary for seed formation as Streetman (1970) found that embryos did not develop until several hours after anthesis. On the basis of extensive cytological observations, the reproductive mechanism in E. curvula appears to be diplospory followed by pseudogamy (Streetman, 1970).

According to Jones and Brown (1951) E. curvula is a heavy pollen

producer. Anther exsertion and pollen dispersal usually occur during the darkness of early morning but may be inhibited if temperatures are lower than 15° C and atmospheric humidity is high, as often occurs following a heavy dew. In the crop Jones and Brown (1951) found that pollen shedding occurred for approximately 3 weeks although heavy pollen shedding lasted about 7-10 days, which is a longer period than that characteristic of most temperate species (Griffiths, Roberts, Lewis, Stoddart and Bean, 1967).

Further study of pollination, seed set and early seed formation in weeping lovegrass has not been attempted. Even in temperate species it appears that the study of the control of seed formation and seed set has largely been neglected.

c) Crop Growth and Development

Established stands of weeping lovegrass can produce two seed crops in the one growing season (Ahring, Taliaferro and Rommann, 1971). However, the second crop which matures in autumn is seldom large enough to merit harvesting (Ahring, 1970). The main crop, contributing up to 95 per cent of the total seasonal seed harvest (Ahring et al., 1971), matures during mid-summer, approximately 12 weeks after spring growth begins (Dalrymple, 1969).

In South Africa established stands normally produce one seed crop each year. A survey of seed production in weeping lovegrass stands grown under dryland conditions in the highland sourveld areas of Natal, showed that the average seed crop matured during December and yielded between 80 and 125 kg of dressed seed per hectare (Field-Dodgson, 1973). The crops were growing in areas where the annual rainfall frequently exceeded 1 000 mm.

According to Dalrymple (1969), seed crops require at least 500 mm of rain each year in order to produce yields of the order of 150 to 300 kg/ha. Seed yields from crops grown under dryland conditions have been recorded as low as 25 kg/ha (Ahring et al., 1971).

Irrigation, in association with adequate fertilisation, has a marked effect on seed production. In Oklahoma yields of 500-800 kg/ha have been obtained with supplementary irrigation (Ahring et al., 1971). In Arizona a maximum total yield of 1 000 kg/ha of seed has been reported (Crider, 1945).

In South Africa the second autumn seed crop is produced 6-10 weeks after the December crop. However seed yields are negligible due not only to a greatly reduced seedhead population when compared with the first crop, but also to failure of these seedheads to set seed. The second crop is not an economic proposition to harvest (Field-Dodgson, 1973).

A similar situation exists in the seed producing areas of the United States. Ahring (1970) reported that only in one season during an 8-year period were two crops harvestable in Oklahoma. In this single growing season when approximately 120 kg/ha of seed was harvested from the second crop, Ahring (1970) suggested that unusually humid weather and cool night temperatures at the time of ear emergence and anthesis, and drier, cooler weather during seed formation and development created a favourable environment for seed set at this time. Lack of seed set in the autumn crop has been attributed to high night temperatures during flowering (Ahring, 1970).

Recently Ahring (pers. comm.)* concluded that factors other than soil fertility and moisture were influencing fertile tiller production and seed set in weeping lovegrass. Although increased nitrogen fertilisation and irrigation significantly increased culm production and seed yield of the autumn crop, the quantity of seed in the crop was not sufficient to merit harvesting. Ahring (pers. comm.)* is of the

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opinion that seed production in E. curvula is primarily a response to a temperature-regulated control mechanism, although it is conceivable that other climatic and possibly management factors may also have some influence.

CHAPTER III

EXPERIMENTAL. THE PHYSIOLOGY OF SEED PRODUCTION IN *Eragrostis curvula*

SECTION 1 TILLER FERTILITY

INTRODUCTION

In herbage grasses the number of fertile tillers produced per unit area, as determined by the number of tillers formed and the proportion of these becoming fertile, is a major component of seed yield (Lewis, 1966). In view of this, a knowledge of tillering, including the growth and development of those tillers contributing to the final crop of seedheads at each harvest, is necessary in any comprehensive investigation of seed crop development (Ryle, 1966). In the temperate species it appears that both the time of origin and the position of tillers within the plant determine the likelihood of any particular tiller becoming fertile irrespective of environmental and cultural conditions.

Langer and Ryle (1959) found in plants of timothy (*Phleum pratense*) sown successively throughout the spring and summer, that the ability of tillers to produce seedheads declined the later they appeared. This trend is apparently inherent in the organisation of the plant since it occurred irrespective of time of sowing. Similar results have been obtained by Lambert (1967b) for cocksfoot (*Dactylis glomerata*) and by Lewis (1963) for meadow fescue (*Festuca pratensis*).

In established seed crops of meadow fescue, perennial (*Lolium perenne*) and Italian ryegrass (*L. multiflorum*) and cocksfoot, the earliest tillers formed each year contribute the largest proportion of seedheads present at seed harvest (Langer and Lambert, 1959; Wilson, 1959; Lambert, 1963a; Lambert and Jewiss, 1970). In addition there is a decline in the ear-bearing capacity the later tillers appear in these

crops. In the ryegrasses grown for seed in New Zealand, Wilson (1959) found that 90 per cent of tillers arising before August became fertile. Fertility declined progressively for later dates of origin in the spring until flowering was inhibited in December-formed tillers.

In the subtropical Andropogon gayanus grown for seed in Nigeria, the greatest contribution to the seedhead population came from tillers tagged 5-6 months prior to the onset of flowering (Haggar, 1966). It is possible that many of the tagged tillers may have been present in the crop earlier than the date of tagging. However, it can be concluded that in this subtropical herbage species, and also in many of the temperate species, early produced tillers are of great importance to the seed crop.

Also, the position of tillers within the plant is closely related to the reproductive capacity of the tillers. In timothy plants primary tillers produced on the main stem are more fertile and produce heavier ears than secondary tillers of the same age (Langer, 1956). The decline in ear-bearing capacity with successive later dates of tiller origin is greater in secondary and later orders of tillers than in primary tillers (Langer and Ryle, 1959).

As far as tillers which produce inflorescences are concerned, there appears to be an annual progression through the orders of tillers in cocksfoot (Moriya, Hoshino and Kanabu, 1956) and meadow fescue (Lambert and Jewiss, 1970). It is also apparent that with increasing age of plants more orders of tillers contribute to the seedhead population even though the production from some orders is small. The results obtained with meadow fescue indicate that there is a ranking order of tillers in plants for the production of inflorescences which limits the proportion of tillers which can become reproductive within a year, even in a species where the percentage fertility of tillers is comparatively high (Lambert and Jewiss, 1970).

In view of the importance of tiller fertility in seed production

and the possible implications in the management of the seed crop on tiller fertility, the present study was carried out to determine first, the time of origin of tillers producing inflorescences; second the orders of tillers producing inflorescences and third, the relative contributions of tillers of different ages and orders to the seed crop.

EXPERIMENT 1 THE TIME OF ORIGIN AND POSITION IN THE PLANT OF TILLERS WHICH PRODUCE INFLORESCENCES

1. EXPERIMENTAL METHODS

a) Materials and Procedure

On 7 August 1972 weeping lovegrass seed (Ermelo strain) was sown directly into jiffy pots containing a 1:1 mixture of peat and vermiculite. The seedlings, culled for uniformity to leave one plant per pot by 25 August 1972 (18 days of age) were maintained with weekly applications of a balanced nutrient solution and grown in a glasshouse until 2 September 1972 (26 days of age) when they were transferred to the experimental site at the Faculty of Agriculture, University of Natal, Pietermaritzburg.

On 11 September 1972 (35 days of age) a weeping lovegrass sward was established for seed production when the jiffy pots, each containing a single plant, were spaced approximately 15 cm apart in rows 6 m long with a 75 cm spacing between rows. The sward received a basal dressing of phosphate and potassium, each at a rate equivalent to 60 kg/ha, at planting. Nitrogen was applied as nitrate at a rate equivalent to 60 kgN/ha on 15 September and thereafter in equal monthly increments at a rate equivalent to 20 kgN/ha.

As the experiment was carried out over two harvest years the monthly dressings of nitrogen fertiliser were continued until March 1973. No further fertiliser was applied until the following spring when, on 10 August 1973, a second basal dressing of both phosphate and potassium was applied (at the same rates as the initial dressing). At the same time nitrogen fertiliser was applied at a rate equivalent to 60 kgN/ha. The monthly dressings of nitrogen (20 kgN/ha) resumed on 10 September and continued until November 1973.

The sward was irrigated throughout the course of the experiment to prevent moisture stress and was regularly cut with hand clippers every

4-6 weeks during periods of active growth. On each occasion the vegetative growth was cut back to 8-10 cm. Frequent defoliations were necessary to facilitate tiller labelling. At the first signs of reproductive growth in both years, the stand was cut and then left undisturbed until the seedheads were harvested.

An investigation of this type requires the permanent identification of all tillers produced within a defined area. Six labelling sites, each consisting of 40 cm lengths of row, were selected at random from the inner three rows of the stand. At each site all tillers were tagged with coloured plastic rings cut from PVC sleeving material 6 mm in diameter. The rings were slipped over the leaves of the tiller, coming to rest at the base of the shoot. These rings at no time interfered with normal shoot growth.

b) Labelling Procedure

Tiller identification began on 13 September 1972 when the plants were 37 days old. At each site all living tillers were tagged according to their position in the plant as soon as they appeared. A colour code was devised so that the position of any tagged tiller, and therefore its order in the plant, could readily be identified at any time. Tagging continued until 15 December and on 10 January 1973 all tagged culms and the remainder of the seedhead population were harvested and the stand was defoliated to 8-10 cm.

In the second harvest year the time of origin as well as the position of tillers which produced inflorescences was traced. On 15 February 1973, when labelling was resumed, all living tillers were tagged with two rings; the basal ring identified the position of the tiller in the plant while the upper ring signified its time of origin.

On 15 April 1973 all untagged tillers, i.e. those that had emerged between 16 February and 15 April, were tagged in the same manner as the first group but using different coloured rings. By this stage it had become obvious that the rate of tillering at each labelling site far

exceeded the time available to tag all tillers. Consequently from 15 April, tagging continued in only four of the six original sites. Tagging was repeated on 15 August and again on 15 October using different colours at each time of tagging and for each tiller order. Tillers emerging after 15 October 1973 were not tagged. There were thus four groups of tillers labelled according to their time of origin in the second harvest year of the experiment (Table 1). Furthermore, each tagged tiller could be identified according to its position in the plant.

The second seed crop was harvested on 5 December 1973.

TABLE 1 The grouping of tagged tillers according to time of origin in 1973

	Time of tiller origin (1973)	Date Tagged
1.	Before 15 February	14, 15 Feb
2.	16 Feb to 15 April	13, 15 Apr
3.	16 April to 15 August	14, 15 Aug
4.	16 August to 15 October	14, 15 Oct

c) Recordings

At the first harvest on 10 January 1973, the labelled culms were separated according to their position in the plant and counted. No further recordings were taken.

Following the second harvest on 5 December 1973, the tagged tillers were separated into the four groups according to time of origin and classified into 'reproductive', 'vegetative' and 'dead' categories. The fertile tillers were further divided into their various orders. Seedheads from each age group were assessed to determine their contribution to the population of heads at harvest.

From each age group 10 seedheads were randomly selected and analysed for head length and spikelet number per head. Similarly 10 heads were removed for analysis from each of those tiller orders

present in the stand between 16 February and 15 April 1973. These analyses gave some indication of the effects of both tiller age and the orders of the tillers (of similar age) on inflorescence size.

2. RESULTS

a) Time of Origin of Tillers which Produce Inflorescences

Throughout 1973 over 4 500 tillers were tagged (Table 2). Almost 80 per cent of these tillers had emerged by 15 April 1973. At the time of harvest (5 December 1973) approximately 70 per cent of the total number of labelled tillers were still living; the remainder had died during the course of the experiment. Only 16 per cent of the surviving tillers were fertile (Table 2).

TABLE 2 The number and percentage of vegetative and fertile tillers per 4 x 40 cm of row, recorded at time of harvest (5 December 1973) of a second year stand of weeping lovegrass grown for seed

Time of tiller origin (1973)	Before 15 Feb	16 Feb to 15 April	16 April to 15 Aug	16 Aug to 15 Oct	Total
Total no. of tillers labelled	1 990	1 550	398	633	4 571
No. of tillers surviving	1 033	1 113	308	626	3 080
% tiller survival	51,9	71,8	77,4	98,9	67,4
No. of tillers vegetative	769	926	283	608	2 586
No. of tillers fertile	264	187	25	18	494
Fertile tillers as % of surviving tillers	25,6	16,8	8,1	2,9	16,0
% age contribution to seedhead population	53,4	37,9	5,1	3,6	100,0

Over 90 per cent of seedheads present at harvest in December 1973 were produced by tillers emerging before winter (before 15 April 1973). Tillers present in the stand on 15 February 1973 produced a greater proportion of inflorescences than those which appeared during the following two months (15 February to 15 April 1973), which in turn were

far superior to those tillers formed after mid-April and into the next spring (Table 2). It would appear that tillers emerging in late-summer and autumn had a greater chance of becoming fertile than later-emerging tillers and provided the bulk of the seedhead population at harvest in stands of weeping lovegrass.

Inflorescence size was influenced by the age of the tiller (Table 3). Tillers present in the stand by mid-February 1973 produced the longest inflorescence containing the greatest number of spikelets. There was a decline in inflorescence size the later tillers appeared in the stand.

TABLE 3 Effect of time of tiller origin on the size of the weeping lovegrass inflorescence produced (recorded at seed harvest 5 December 1973)

Time of tiller origin (1973)	Before 15 Feb	16 Feb to 15 April	16 April to 15 Aug	16 Aug to 15 Oct
Length of inflorescence (cm)	23,6 ± 2,31	23,1 ± 2,26	21,7 ± 2,22	18,8 ± 2,68
No. spikelets per unit length of inflorescence	10,2 ± 0,73	9,9 ± 0,69	9,7 ± 0,72	9,0 ± 0,79
No. spikelets per inflorescence	241 ± 36,4	230 ± 36,1	210 ± 33,9	171 ± 36,5

b) The Orders of Tillers which Produce Inflorescences

In the Gramineae primary tillers are produced from buds in the axils of leaves on the main stem. Leaves produced on the primary tillers may form shoots from their axillary buds. These shoots are the secondary tillers. Tertiary tillers are in turn produced from axillary buds of leaves on the secondary tillers. Thus the process continues giving rise, successively, to quaternary, quinary and sextary tillers and so on, resulting in a complicated system of tillers of various orders on the same plant.

Data obtained from this experiment show an annual progression of

flowering through the successive orders of tillers (Table 4). In 1972 the majority of seedheads were produced by the secondary tillers while the tertiary and quaternary tillers between them contributed over 70 per cent of the seedhead population in 1973.

TABLE 4 The flowering behaviour of successive orders of tillers in weeping lovegrass, 1972-1973

Establishment year 1972	Tiller Order*							Total
	M.S.	1	2	3	4	5	6	
Total no. tillers labelled	15	136	460	427	62	-	-	1100
No. inflorescences at harvest	15	105	195	17	-	-	-	332
% of total no. inflorescences	4,5	31,6	58,7	5,1	-	-	-	100,0
Second year - 1973								
Total no. tillers labelled	-	27	386	1176	1868	785	329	4571
No. inflorescences at harvest	-	2	77	168	192	44	11	494
% of total no. inflorescences	-	0,4	15,6	34,0	38,9	8,9	2,2	100,0

* Tiller Order M.S. = Main Shoot
1 = Primary
2 = Secondary
3 = Tertiary
4 = Quaternary
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6 = Sextary

It is also apparent that in any one year the highest orders of tillers present in sufficient numbers provided the majority of inflorescences. As the age of the stand increased it was also noticeable that more orders of tillers contributed to the seedhead population.

The majority of tillers present in the sward at 15 April and which flowered before 5 December were tertiary and quaternary (Table 5). No tertiary and few quaternary tillers which emerged subsequent to 15 April had flowered by 5 December (Table 5). Tillering in the spring was restricted to a new crop of tillers comprising both quinary and

sextary tillers, some of which flowered but contributed relatively little to the total seedhead population (Table 6).

TABLE 5 Percentage contribution of successive orders of tillers to the seedhead population contributed by each tiller age-group in 1973

Tiller Order	Time of Tiller Origin (1973)				Total
	Before 15 Feb	16 Feb to 15 April	16 Apr to 15 August	16 Aug to 15 Oct	
Primary	0,8	-	-	-	0,4
Secondary	22,0	10,2	-	-	15,6
Tertiary	42,4	29,9	-	-	34,0
Quaternary	34,8	51,3	16,0	-	38,9
Quinary	-	8,6	80,0	44,4	8,9
Sextary	-	-	4,0	55,6	2,2
	100,0	100,0	100,0	100,0	100,0

TABLE 6 Percentage contribution of tillers originating at different times to the seedhead population contributed by each successive order of tillers in 1973

Tiller Order	Time of Tiller Origin (1973)				Total
	Before 15 Feb	16 Feb to 15 April	16 Apr to 15 August	16 Aug to 15 Oct	
Primary	100,0	-	-	-	100,0
Secondary	75,3	24,7	-	-	100,0
Tertiary	66,7	33,3	-	-	100,0
Quaternary	47,9	50,0	2,1	-	100,0
Quinary	-	36,4	45,4	18,2	100,0
Sextary	-	-	9,1	90,9	100,0
Total	53,4	37,9	5,1	3,6	100,0

An analysis of inflorescences produced by tillers emerging during the period between 16 February and 15 April 1973 indicated a decline in the size of the inflorescence with each successive lower order of

tillers (Table 7). The position of the tiller in the plant therefore appears to have some influence on the size of inflorescence produced, largely perhaps because these tillers are in competition with the already present better developed higher order tillers.

TABLE 7 The effect of tiller order on the size of inflorescence produced by tillers originating between 16 February and 15 April 1973

Tiller Order	Secondary	Tertiary	Quaternary	Quinary
Inflorescence length (cm)	24,4 ± 1,28	23,7 ± 1,04	22,3 ± 1,65	19,6 ± 1,59
No. spikelets per unit length of inflorescence	10,3 ± 0,90	9,9 ± 0,82	9,7 ± 0,65	9,1 ± 0,81
No. spikelets per inflorescence	253 ± 32,1	236 ± 28,2	216 ± 30,0	180 ± 29,0

3. DISCUSSION

The data in Table 1 indicate that tillers originating in late summer contributed the greatest number of seedheads at harvest, nine months later. The substantial contribution of these tillers to seed yield is associated with a peak period of tiller production at this time and a high level of fertility among these tillers as compared with those emerging later. Thus the results from weeping lovegrass are similar to those obtained by Robson (1968) with tall fescue (Festuca arundinaceae) and by Lambert and Jewiss (1970) with meadow fescue. In cocksfoot and timothy, tillers appearing before the winter also appear to make the major contribution to the number of seedheads present at harvest (Langer and Lambert, 1959; Wilson, 1959). In weeping lovegrass over 90 per cent of seedheads were produced by tillers appearing before winter.

In most temperate species approximately 30 per cent of tillers in the crop become fertile, although the range varies between 10 and 40 per cent (Langer, 1959b; Langer and Lambert, 1959; Lambert, 1967a)

Robson, 1968). In the subtropical species the percentage of tillers fertile at harvest appears to be lower. In Andropogon gayanus Haggar (1966) obtained a mean value of 20 per cent. In the present study only 16 per cent of the surviving tiller population produced seedheads (Table 2). The inability of later-formed tillers to become fertile in weeping lovegrass has contributed to the low value obtained. However, perennial herbage species produce many more tillers than are capable of producing an inflorescence so that the perenniality of the species is ensured (Langer and Lambert, 1959).

Under natural conditions E. curvula will flower throughout the summer, as long as temperature and moisture conditions are suitable. It is possible that many of the vegetative tillers present at harvest in the second year of this present experiment may have become fertile if a second seed crop had been able to develop. Unfortunately, for ease of counting tillers, plants within the labelling sites were removed at harvest so prohibiting the study of a second crop. It is therefore possible that the proportion of tillers becoming fertile may have been greater if a second seed crop had been taken into consideration.

The number of tillers per unit area in the established sward of weeping lovegrass was found to be high, possibly the result of low plant density. Intense intra-plant competition for nutrients and assimilates may have restricted the ability of many tillers to produce a seedhead (Langer, 1959a). Seed yield and seedhead production may be increased by reducing tiller density and consequently the severity of this competition (Langer and Lambert, 1963). Langer and Lambert (1963) suggested that differences in the proportion of tillers that become fertile may result from changes in the levels of nutrient, light and water supply brought about through variations in population density. However, comparatively little is known about the way in which plant density governs competition at various critical stages of plant

development (Donald, 1954).

The physiological factors involved in the relationship between the order of succession of tillers and their ability to produce an inflorescence are not fully understood (Langer and Ryle, 1959). However competition between tillers for nutrients and assimilates, and the suitability of environmental conditions during growth, could play an important role (Langer, 1959b). Severe nitrogen deficiency may completely inhibit reproduction in plants (Langer, 1959a; Ryle, 1964). Inflorescence production can therefore often be increased by increasing the supply of nitrogen (Langer, 1959b; Wilson, 1959; Ryle, 1964) although the percentage of fertile tillers generally remains unchanged because of a simultaneous increase in the total number of tillers (Langer, 1959b; Evans, 1963; Lambert, 1966a).

Differences in light intensity also appear to affect tiller fertility. Increased shading will reduce the proportion of tillers producing an inflorescence (Ryle, 1961; 1966; 1967) although the effect is greater in some herbage species than in others (Ryle, 1966; 1967).

The decline in spikelet number per inflorescence with decrease in the age of the tiller (Table 3) may have arisen primarily from differences in the number of leaf primordia accumulated at the shoot apex at inflorescence initiation (Ryle, 1964) rather than any competitive factor (Ryle, 1966). In older shoots a greater number of leaf primordia accumulate than in younger shoots, which presumably means that more sites are available for primary branch formation and spikelet production (Ryle, 1963). Ryle (1964) found that in perennial ryegrass, meadow fescue and cocksfoot the number of primary spikelet branches in the inflorescence was greatest in shoots arising in early autumn; those arising at later dates carried progressively smaller numbers of branches until the lowest number was found in shoots arising in early spring.

The position of a tiller in the plant determines the likelihood of

that tiller becoming fertile in any one year, according to the data presented in Table 4. Although the highest orders of tillers produced the bulk of the seedhead population, they had to be present in sufficient numbers in order to contribute substantially to the overall yield. Within each labelling site there was a physical limitation on the highest orders especially in the first year. The number of main shoots were directly limited by the number of plants in each site, and primary tillers by the number and rate of growth of main shoots. In the second year the number of primary tillers present in the sward was further reduced since by then many had already flowered and died, while others had possibly died for other reasons. The secondary tillers are produced over a wider range of time than the primary tillers, depending on the rate of development of the primary tillers from which they are produced. For tillers of lower orders there is still greater flexibility in their time of origin.

In weeping lovegrass it is likely that the positional effect within the plant on tiller fertility and size of inflorescence produced (Table 7) may be operative through the size, as determined by internal competition for nutrients, and leaf area of individual tillers. Langer (1959b) has shown that the growth of lower orders of tillers was depressed more than that of primary tillers by a shortage of nutrients resulting in smaller tillers which developed a restricted leaf area compared with the higher order tillers (Langer, 1957; Lambert, 1967a).

The annual progression through the orders of tillers which produced inflorescences in weeping lovegrass was similar to that reported for cocksfoot by Moriya et al. (1956) who found that the tertiary, quaternary and quinary tillers produced inflorescences only in the second year. However, for meadow fescue, Lambert and Jewiss (1970) found that the progression through the orders was slower, with secondary and tertiary tillers producing the majority of

inflorescences in the second year.

Therefore, the seed crop appears to depend to a large extent on the number of tillers formed before winter, as found in most temperate species studied. These tillers are generally of the highest orders present in the plant at this time provided they are present in sufficient numbers. It is possible, as Langer and Lambert (1959) have suggested, that any cultural treatment encouraging tillering is likely to have a beneficial effect on the seed crop if applied at the time of origin of those tillers which ultimately contribute most actively to the number of inflorescences produced. In weeping lovegrass, as in other herbage species, such treatments should be applied in the late summer and autumn of each year.

SECTION 2 INFLORESCENCE GROWTH AND DEVELOPMENT

INTRODUCTION

No investigation of seed production in herbage species would be complete without some study of inflorescence growth and development. Modern cultural techniques for seed production in herbage grasses require a detailed knowledge of the development of the inflorescence and the influence of both internal and external factors on the capacity of the seedhead to produce seed. The number of seeds produced in the inflorescence is dependent ultimately on the total number of florets formed in the inflorescence.

With the initiation of floral primordia the shoot enters a new phase of development with the differentiation of the inflorescence, which proceeds until some time prior to ear emergence. During this time spikelets and florets are formed and their number, and thus the size of the inflorescence, is determined (Griffiths et al., 1967). In the Gramineae the total number of florets formed in each inflorescence depends on the number of primary spikelet branches developed either from the axils of unexpanded leaf primordia on the shoot apex, or subsequently from new axillary sites produced by continued growth of the apical meristem, and on the number of florets developing from each spikelet branch (Ryle, 1966).

In the previous experiment (Experiment 1) the age of the tiller and its morphological position in the plant were both found to influence the size of inflorescence produced, as determined by spikelet numbers. The date of origin of the tiller also affects the number of florets. In timothy (Ryle, 1963), ryegrass, cocksfoot and meadow fescue (Ryle, 1964) tillers arising in early autumn develop inflorescences with a greater number of florets than those arising at later dates. The smaller ear size in tillers arising at successively later dates resulted from decreased numbers of primary branches in the

inflorescence and also from the development of fewer spikelets on each branch (Ryle, 1964). An increase in the duration of vegetative growth before the onset of flowering was followed by an increase in the number of florets in the inflorescence (Ryle, 1963).

In timothy, tillers formed directly from sites on the main stem, the primary tillers, produced larger inflorescences than did secondary tillers of the same age (Langer, 1956; 1959b).

In temperate species the environment determines not only time of ear emergence and rate of inflorescence differentiation (Cooper, 1952; Cooper and McWilliam, 1966; Ryle and Langer, 1963a) but also the size of the inflorescence (Ryle, 1965; Ryle and Langer, 1963b). For any particular genotype the number of spikelets and florets varies according to external conditions, particularly after floral initiation. In single plants of timothy (Ryle and Langer, 1963b) and of ryegrass (Ryle, 1965) the total number of florets in the inflorescence increases as daylength or temperature is decreased. It would appear that the imposition of less favourable environmental conditions for reproductive growth prolongs the activity of the apical meristem by delaying inflorescence initiation. As a result additional primordia are formed or alternatively fewer develop into vegetative structures. Spikelets may then develop in the axils of these primordia. Relatively short daylengths and low temperatures also retard the rate of differentiation of the inflorescence, resulting in a longer period of development before ear emergence and greater numbers of florets in each spikelet. The number of florets developed in each spikelet appears to depend upon the balance between factors controlling the rate of differentiation and the availability of metabolites (Ryle, 1965).

A sufficient supply of nutrients must be available to allow the inflorescence to grow to maximum size. In temperate species the main effect of a higher level of nitrogen is to increase the number of

florets in each primary spikelet branch (Evans, 1954; Langer, 1959b; Ryle, 1963b; Stoddart, 1961; Lambert, 1967b). Spikelet production does not appear to be affected until deficiency becomes particularly acute (Ryle, 1964; 1966). In tropical and subtropical species in which the affect of nitrogen nutrition on inflorescence growth has been studied, increased nitrogen supply has a marked effect on inflorescence size. In Chloris gayana the number of racemes per inflorescence and the mean length of racemes are significantly increased following the application of nitrogen (Boonman, 1972b). The average size of the inflorescence in plants of Andropogon gayanus (Haggar, 1966) and Setaria sphacelata (Boonman, 1972a) are also greatly increased by applied nitrogen. In Paspalum plicatulum Chadhokar and Humphreys (1970) found that nitrogen stress after inflorescence initiation reduced the number of racemes and the number of florets per raceme in the inflorescence, especially in late-formed tillers.

A similar situation with regard to tiller age occurs in timothy in which later-formed tillers are affected more from a reduced nitrogen supply than shoots arising from sites on the main stem (Langer, 1959b). Inflorescences borne on later-formed tillers are smaller not only because of their age at the time of flowering but also because they are generally subjected to increased nutritional stress (Ryle, 1963b).

Because of the obvious implications of inflorescence size and nitrogen nutrition in seed production an experiment was undertaken in a glasshouse to determine the effect of nitrogen supply on the development and size of the inflorescence formed in selected tillers at different morphological positions within the weeping lovegrass plant. Since time of application is as important as the rate at which nitrogen is applied in practical management, nitrogen was applied at various developmental stages in the reproductive phase of

flowering through the successive orders of tillers (Table 4). In 1972 the majority of seedheads were produced by the secondary tillers while the tertiary and quaternary tillers between them contributed over 70 per cent of the seedhead population in 1973.

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florets in each primary spikelet branch (Evans, 1954; Langer, 1959b; Ryle, 1963b; Stoddart, 1961; Lambert, 1967b). Spikelet production does not appear to be affected until deficiency becomes particularly acute (Ryle, 1964; 1966). In tropical and subtropical species in which the affect of nitrogen nutrition on inflorescence growth has been studied, increased nitrogen supply has a marked effect on inflorescence size. In Chloris gayana the number of racemes per inflorescence and the mean length of racemes are significantly increased following the application of nitrogen (Boonman, 1972b). The average size of the inflorescence in plants of Andropogon gayanus (Haggar, 1966) and Setaria sphacelata (Boonman, 1972a) are also greatly increased by applied nitrogen. In Paspalum plicatulum Chadhokar and Humphreys (1970) found that nitrogen stress after inflorescence initiation reduced the number of racemes and the number of florets per raceme in the inflorescence, especially in late-formed tillers.

A similar situation with regard to tiller age occurs in timothy in which later-formed tillers are affected more from a reduced nitrogen supply than shoots arising from sites on the main stem (Langer, 1959b). Inflorescences borne on later-formed tillers are smaller not only because of their age at the time of flowering but also because they are generally subjected to increased nutritional stress (Ryle, 1963b).

Because of the obvious implications of inflorescence size and nitrogen nutrition in seed production an experiment was undertaken in a glasshouse to determine the effect of nitrogen supply on the development and size of the inflorescence formed in selected tillers at different morphological positions within the weeping lovegrass plant. Since time of application is as important as the rate at which nitrogen is applied in practical management, nitrogen was applied at various developmental stages in the reproductive phase of

growth.

Later it became obvious that plant and tiller response to nitrogen during early stages of vegetative growth could also be implicated in seedhead production. Hence, a second experiment was carried out in which different levels of nitrogen were applied at different stages of vegetative growth prior to inflorescence initiation.

EXPERIMENT 2 EFFECT OF THE POSITION OF THE TILLER IN THE PLANT AND OF NITROGEN, APPLIED AT DIFFERENT PHYSIOLOGICAL STAGES OF REPRODUCTIVE GROWTH, ON THE CAPACITY OF THE INFLORESCENCE TO PRODUCE SEED

1. EXPERIMENTAL METHODS

a) Procedure

120 plants of the Ermelo strain of weeping lovegrass were grown in 15 cm (2 litre) pots containing 550 g of a 1:1 mixture of peat and vermiculite. Seed was sown directly into the pots on 10 March 1972. At the two-leaf stage the seedlings were thinned to five per pot and then subsequently to one plant per pot as the first primary tiller emerged.

From the outset the plants were grown in a controlled temperature glasshouse with a 30° C day and a 24° C night temperature in natural daylight. A constant 14 hour photoperiod was maintained throughout the experiment with supplementary lighting provided by sixteen 250 watt incandescent light bulbs. This light source was held 60 cm above the plants. Relative humidity was kept at between 50 and 60 per cent throughout the experiment.

Each plant received 100 ml of culture solution every second week until the emergence of the fifth primary tiller, at which stage the solution was applied at weekly intervals until harvest. All essential nutrients apart from nitrogen were supplied in fixed amounts in the solution. The potting mix was maintained as close as possible to field moisture capacity by adding distilled water when necessary.

The main shoot, the first two primary and the first two secondary tillers to emerge were tagged with coloured plastic rings for subsequent identification. The five tillers were labelled as soon as the second leaf blade became fully emerged from the sheath of the first leaf.

The experiment was laid out in three completely randomised blocks

with each treatment represented by five randomly distributed plants per block. Each block was surrounded by a border row to minimise environmental side effects. Each week until the emergence of the main shoot inflorescences the blocks were rearranged to eliminate positional effects.

At the onset of the experiment 40 plants were randomly selected for microdissection to determine time of initiation of the main shoot inflorescence. At this stage, approximately 40 days after sowing, the treatments began. The harvesting of mature culms began 25 days after peak anthesis of respective inflorescences on 9 June 1972.

b) Treatments

Nitrogen, as nitrate, was applied in seven treatment combinations (Table 8). Times of application were dependent on the stage of development of the main shoot inflorescence and correspond with inflorescence initiation, ear emergence and initial anthesis. Each treatment received the same total amount of nitrogen, represented as 3N and equivalent to 0,24g N per pot. At each time of application the nitrogen was applied in 50 ml aliquots.

TABLE 8 The rate and time of nitrogen application for each treatment (treatment no. 1 - control treatment)

Time of Nitrogen Application	Nitrogen Treatment Number							
	1	2	3	4	5	6	7	8
Inflorescence initiation	-	3N	-	-	1½N	1½N	-	1N
Ear emergence	-	-	3N	-	1½N	-	1½N	1N
Initial anthesis	-	-	-	3N	-	1½N	1½N	1N

1N equivalent to 0,08g/pot

The control treatment was supplied with no nitrogen during the treatment period. However, to sustain growth until the commencement of the reproductive phase, all plants received a basal application of 0,08g per pot (1N) at emergence of the third primary tiller.

c) Observations and Recordings

The dates of emergence of the five labelled tillers were noted. A tiller was considered to be fully emerged when tagged.

Times of inflorescence initiation, ear emergence and initial and peak anthesis of each tagged tiller were noted. Initiation of the inflorescence was taken as the first definite sign of the development of primary branch primordia on the shoot apex. Ear emergence was defined as that time when the first two terminal spikelets were fully emerged from the sheath of the flagleaf. Initial anthesis occurred when the first anthers exserted. When approximately 75 per cent of all spikelets in the inflorescence had at least one floret with exserted anthers the inflorescence was defined as being at peak anthesis.

At harvest the number of vegetative and reproductive tillers in each plant was recorded. The herbage was oven-dried at 90° C for 24 hours and weighed. The tagged culms were separated from the rest of the reproductive tillers for analysis.

Both stem and inflorescence lengths were measured and the number of primary branches and spikelets on the inflorescence counted. The total number of florets and the number of these which were fertile was counted in those spikelets on a basal, intermediate and upper primary branch taken from the inflorescence ¼, ½ and ¾ along the central axis. This gave some estimation of the mean number of florets per spikelet for each labelled inflorescence and also the total number of florets per inflorescence.

The capacity of the floret to set seed, or the percentage of fertile florets, was determined from the number of florets which survived and were counted at maturity and not from the number originally present at time of ear emergence. Consequently no account was taken of florets which may have degenerated prior to the maturity of the inflorescence.

Seed was collected from selected basal, intermediate and upper primary branches and separately weighed at a constant 12,5 per cent moisture content. Seed size was determined as the mass of 100 seeds. Finally the mass of seed produced in each of the five labelled inflorescences was determined.

The components of inflorescence size were analysed statistically as a split-plot with nitrogen treatments as the main plot treatment and tiller position as the subplot treatment. Where applicable the primary branch position within the inflorescence was taken as a sub-subplot treatment in a split-plot design. Analysis of variance was carried out on the data and where F tests showed significance (Appendix A Tables 1-3) least significant difference (L.S.D.) tests were applied at both the 5 and 1 per cent levels of probability.

2. RESULTS

a) Development of the Inflorescence (Table 9)

The labelled primary and secondary tillers emerged 13 and 23 days respectively after the main shoot. The onset of the reproductive phase in the first primary and first secondary inflorescences occurred only 7 and 20 days respectively after that of the main shoot inflorescence. Therefore both these lower order tillers, and particularly the first primary tiller, appeared to develop at a faster rate than the main shoot at least to inflorescence initiation.

In all labelled tillers the inflorescence appeared to develop at approximately the same rate. Emergence and peak anthesis in primary and secondary inflorescences both occurred at constant intervals after the respective stages had occurred in the main shoot inflorescence.

The application of nitrogen during reproductive development had no effect on the rate of development of any of the labelled inflorescences.

TABLE 9 Time of inflorescence initiation and differentiation in the main shoot and the labelled primary and secondary tillers (average for all nitrogen treatments)

	Labelled Tiller				
	Main Shoot	First Primary	Second Primary	First Secondary	Second Secondary
Days to tiller emergence from sowing	8,0	19,7	22,4	30,7	31,5
Days to inflorescence initiation from tiller emergence	32,4	27,8	*	30,0	*
Days to ear emergence from tiller emergence	39,0	34,6	30,6	37,2	36,2
Days to peak anthesis from tiller emergence	54,0	48,8	45,4	51,3	50,2
Days to peak anthesis from sowing	62,0	68,5	68,8	81,0	81,7

* not recorded

b) Culm Size

i. Stem length (Table 10). At each treatment the main stem was shorter than those stems produced by the primary tillers, and these stems were shorter than the secondary stems. Differences in stem length between the main shoot, first primary and first secondary tiller means were highly significant ($p = 0,01$). The second secondary tiller produced the longest stem in most treatments and its mean length was significantly longer than the mean stem length of the first secondary tiller ($p = 0,01$).

The application of nitrogen had no significant effect on stem length in any labelled tiller.

ii. Stem mass (Table 11). The dry mass of stems appeared to be associated closely with stem length. The main shoot was generally the lightest in each treatment. While the variation in stem mass between the main shoot and first primary tiller means was not significant, the difference in dry mass between the second primary and both the main

TABLE 10 Effect of tiller position in the plant and nitrogen supply on the length of stem (cm) of the weeping lovegrass culm

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main Shoot	83,6	91,2	78,6	87,8	79,8	87,4	86,0	84,8	85,2
1st primary	93,6	98,6	92,0	103,8	92,4	98,0	99,2	95,4	96,6
2nd primary	103,0	95,8	93,4	102,2	95,2	97,4	98,2	94,4	97,5
1st secondary	119,0	108,6	111,4	112,0	102,4	117,6	119,0	114,0	113,0
2nd secondary	125,0	120,0	113,6	123,2	117,2	116,2	119,4	113,2	118,5
N Treatment Mean	104,8	102,8	97,8	106,2	97,4	103,3	104,4	100,4	102,1

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 3,02		
Between labelled tiller means	± 1,94	3,85	5,09
Between tillers at same nitrogen treatment	± 5,50	10,88	14,38
Between nitrogen treatments for same tiller	± 5,77		

TABLE 11 Effect of tiller position in the plant and nitrogen supply on the stem dry mass (mg) of the weeping lovegrass culm

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	726	837	765	846	739	864	775	763	789
1st primary	817	813	819	873	755	806	851	736	809
2nd primary	991	882	977	950	857	879	920	765	903
1st secondary	934	896	884	882	821	795	955	758	865
2nd secondary	1202	1098	1036	1140	912	956	1112	910	1046
N Treatment Mean	934	905	896	938	817	860	923	787	882

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 50,9		
Between labelled tiller means	± 23,5	46,4	61,4
Between tillers at same nitrogen treatments	± 66,3	131,3	173,6
Between nitrogen treatments for same tiller	± 82,9	166,9	222,9

shoot and first primary tiller means was highly significant ($p = 0,01$).

The second secondary tiller produced the heaviest stem in each treatment. The mean mass of the second secondary stem was significantly greater than the means of all four remaining labelled tillers ($p = 0,01$).

Differences in stem mass between nitrogen treatments and the control treatment for each labelled tiller were generally small and not significant. The variation between nitrogen treatment means, including the control treatment mean, was not significant.

iii. Inflorescence length (Table 12). The main shoot inflorescence was generally longer than the first primary inflorescence which, in turn, was longer than the inflorescence produced by the first secondary tiller. Differences between the mean inflorescence lengths of these three tillers were highly significant ($p = 0,01$). The second primary inflorescence was longer than the first primary inflorescence in each treatment and the difference between the inflorescence means was significant ($p = 0,01$). Similarly, the second secondary inflorescence mean was significantly greater than that of the first secondary inflorescence ($p = 0,01$).

The response to nitrogen increased as tiller order increased. Applied nitrogen had no effect on the length of the main shoot inflorescence. The longest inflorescence produced by the first primary and second primary tillers was obtained when nitrogen was applied at initiation of the main shoot inflorescence (treatment 2) and at ear emergence (treatment 3) respectively. These inflorescences were significantly longer than those produced in the control treatment to at least the 5 per cent level of probability.

The length of inflorescence produced by the secondary tillers showed the greatest response to applied nitrogen. The first secondary inflorescence was significantly longer in each treatment to which nitrogen was applied than in the control treatment ($p = 0,01$). The

TABLE 12 Effect of tiller position in the plant and nitrogen supply on the length of the weeping lovegrass inflorescence (cm)

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	41,6	42,4	41,4	41,4	41,2	41,4	41,4	41,2	41,5
1st primary	38,4	42,2	41,8	40,6	40,0	40,4	38,6	39,8	40,2
2nd primary	40,6	42,4	43,8	41,8	42,0	41,4	41,4	42,0	41,9
1st secondary	29,8	37,4	36,2	38,0	38,2	37,2	37,6	36,0	36,3
2nd secondary	35,6	39,4	37,8	40,4	36,8	37,2	39,8	37,2	38,0
N Treatment Mean	37,2	40,8	40,2	40,4	39,6	39,5	39,8	39,2	39,6

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	±0,79	1,63	2,19
Between labelled tiller means	±0,47	0,93	1,23
Between tillers at same nitrogen treatment	±1,32	2,62	3,46
Between nitrogen treatments for same tiller	±1,43	2,85	3,80

TABLE 13 Effect of tiller position in the plant and nitrogen supply on the number of primary branches produced in the weeping lovegrass inflorescence

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	30,8	33,2	31,4	30,8	31,8	32,8	31,6	31,8	31,8
1st primary	31,6	33,4	33,0	32,4	33,4	32,8	33,4	33,2	32,9
2nd primary	32,0	33,2	33,2	33,6	33,8	33,0	34,2	34,8	33,5
1st secondary	35,0	38,0	36,6	36,8	35,2	36,6	38,0	37,4	36,7
2nd secondary	37,0	39,2	38,0	39,0	37,6	37,8	39,2	39,2	38,4
N Treatment Mean	33,3	35,4	34,4	34,5	34,4	34,6	35,3	35,3	34,6

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	±0,91		
Between labelled tiller means	±0,48	0,95	1,26
Between tillers at same nitrogen treatment	±1,36	2,69	3,55
Between nitrogen treatments for same tiller	±1,52		

longest first and second secondary inflorescences were recorded in treatment 4, when nitrogen was applied at initial anthesis of the main shoot inflorescence. However, actual time of nitrogen application during inflorescence development generally had little effect on the length of the inflorescence produced by each labelled tiller.

c) Inflorescence Size

i. Number of primary branches per inflorescence (Table 13). The position of the tiller in the plant had a considerable effect on the number of primary branches in the inflorescence. The second secondary inflorescence contained an average of 7 branches more than the main shoot inflorescence. An analysis of tiller means shows that the main shoot inflorescence produced significantly fewer primary branches than either the first primary ($p = 0,05$) or second primary inflorescence ($p = 0,01$). Both primary inflorescences had fewer primary branches than the secondary inflorescences; the variation between both orders was highly significant ($p = 0,01$).

Nitrogen applied at any stage during inflorescence development had no significant effect on primary branch production.

ii. Number of spikelets per inflorescence (Table 14). The main shoot inflorescence contained consistently fewer spikelets than the lower order tillers in each treatment. As a consequence the primary and secondary inflorescence means were significantly larger than the main shoot mean ($p = 0,01$). Also, the second primary and second secondary inflorescence means were significantly larger than the first primary and first secondary means respectively ($p = 0,01$).

Applied nitrogen increased the number of spikelets in all labelled inflorescences. However the response was generally small and not significant except in the second secondary inflorescence. This inflorescence responded significantly to the application of nitrogen in all treatments except 5 and 8, to at least the 5 per cent level of probability.

TABLE 14 Effect of tiller position in the plant and nitrogen supply on the number of spikelets produced per inflorescence in weeping lovegrass

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	314	355	326	310	330	343	340	345	333
1st primary	374	398	381	412	389	403	380	384	390
2nd primary	416	441	424	439	448	438	421	439	433
1st secondary	340	382	396	392	375	362	389	383	377
2nd secondary	372	434	438	453	366	454	434	416	421
N Treatment Mean	363	402	393	401	382	400	393	393	391

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	±18,8		
Between labelled tiller means	± 8,2	16,3	21,5
Between tillers at same nitrogen treatment	±23,3	47,6	60,8
Between nitrogen treatments for same tiller	±28,0	56,3	75,2

TABLE 15 Effect of tiller position in the plant and nitrogen supply on the number of florets produced per spikelet in the weeping lovegrass inflorescence

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main Shoot	7,2	8,7	8,2	8,0	7,6	7,5	7,1	7,2	7,7
1st primary	4,7	6,4	5,3	5,1	5,3	5,0	5,0	5,0	5,2
2nd primary	4,9	6,1	5,3	5,4	5,1	5,0	5,2	5,3	5,3
1st secondary	4,4	5,3	5,2	5,2	5,3	5,2	5,1	5,0	5,1
2nd secondary	4,6	5,5	5,5	5,6	5,2	5,0	5,4	5,1	5,3
N Treatment Mean	5,2	6,4	5,9	5,9	5,7	5,5	5,6	5,5	5,7

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	±0,23	0,47	0,64
Between labelled tiller means	±0,13	0,26	0,34
Between tillers at same nitrogen treatment	±0,37	0,72	0,96
Between nitrogen treatments for same tiller	±0,40	0,80	1,07

iii. Number of florets per spikelet (Table 15). The largest spikelets were developed by the main shoot inflorescence and contained as many as 3 florets more than those spikelets developed in the primary and secondary inflorescences. Differences in floret numbers per spikelet between the main shoot inflorescence and the four lower order inflorescences were highly significant ($p = 0,01$) in each treatment.

The application of nitrogen had a marked effect on the number of florets produced per spikelet in each labelled inflorescence but only when applied as a single dressing. Nitrogen applied as a split dressing to treatments 5 to 8 had no significant effect on spikelet size, even though the total amount of nitrogen applied was the same in all treatments.

The largest spikelets in the main shoot and both primary inflorescences were recorded in treatment 2 when nitrogen was applied at initiation of the main shoot inflorescence. The variation in spikelet size between this treatment and treatment 1 (control) for each of the three inflorescences was highly significant ($p = 0,01$). Also, the spikelet in the main shoot inflorescence in treatments 3 and 4 was significantly larger than that in the control treatment ($p = 0,05$). In the primary inflorescences the variation between treatment 3, treatment 4 and the control treatment was small and not significant. Furthermore the average spikelet in the first primary inflorescence in treatment 2 contained significantly more florets than those spikelets in treatments 3 and 4 ($p = 0,05$).

The number of florets per spikelet in both secondary inflorescences was increased significantly when nitrogen was applied ($p = 0,05$). There was little variation in spikelet size when nitrogen was applied at initiation, emergence or initial anthesis of the main shoot inflorescence.

An analysis of nitrogen treatment means shows that the largest

spikelet was obtained when nitrogen was applied at inflorescence initiation (treatment 2). The mean number of florets per spikelet in treatment 2 was significantly greater than in treatments 3 and 4 ($p = 0,05$) and all remaining treatments including treatment 1 ($p = 0,01$).

The effect of spikelet location in the inflorescence on the size of the spikelet is recorded in Table 16. Although the average size of spikelets was the same at each primary branch, the actual position of the tiller in the plant had a noticeable effect on the number of florets carried in spikelets at each primary branch position. Spikelets on the basal primary branch in the main shoot inflorescence were smaller than those on the intermediate and upper primary branches. This trend was reversed in the primary and secondary inflorescences where the basal spikelets contained more florets than those spikelets at the upper locations in the inflorescence. The variation in spikelet size between basal and upper primary branches in the main shoot, first primary and second secondary inflorescences was highly significant ($p = 0,01$).

As a consequence of the reversed trend in spikelet size within the inflorescence the decline in the number of florets per spikelet through the tiller orders was greater on the upper primary branch than on the basal branch. This decline was however highly significant at each primary branch position ($p = 0,01$).

The influence of nitrogen on spikelet size at different locations in the inflorescence is shown in Table 17. The response to nitrogen appeared to be similar at the basal, intermediate and upper primary branch positions while the variation in floret numbers per spikelet between the three position in each nitrogen treatment were small and not significant.

iv. Number of florets per inflorescence (Table 18). The average main shoot inflorescence contained over 2 500 florets, significantly

TABLE 16 The number of florets per spikelet in basal, intermediate and upper primary branches of inflorescences produced by the main shoot and labelled primary and secondary tillers of weeping lovegrass (average for all nitrogen treatments)

Primary Branch Position	Labelled Tiller					Primary Branch Mean
	Main Shoot	First Primary	Second Primary	First Secondary	Second Secondary	
Basal	7,1	5,4	5,4	5,2	5,6	5,7
Intermediate	7,9	5,2	5,2	5,1	5,2	5,7
Upper	8,1	5,1	5,2	5,0	5,0	5,7
Labelled Tiller Mean	7,7	5,2	5,3	5,1	5,3	5,7

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between labelled tiller means	±0,13	0,26	0,34
Between primary branch means	±0,05		
Between primary branches for same tiller	±0,11	0,22	0,26
Between tillers for same primary branch	±0,16	0,31	0,41

TABLE 17 Effect of nitrogen supply on the number of florets produced per spikelet in basal, intermediate and upper primary branches of the weeping lovegrass inflorescence (average for labelled tillers)

Primary Branch Position	Nitrogen Treatment Number								Branch Mean
	1	2	3	4	5	6	7	8	
Basal	5,1	6,4	5,9	6,0	5,6	5,6	5,6	5,5	5,7
Intermediate	5,2	6,6	5,9	5,9	5,7	5,5	5,6	5,5	5,7
Upper	5,2	6,3	5,9	5,7	5,8	5,5	5,5	5,5	5,7
N Treatment Mean	5,2	6,4	5,9	5,9	5,7	5,5	5,6	5,5	5,7

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	±0,23	0,47	0,64
Between primary branch means	±0,05		
Between primary branches at same nitrogen treatment	±0,14		
Between nitrogen treatments for same primary branch	±0,26	0,52	0,70

more than any other labelled tiller mean (p = 0,01). Also, the mean number of florets in the second primary and second secondary inflorescences was greater than the first primary and first secondary inflorescence means respectively; the differences were highly significant (p = 0,01).

On average the greatest number of florets per inflorescence was obtained when nitrogen was applied at the onset of tiller fertility in the plant (treatment 2). This treatment mean was significantly greater than all other treatment means to at least the 5 per cent level of probability. No significant gain was made by applying nitrogen as a split dressing in treatments 5 to 8 as compared with a single dressing in treatments 3 and 4. However, all treatments receiving nitrogen whether as a single or split application had a significantly higher mean number of florets per inflorescence compared with the control treatment (p = 0,01).

The largest main shoot inflorescence was obtained when nitrogen was applied at treatment 2. The differences between this treatment and all remaining treatments were highly significant (p = 0,01). The largest number of florets in the primary inflorescences was also obtained at treatment 2 although the response was not as distinct, particularly in the second primary inflorescence.

Time of application was of little consequence in the secondary inflorescences although the maximum number of florets in the second secondary inflorescence was recorded when nitrogen was applied at initial anthesis (Treatment 4).

The greatest response to nitrogen was obtained in the secondary inflorescences. Nitrogen as applied in most treatments significantly increased the number of florets in the secondary inflorescences as compared with the control treatment. In comparison, the number of florets in the main shoot inflorescence was increased significantly only by treatment 2 (p = 0,01) and treatment 3 (p = 0,05).

TABLE 18 Effect of tiller position in the plant and nitrogen supply on the number of florets per inflorescence of weeping lovegrass

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	2266	3113	2638	2468	2497	2584	2383	2469	2552
1st primary	1751	2569	1990	2110	2044	2024	1926	1889	2038
2nd primary	2019	2625	2247	2400	2367	2181	2188	2324	2294
1st secondary	1488	2016	2062	2027	2006	1831	1967	1903	1912
2nd secondary	1691	2383	2387	2544	1863	2247	2286	2156	2195
N Treatment Mean	1843	2541	2265	2310	2156	2173	2150	2148	2198

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	±99,3	203,4	274,4
Between labelled tiller means	±56,1	111,0	146,7
Between tillers at same nitrogen treatment	±158,5	313,9	414,9
Between nitrogen treatments for same tiller	±173,1	346,7	461,4

TABLE 19 Effect of tiller position in the plant and nitrogen supply on the percentage fertility of florets in the weeping lovegrass inflorescence

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	49	47	45	47	44	46	49	47	47
1st primary	45	39	45	37	41	46	41	43	42
2nd primary	46	41	42	43	41	45	40	43	43
1st secondary	43	41	39	35	41	39	38	36	39
2nd secondary	46	42	41	33	33	42	40	39	40
N Treatment Mean	46	42	43	39	40	44	42	42	42

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 2,7		
Between labelled tiller means	± 1,2	2,4	3,1
Between tillers at same nitrogen treatment	± 3,9	6,7	8,9
Between nitrogen treatments for same tiller	± 4,0	8,1	10,8

d) Seed Production per Inflorescence

i. Floret fertility (Table 19). The capacity of florets to set seed declined through the tiller orders. This was evident in each treatment, but more especially in treatment 4. As a result, the average fertility of the main shoot inflorescence was significantly higher than the average fertility of first primary inflorescence ($p = 0,01$) which, in turn, was significantly more fertile than the first secondary inflorescence ($p = 0,05$).

The capacity of florets to set seed was similar in the first and second primary inflorescences and also in both secondary inflorescences.

Applied nitrogen had no significant effect on the capacity of florets to set seed.

The influence of the position of the floret in the inflorescence on its fertility is shown in Table 20. Florets in spikelets on the basal primary branch were more fertile than those florets on the upper primary branch in each labelled inflorescence. The fertility mean at the basal primary branch was significantly higher than that at the upper branch ($p = 0,01$).

The main shoot inflorescence not only had the highest average fertility but also the greatest range in fertility. A decline in floret fertility of 3 per cent from the basal to the upper primary branch was significant ($p = 0,05$).

As recorded in Table 21 nitrogen had little effect on the capacity of florets to set seed at each primary branch position in the inflorescence. Compared with treatment 1, nitrogen reduced floret fertility at each primary branch. The response was the same at each location but this reduction failed to reach significance.

In treatment 2 spikelets on the basal primary branch were 5 per cent more fertile than those on the upper branch; this variation was significant ($p = 0,01$) and was due largely to the reduced fertility of

TABLE 20 The percentage fertility of florets in basal, intermediate and upper primary branches of inflorescences produced by the main shoot and labelled primary and secondary tillers of weeping lovegrass (average for all nitrogen treatments)

Primary Branch Position	Labelled Tiller					Primary Branch Mean
	Main Shoot	First Primary	Second Primary	First Secondary	Second Secondary	
Basal	49	43	43	40	41	43
Intermediate	46	43	43	39	39	42
Upper	46	41	42	38	40	41
Labelled Tiller Mean	47	42	43	39	40	42

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between labelled tiller means	± 1,2	2,4	3,1
Between primary branch means	± 0,6	1,2	1,6
Between primary branches for same tiller	± 1,3	2,6	3,5
Between tillers for same primary branch	± 1,6	3,2	4,2

TABLE 21 Effect of nitrogen supply on the percentage fertility of florets in basal, intermediate and upper primary branches of the weeping lovegrass inflorescence (average for labelled tillers)

Primary Branch Position	Nitrogen Treatment Number								Branch Mean
	1	2	3	4	5	6	7	8	
Basal	47	44	44	41	40	44	44	41	43
Intermediate	45	43	43	38	41	44	41	42	42
Upper	45	39	41	38	40	43	42	42	41
N Treatment Mean	46	42	43	39	40	44	42	42	42

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 2,7		
Between primary branch means	± 0,6	1,2	1,6
Between primary branches at same nitrogen treatment	± 1,7	3,2	4,4
Between nitrogen treatments for same primary branch	± 3,0		

the upper florets. In all other treatments the variation in fertility was between 1 and 3 per cent and not significant.

ii. 100 seed mass (Table 22). The position of the tiller in the plant had a considerable effect on seed size. The heaviest seed was produced in the main shoot inflorescence and the lightest in the second secondary inflorescence in most treatments. The mean mass of 100 seeds in the first secondary inflorescence was significantly lower than that of either the first primary inflorescence ($p = 0,05$) or the main shoot inflorescence ($p = 0,01$). The difference in seed size between the two latter inflorescence means was not significant.

Nitrogen significantly increased the mass of 100 seeds. The average mass of 100 seeds in each nitrogen treatment was significantly greater than that of the control mean ($p = 0,01$). The heaviest seed was obtained after nitrogen had been applied at initial anthesis (treatment 4). The application of nitrogen as a split dressing had no beneficial effect on seed size as compared with a single dressing.

The heaviest seed produced in the main shoot inflorescence and both primary inflorescences was obtained when nitrogen was applied at emergence of the main shoot inflorescence (treatment 3). However, seed from the main shoot and second primary inflorescences in this treatment and in all other nitrogen treatments was not significantly heavier than in the control treatment. Seed produced in the first primary inflorescence in treatment 3 and also in treatments 4 and 5 was significantly heavier than in the control treatment ($p = 0,05$).

The greatest response to nitrogen was obtained from seed in both secondary inflorescences. The mass of 100 seeds developed in the first and second secondary inflorescences showed a highly significant increase when nitrogen was applied in all treatments as compared with the control treatment ($p = 0,01$).

The increased average seed size in treatment 4 can be attributed largely to the increase in mass of seeds in the secondary

TABLE 22 Effect of tiller position in the plant and nitrogen supply on the mass of 100 seeds (mg) from the weeping lovegrass inflorescence

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	41,8	41,8	43,3	43,1	42,4	42,6	42,6	43,9	42,7
1st primary	39,4	42,4	43,0	42,9	42,8	41,6	41,3	41,1	41,8
2nd primary	40,2	42,9	43,3	41,6	41,4	41,1	39,8	40,8	41,4
1st secondary	35,5	39,9	41,5	44,7	39,7	40,8	41,5	41,7	40,7
2nd secondary	34,1	39,7	39,1	43,5	42,2	40,5	39,6	40,1	39,8
N Treatment Mean	38,2	41,3	42,0	43,2	41,7	41,3	40,9	41,5	41,3

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 0,93	1,90	2,56
Between labelled tiller means	± 0,51	1,01	1,33
Between tillers at same nitrogen treatment	± 1,44	2,85	3,77
Between nitrogen treatments for same tiller	± 1,59	3,18	4,23

TABLE 23 The mass of 100 seeds (mg) from basal, intermediate and upper primary branches of inflorescences produced by the main shoot and labelled primary and secondary tillers of weeping lovegrass (average for all nitrogen treatments)

Primary Branch Position	Labelled Tiller					Primary Branch Mean
	Main Shoot	First Primary	Second Primary	First Secondary	Second Secondary	
Basal	41,7	40,4	40,1	39,9	39,7	40,4
Intermediate	42,7	41,9	41,5	40,5	39,6	41,2
Upper	43,7	43,1	42,4	41,6	40,2	42,2
Labelled Tiller Mean	42,7	41,8	41,4	40,7	39,8	41,3

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between labelled tiller means	± 0,51	1,01	1,33
Between primary branch means	± 0,16	0,31	0,41
Between primary branches of same tiller	± 0,35	0,69	0,91
Between tillers for same primary branch	± 0,58	1,16	1,53

inflorescences. Seed in both these inflorescences was heavier than seed in the main shoot inflorescence (at treatment 4).

Seed size varied considerably within the inflorescence as illustrated in Table 23. The mass of 100 seeds in spikelets on the upper primary branch was consistently higher than the 100 seed mass on the intermediate and basal primary branches. The variation in seed size between the basal, intermediate and upper branch means was highly significant ($p = 0,01$). In the second secondary inflorescence the variation in 100 seed mass between basal and upper primary branches was only 0,5 mg and not significant.

The decline in seed size between the main shoot inflorescence and the second secondary inflorescence was greater on the upper primary branches than on the basal primary branches. The variation in seed size between these two inflorescences increased from 2,0 mg on the basal primary branch to 3,1 mg and 3,9 mg on the intermediate and upper branches respectively. These differences were all highly significant ($p = 0,01$).

The results in Table 24 show that the response to nitrogen was similar at each primary branch position, except in treatment 8 where the increase in seed mass from the upper primary branch over that in the control was almost double the increase at the basal branch position. The application of nitrogen in each treatment significantly increased the 100 seed mass at each primary branch position when compared with the data in the control treatment, to at least the 5 per cent level of probability.

iii. Seed mass per inflorescence (Table 25). Seed production per inflorescence declined through the tiller orders. In each nitrogen treatment the mass of seed produced in the main shoot inflorescence was significantly greater than the seed mass in either the first primary or first secondary inflorescence ($p = 0,01$). Also, the second primary and second secondary inflorescence produced a heavier mass of

TABLE 24 Effect of nitrogen supply on the mass of 100 seeds (mg) from basal, intermediate and upper primary branches of the weeping lovegrass inflorescence (average for all labelled tillers)

Primary Branch Position	Nitrogen Treatment Number								Branch Mean
	1	2	3	4	5	6	7	8	
Basal	37,4	40,7	41,3	42,4	40,8	40,3	40,2	39,9	40,4
Intermediate	38,2	41,0	42,0	43,0	41,9	41,4	40,7	41,6	41,2
Upper	39,0	42,3	42,8	44,1	42,3	42,3	41,9	43,1	42,2
N Treatment Mean	38,2	41,3	42,0	43,2	41,7	41,3	40,9	41,5	41,3

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 0,93	1,90	2,56
Between primary branch means	± 0,16	0,31	0,41
Between primary branches at same nitrogen treatment	± 0,44	0,88	1,16
Between nitrogen treatments for same primary branch	± 0,99	2,03	2,72

TABLE 25 Effect of tiller position in the plant and nitrogen supply on the seed mass per inflorescence (mg) of weeping lovegrass

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	444	599	495	482	446	490	483	496	492
1st primary	304	422	370	327	347	379	322	324	349
2nd primary	357	455	403	409	385	396	351	397	394
1st secondary	220	323	325	311	312	287	304	281	295
2nd secondary	259	384	356	356	269	375	376	329	338
N Treatment Mean	317	437	390	377	352	385	367	365	374

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 28,1	57,6	77,7
Between labelled tiller means	± 12,3	24,3	32,1
Between labelled tillers at same nitrogen treatment	± 34,7	68,6	90,7
Between nitrogen treatments for same labelled tiller	± 41,9	84,2	112,3

seed than the first primary and first secondary inflorescence respectively. The variation between main shoot, first primary and first secondary inflorescence means and between first and second inflorescence means at both primary and secondary orders was highly significant ($p = 0,01$).

The optimum time of application of nitrogen for maximum seed production in each tiller was at the onset of the reproductive stage of growth in the plant (treatment 2). The response to a single dressing of nitrogen declined the later it was applied during the development of the inflorescence. The application of nitrogen as a split dressing also increased seed production per inflorescence particularly when nitrogen was applied at inflorescence initiation and again at initial anthesis (treatment 6). However, the effect was generally not as great as obtained with single dressings.

The greatest response to nitrogen when applied at inflorescence initiation (treatment 2) was obtained from seed in the main shoot inflorescence. The mass of seed produced by this inflorescence at treatment 2 was significantly greater than of any other nitrogen treatment to at least the 5 per cent level of probability.

The greatest response to nitrogen in terms of the mass of the seed produced was obtained in the secondary inflorescences. In both secondary inflorescences seed mass was increased considerably when single or split dressings of nitrogen were applied at any time during the development of the main shoot inflorescence. The variation in seed size between nitrogen treatments and the control treatment was generally significant to at least the 5 per cent level of probability. As a comparison, the mass of seed produced in the main shoot inflorescence and in each primary inflorescence was only significantly heavier in treatment 2, when compared with the respective seed mass in these inflorescences in the control treatment ($p = 0,01$).

e) Correlation Coefficients between Certain Characters

The association between seed mass produced per inflorescence and some of its components was considered. The correlation coefficients presented in Table 26 were obtained from the combined data of all labelled inflorescences.

The number of florets per spikelet (4) and per inflorescence (5) and the number of these which became fertile (6) all showed a high positive correlation with seed yield. These correlations, and the negative relationship between the number of primary branches per inflorescence (2) and seed yield per inflorescence, were highly significant ($p = 0,01$).

The number of primary branches and spikelets per inflorescence (3) generally showed a high negative correlation with the other yield components. However, spikelet number per inflorescence was positively correlated with floret number per inflorescence (5).

While spikelet size (4) showed a high positive correlation with fertility (6) and to a lesser extent with seed size (7) the relationship between the two latter yield components was significantly negative ($p = 0,01$).

Inflorescence length (1) was positively correlated with all characters except the number of primary branches in the inflorescence. The relationship between inflorescence length and floret numbers per inflorescence was highly significant ($p = 0,01$). This was due almost solely to the number of florets per spikelet as the correlation between inflorescence length and spikelet numbers per inflorescence was negligible. Inflorescence length showed a high positive correlation with seed yield per inflorescence ($p = 0,01$).

The relationships between associated characters and seed mass in each order of labelled tillers are shown individually in Table 27.

In all labelled inflorescences the number of florets per inflorescence (5) showed the highest positive correlation with seed yield per inflorescence, while the number of florets per spikelet (4)

TABLE 26 Correlation coefficients between seven characters with each other and with yield of seed in the weeping lovegrass inflorescence (analysis from data of all labelled inflorescences)

	2	3	4	5	6	7	8
1. Inflorescence length (cm)	-0,308**	+0,011	+0,371**	+0,423**	+0,251*	+0,337**	+0,507**
2. Primary branches/ inflorescence		+0,405**	-0,371**	-0,069	-0,349**	-0,192	-0,310**
3. Spikelets per inflorescence			-0,484**	+0,281**	-0,209*	-0,146	-0,024
4. Florets per spikelet				+0,692**	+0,335**	+0,223*	+0,754**
5. Florets per inflorescence					+0,205*	+0,121	+0,816**
6. Floret fertility (%)						-0,303**	+0,640**
7. 100 seed mass (mg)							+0,191
8. Seed yield/ inflorescence (mg)							-

* Significant at 5% level

** Significant at 1% level

Multiple correlation coefficient

r = 0,998** (198 d.f.)

TABLE 27 Correlation coefficients between seven characters with each other and with yield of seed in five labelled inflorescences of weeping lovegrass

(a) Main shoot inflorescence

	2	3	4	5	6	7	8
1. Inflorescence length (cm)	+0,285	+0,021	-0,089	-0,049	+0,173	-0,013	+0,106
2. Primary branches/ inflorescence		+0,372*	+0,006	+0,271	+0,113	+0,081	+0,363*
3. Spikelets per inflorescence			-0,234	+0,505**	-0,128	+0,153	+0,409**
4. Florets per spikelet				+0,716**	-0,088	-0,046	+0,550**
5. Florets per inflorescence					-0,158	+0,062	+0,790**
6. Floret fertility (%)						-0,550**	+0,418**
7. 100 seed mass (mg)							-0,051
8. Seed yield per inflorescence (mg)							-

* Significant at 5% level

** Significant at 1% level

Multiple correlation coefficient

r = 0,993** (38 d.f.)

TABLE 27 (b) First primary inflorescence

	2	3	4	5	6	7	8
1. Inflorescence length (cm)	-0,041	+0,038	+0,368*	+0,378*	-0,026	+0,104	+0,304
2. Primary branches/ inflorescence		+0,439**	-0,119	+0,169	+0,011	+0,048	+0,165
3. Spikelets per inflorescence			-0,235	+0,427**	+0,025	+0,111	+0,390*
4. Florets per spikelet				+0,775**	-0,086	+0,011	+0,594**
5. Florets per inflorescence					-0,070	+0,083	+0,804**
6. Floret fertility (%)						-0,435**	+0,447**
7. 100 seed mass (mg)							+0,108
8. Seed yield per inflorescence (mg)							-

* Significant at 5% level

** Significant at 1% level

Multiple correlation coefficient

r = 0,992** (38 d.f.)

TABLE 27 (c) Second primary inflorescence

	2	3	4	5	6	7	8
1. Inflorescence length (cm)	+0,052	-0,060	+0,327*	+0,250	-0,048	+0,206	+0,214
2. Primary branches/ inflorescence		+0,614**	-0,074	+0,439**	-0,436**	-0,111	+0,006
3. Spikelets per inflorescence			-0,204	+0,668**	-0,170	-0,121	+0,322*
4. Florets per spikelet				+0,572**	-0,039	-0,010	+0,470**
5. Florets per inflorescence					-0,163	-0,050	+0,650**
6. Floret fertility (%)						+0,083	+0,563**
7. 100 seed mass (mg)							+0,322*
8. Yield of seed/ inflorescence (mg)							-

* Significant at 5% level

** Significant at 1% level

Multiple correlation coefficient

r = 0,990** (38 d.f.)

TABLE 27 (d) First secondary inflorescence

	2	3	4	5	6	7	8
1. Inflorescence length (cm)	+0,160	+0,038	+0,405**	+0,319*	-0,106	+0,399*	+0,310*
2. Primary branches/ inflorescence		+0,376*	+0,035	+0,292	-0,291	-0,035	+0,022
3. Spikelets per inflorescence			-0,150	+0,621**	-0,047	-0,186	+0,335*
4. Florets per spikelet				+0,670**	+0,217	+0,119	+0,656**
5. Florets per inflorescence					+0,153	-0,078	+0,771**
6. Floret fertility (%)						-0,571**	+0,615**
7. 100 seed mass (mg)							-0,064
8. Yield of seed/ inflorescence (mg)							-

* Significant at 5% level

** Significant at 1% level

Multiple correlation coefficient

r = 0,984** (38 d.f.)

TABLE 27 (e) Second secondary inflorescence

	2	3	4	5	6	7	8
1. Inflorescence length (cm)	+0,279	+0,123	+0,364*	+0,362*	+0,074	+0,337*	+0,428**
2. Primary branches/ inflorescence		+0,217	+0,006	+0,172	-0,189	+0,335*	+0,071
3. Spikelets per inflorescence			-0,171	+0,702**	-0,127	+0,053	+0,324*
4. Florets per spikelet				+0,569**	+0,264	+0,162	+0,621**
5. Florets per spikelet					+0,121	+0,121	+0,731**
6. Floret fertility (%)						-0,595**	+0,657**
7. 100 seed mass (mg)							-0,007
8. Yield of seed/ inflorescence (mg)							-

* Significant at 5% level

** Significant at 1% level

Multiple correlation coefficient

r = 0,985** (38 d.f.)

appeared to have a greater effect than the number of spikelets in each inflorescence (3). In the main shoot and primary inflorescences the relationship between spikelet size and number of florets per inflorescence was much greater than that between spikelet numbers and the number of florets per inflorescence.

In all inflorescences floret fertility (6) showed a high positive correlation with seed yield per inflorescence. The fertility effect on yield appeared to increase through the tiller orders, as the position of the fertile tiller moved further out from the main shoot.

Seed size (7) had little influence on seed yield per inflorescence except in the second primary inflorescence when a high positive correlation between this character and seed yield was obtained.

f) Plant Growth and Development (Table 28)

The greatest number of inflorescences per plant at harvest was obtained in treatment 2. The number of inflorescences declined as nitrogen was applied at a later stage in the development of the main shoot inflorescence. The difference of approximately 4 seedheads per plant between treatments 2 and 4 was highly significant ($p = 0,01$). There appeared to be little benefit in applying nitrogen as a split dressing as compared with a single application at the onset of the reproductive phase or at ear emergence. However, all nitrogen treatments significantly increased the number of seedheads per plant to at least the 5 per cent level of probability, as compared with the control treatment.

The percentage of tillers which became fertile in each plant ranged between 11,0 per cent and 15,5 per cent. Nitrogen appeared to have a slight detrimental effect on tiller fertility except in treatment 2.

Plant size, in terms of tiller production and herbage dry matter production was increased significantly at each nitrogen treatment as compared with the control treatment ($p = 0,01$). The time of appli-

TABLE 28 Effect of nitrogen, applied at different physiological stages of reproductive growth on plant growth and development of weeping lovegrass

Nitrogen Treatment Number	Growth and Development per Plant				
	No. inflo-rescences	No. veg. tillers	Total No. Tillers	% tillers fertile	Herbage dry matter (g)
1	8,4	51,2	59,6	14,1	13,7
2	15,4	83,8	99,2	15,5	28,4
3	14,2	90,8	105,0	13,5	31,0
4	11,2	90,6	101,8	11,0	29,9
5	13,6	91,8	105,4	12,0	29,3
6	11,4	75,0	86,4	13,2	23,6
7	11,6	90,4	102,0	11,4	29,3
8	13,0	81,8	94,8	13,7	27,0
Between Treatments:					
S.E.	± 1,16	± 6,26	± 6,37		± 1,82
L.S.D. 5%	2,36	12,75	12,99		3,71
L.S.D. 1%	3,18	17,15	17,47		4,99

cation of either a single or split nitrogen dressing was of little consequence to either tiller or herbage production.

3. DISCUSSION

The results obtained in this experiment have shown in some detail certain aspects of the physiology of seed production in an individual weeping lovegrass seedhead. The position of the tiller in the plant appeared to have a considerable effect on the size of the inflorescence and on the capacity of this inflorescence to produce seed. The response of both these characters to variations in the time at which nitrogen was applied to the plant was also considerable.

a) Tiller Position in Relation to Inflorescence Size and Seed Yield

i. Inflorescence size. Experiments with temperate grasses have shown that inflorescence size is largely dependent upon the date of

origin of the shoot and hence its age when flowering begins (Langer, 1956; Ryle, 1963b; 1964). The position of the tiller in the plant also influences the size of the inflorescence. Langer and Ryle (1959) found in timothy that primary tillers produced heavier and larger ears when compared with secondary tillers of the same age.

The present experiment has shown that inflorescence size in weeping lovegrass depended also on the position of the tiller in the plant. However, it is debatable whether the tillers selected in this experiment were of the same generation. As shown in Table 9 the primary tillers emerged about 12 days after the main shoot and the secondary tillers after approximately 23 days. Reproductive growth began in the main shoot only 40 days after sowing and 10-11 days after emergence of the secondary tillers. In the field, it is expected that the labelled tillers would emerge at approximately the same time relative to the growth and development of the crop. However, in this glasshouse experiment the influence of the position of the tiller on development of the inflorescence is considered to be confounded with the influence of tiller age.

In weeping lovegrass the main shoot inflorescence contained the largest number of florets and the primary and secondary tillers, arising in lower orders of succession and at later dates, carried progressively smaller ears in terms of floret numbers (Table 18). The number of florets per inflorescence is dependent upon the number of spikelets in the inflorescence and the number of florets developed per spikelet. Both these characters were highly correlated with floret production per inflorescence (Table 19).

Analysis of each component showed that the decrease in inflorescence size from main shoot to secondary tiller was caused solely by a marked decrease in spikelet size. Spikelet size showed a high negative correlation with spikelet number per inflorescence (Table 27) and the main shoot inflorescence had significantly fewer primary

branches (Table 15) and spikelets (Table 16) than either the primary or secondary inflorescences ($p = 0,01$).

In temperate species it is generally acknowledged that an increase in the duration of vegetative growth before the onset of reproduction will be followed by an increase in the number of florets in the inflorescence brought about by an increase in the number of spikelets and number of florets per spikelet (Ryle, 1966). The increase in duration of vegetative growth, or an increase in the age of the tiller prior to reproductive growth has been shown to increase the accumulation of leaf primordia on the vegetative apical meristem (Ryle and Langer, 1963b). The number of spikelet primordia developed depends largely on the number of leaf primordia on the shoot apex at inflorescence initiation (Ryle, 1966). A high positive correlation between the number of spikelet branches in the inflorescence and the accumulation of leaf primordia on the vegetative apical meristem immediately prior to reproductive growth has been recorded in three temperate grasses (Ryle, 1964).

There is no evidence to suggest that inflorescence development in weeping lovegrass does not follow the same pattern. Therefore an increase in the number of leaf primordia accumulated on the apical meristem at inflorescence initiation should result in an increase in the number of primary branches and number of spikelets in the inflorescence. In this experiment it would appear that the primary and secondary tillers were larger at the onset of reproductive growth and contained a larger apical meristem than the main shoot, despite the shorter period between tiller emergence and inflorescence initiation in these lower order tillers. The primary tillers, and to a lesser extent, the secondary tillers developed at a faster rate to inflorescence initiation than the main shoot (Table 9). It is possible that leaves developed at a faster rate in the primary and secondary tillers as compared with leaf development in the main shoot and that more leaf

primordia had accumulated on the apical meristems of these tillers at inflorescence initiation.

In the main shoot the large number of florets per spikelet more than compensated for the reduced number of spikelets in the inflorescence. The development of fewer florets per spikelet is presumably related to the status of the shoot as a whole and influenced by other shoots and therefore intraplant competition similar to that reported by Donald (1954) in wimmera ryegrass (Lolium rigidum). It appears that the availability of metabolites sets an upper limit to the number of florets that can be developed not only in the spikelet but also in the inflorescence as a whole. The main shoot was able therefore to compete more successfully for metabolites than the lower order tillers, thus restricting the movement of metabolites to these tillers during inflorescence differentiation and reducing the number of florets developed in the spikelet.

In addition, competition between spikelets in inflorescences produced by the primary and secondary tillers may have intensified because of the increased spikelet number in these inflorescences. This may have further restricted floret production in each spikelet and/or caused more florets to degenerate during inflorescence development. Competition for metabolites between spikelets in the main shoot inflorescence was possibly reduced because of the smaller number of spikelets in the inflorescence allowing each spikelet to carry more florets.

In weeping lovegrass the reduction in spikelet size between inflorescences was almost double that on the upper primary branches as compared with the basal branches (Table 16). This was due largely to the increased size of spikelets in the upper primary branches in the main shoot inflorescence as compared with those spikelets on the basal primary branches.

This also suggests that there was little if any competition for

assimilates between spikelets in the main shoot inflorescence, and that competition increased in the lower order tillers. With further development competition intensified not only between inflorescences but also between spikelets in the same seedhead. Consequently the spikelets developed in the upper parts of the primary and secondary inflorescences were smaller and carried fewer florets than the more basally located and earlier formed spikelets.

In this experiment results show that the second primary and second secondary inflorescences carried more primary branches (Table 15), more spikelets (Table 16) and slightly larger spikelets (Table 17) than the first primary and first secondary inflorescences respectively. Consequently the second tiller to emerge in each order developed the larger inflorescence than the first tiller (Table 18). Both tillers in each order emerged at about the same time and developed at approximately the same rate (Table 9) so that these factors were not responsible for the differences.

In all plants the first secondary tiller developed from an axillary bud on the first primary tiller and the second secondary tiller from the second primary tiller. It is possible that the parent tiller may have exerted some influence on the development of the associated tillers. This would explain the smaller ear size of the first secondary tiller as compared with that of the second secondary tiller.

The reduced seed-producing potential of the first primary tiller as compared with the second is difficult to explain. Any explanation offered must attribute the reduced ear size to restricted growth of the first primary tiller, the result of some environmental, hormonal or genetic factor within the plant.

ii. Seed yield per inflorescence. The number of florets in each inflorescence is a measure of the potential number of seeds the inflorescence is able to produce. The actual number of seeds in the inflo-

rescence is dependent upon the success or failure of florets to set seed. Research has indicated that floret fertility is not only genetically controlled but also controlled by environmental factors (Ryle, 1966). The position of the tiller in the plant and presumably the associated age of the tiller appear to influence floret fertility in weeping lovegrass according to results obtained in this experiment (Table 19).

The capacity of florets to set seed was higher in the main shoot inflorescence than in the lower order tillers and there was a progressive decline in fertility between the lower orders. An analysis of seed yield components between inflorescences showed that fertility was highly correlated with spikelet size and to a lesser extent with inflorescence size (Table 26). It would appear therefore that the florets in a larger spikelet or larger seedhead had the greater opportunity to set seed than those florets in a smaller spikelet or seedhead. In ryegrass, Anslow (1963) found that the proportion of florets setting seed declined as heads emerged later. In weeping lovegrass the primary and secondary inflorescences were not only smaller but also emerged progressively later than the main shoot.

Spikelets on the basal primary branches of labelled inflorescences were more fertile than those on the upper primary branches (Table 20). Similar gradations in fertility in the inflorescence have been obtained in ryegrass (Anslow, 1963) and in wheatgrass and bromegrass (Knowles and Baenziger, 1962).

When seed is set, the evidence suggests that some embryos die soon after pollination (Johnston, 1960) and that even when development continues there is great variation in the final mass attained by the individual seeds (Anslow, 1964). In single plants of weeping lovegrass the main shoot inflorescence produced the heaviest seed (Table 22) and within each inflorescence the upper spikelets developed heavier seed than those more basally located (Table 23).

The primary inflorescences, and to an even greater extent the secondary inflorescences, contained fewer florets and fewer and lighter seeds than the main shoot inflorescence. This suggests that the ability of the lower order tillers to compete for assimilates decreased during inflorescence development and also during development of the seed. Donald (1954) implied that evidence of differences in seed mass and in number of seeds per inflorescence indicated intra-plant competition or, more precisely, competition between inflorescences.

Seed size showed little correlation with the size of the spikelet in which the seed developed (Table 27). However, seed size showed a high negative correlation with floret fertility (Table 27), suggesting that final seed size was influenced to a large extent by competition between developing seeds for assimilates.

The basal primary branches in the weeping lovegrass inflorescence carried a greater number of spikelets than the upper primary branches. In the average inflorescence the basal spikelets varied little in size from the upper ones but were slightly more fertile. Therefore, a greater number of seeds were formed and developed on the basal primary branches. Competition for assimilates between spikelets and between developing seeds in each spikelet on the basal primary branches was presumably much more intense than between and within the spikelets on the upper primary branches. Thus the heavier seed developed in spikelets on the upper branches of the weeping lovegrass inflorescence. However, it must also be assumed that competition between and within spikelets on the one primary branch was greater than competition for assimilates between primary branches in the inflorescence. This assumption would not be so important if the ear itself photosynthesises actively and retains its own assimilates as occurs in many cereals (Thorne, 1965; 1966).

The yield or mass of seed produced in each inflorescence is therefore dependent upon the number of florets in the inflorescence, the

proportion of these which become fertile and the size or mass of each individual seed. In each tiller seed yield showed a high positive correlation with the number of florets per inflorescence and with floret fertility (Table 27). There was no close relationship between seed size and seed yield except in the second primary inflorescence, in which it was also noted that floret fertility showed a low positive correlation with seed size; the only inflorescence to show this. Therefore, there appeared to be some interaction between seed size and floret fertility which affected the relationship of seed size with seed yield per inflorescence.

b) Nitrogen Supply, Inflorescence Size and Seed Yield

Potential ear size depends on the age of the shoot at flowering and its position in the plant. Whether this potential is realised depends to a large extent on the influence of several environmental factors at flowering, including day length and temperature (Ryle, 1965; Ryle and Langer, 1963b), light intensity or the degree of shading (Ryle, 1967) and the level of nitrogen supply (Langer, 1959b; Ryle, 1963b; 1964). A sufficient supply of mineral nutrients must be available to allow the inflorescence to grow to maximum size. The results reported in this experiment show the effect of applying the same level of nitrogen at various stages of reproductive growth in the weeping lovegrass inflorescence.

Nitrogen had no effect on the rate of reproductive development to anthesis in any of the inflorescences studied and had no significant effect on the number of primary branches (Table 13) and number of spikelets produced per inflorescence (Table 14). Floret fertility was also little affected by the application of nitrogen at or after inflorescence initiation (Table 19).

The greatest effect of nitrogen, applied during inflorescence development, was the significant increase in the number of florets developed per spikelet (Table 15). This increase in spikelet size was

largely responsible for the marked increase in floret numbers per inflorescence in each nitrogen treatment (Table 18).

In ryegrass, meadow fescue and cocksfoot Ryle (1964) found that the main effect of a higher level of nitrogen was to increase the number of florets developed on the primary branches. In single plants of timothy increased levels of nitrogen increased the number of florets in inflorescences of most tillers (Langer, 1959b; Ryle, 1963b). A high nitrogen supply during inflorescence development in plants of Paspalum plicatulum significantly increased the number of seeds per inflorescence (Chadhokar and Humphreys, 1970).

The greatest increase in mean spikelet size followed the single application of nitrogen at initiation of the main shoot inflorescence. Similarly, the mean number of florets per inflorescence was maximal when nitrogen was applied at this stage (treatment 2). However, an analysis of each individual tiller showed that the response to nitrogen as applied in treatment 2 declined with increasing order of succession of tillers. There was little difference in floret number per spikelet or per inflorescence in the secondary inflorescences when nitrogen was applied as a single dressing at initiation, or emergence or initial anthesis of the main shoot inflorescence.

The optimum time of nitrogen application for maximum floret production in each inflorescence appeared to be prior to the onset of reproductive growth in each respective tiller. For example, inflorescence initiation occurred in the first secondary tiller approximately 61 days after sowing (Table 9). As a result nitrogen applied at initial anthesis in the main shoot inflorescence (treatment 4) coincided with a stage immediately prior to inflorescence initiation in the first secondary tiller, and was able therefore to stimulate floret production in this inflorescence. The effect of nitrogen applied at this time was even greater in the second secondary inflorescence.

The increase in number of florets per spikelet was greatest in the

secondary inflorescences. In addition, while nitrogen had only a small positive effect on spikelet production in the main shoot and primary inflorescences, it significantly increased the number of spikelets in the second secondary inflorescence (Table 14). Consequently the greatest response to nitrogen, in terms of floret production per inflorescence, was obtained in the secondary tillers.

Under conditions of low nitrogen supply, as obtained in the control treatment, the secondary tillers, because of their position in the plant, were presumably affected adversely by intense competition for assimilates during inflorescence development. This resulted in a marked decline in floret number due largely to a reduction in spikelet size. An increase in nitrogen supply apparently improved the supply of assimilates to the developing inflorescences, and particularly the secondary inflorescences, resulting in an increase in floret production and/or a reduction in the incidence of floret degeneration in the developing spikelet.

Nitrogen was responsible for the production of heavier seed in the primary and secondary inflorescences but had little effect on seed mass in the main shoot inflorescence (Table 22). Maximum seed size in the primary tillers was obtained when nitrogen was applied at ear emergence in the main shoot (treatment 3) and this coincided closely with inflorescence initiation in the first primary tiller.

The greatest increase in seed mass was obtained in the secondary inflorescences. The heaviest seed in these inflorescences was recorded following the application of nitrogen at initial anthesis in the main shoot inflorescence (treatment 4) and immediately prior to inflorescence initiation in the first secondary tiller. Therefore it would appear that the optimum time of nitrogen application to increase seed size was also immediately prior to the onset of reproductive growth in each tiller.

Apart from some recent research by Ryle (1970; 1972) and Ryle and

Powell (1972) little is known of the mechanism involved in seed fill in the grasses. According to Donald (1954) variability in seed size depends to a large extent on the incidence of intraplant competition for assimilates. Anslow (1964) has emphasised the influence of competition for light and the products of photosynthesis. In cocksfoot, the mass of seed produced per plant was reduced by aerial competition which was considered to be competition for light (Lambert, 1968).

In recent times much attention has been given to the source of carbohydrates deposited in the grain, particularly in cereals. In high yielding cereal crops Thorne (1966) and Yoshida (1972) have suggested that carbohydrates translocated to the endosperm are mostly derived from photosynthesis after ear emergence. The carbon assimilated by the flag-leaf is translocated predominantly to the developing ear and ear photosynthesis itself may contribute a major portion of the total carbohydrate in the seedhead (Thorne, 1966; Yoshida, 1972).

Increasing the nitrogen supply to the plant not only increases the availability of nitrogenous products necessary for grain development but also increases the supply of carbohydrate to the seeds. According to Murata (1969) nitrogen promotes leaf area expansion if applied prior to ear emergence, and stimulates the photosynthetic activity of the leaf and prevents any decline in the photosynthetically active area if applied after ear emergence. As a result photosynthetic activity vital for seed development is maintained for longer periods, the supply of carbohydrate is increased, competition for assimilates is reduced and seed size subsequently increased.

The results recorded in Table 25 show that nitrogen applied during inflorescence development in weeping lovegrass had a marked effect on the mass of seed produced per inflorescence. The optimum time of nitrogen application in this experiment was at the onset of reproductive growth in the main shoot, and the response declined as the time

of application was delayed. There was little benefit when nitrogen was applied as a split dressing for it is suspected that the second application followed too soon after the first to show any distinct effect. If this is so, different conclusions would be expected in the field where the rate of development of the tillers is much slower than in the glasshouse. However, this glasshouse experiment did show that applying nitrogen as a split dressing at inflorescence initiation and again at initial anthesis yielded a greater seed mass per inflorescence than a single application of nitrogen at initial anthesis.

Because the greatest response to applied nitrogen was obtained when the primary and, more especially, the secondary tillers had not yet reached the reproductive phase of growth it seemed desirable to gain some knowledge of the influence of nitrogen on seed production in the same tillers when applied prior to reproductive growth. Therefore, a second experiment was carried out when increased levels of nitrogen were applied at different physiological stages of vegetative growth.

EXPERIMENT 3 EFFECT OF THE POSITION OF THE TILLER IN THE PLANT AND OF NITROGEN, APPLIED AT DIFFERENT PHYSIOLOGICAL STAGES OF VEGETATIVE GROWTH, ON THE CAPACITY OF THE INFLORESCENCE TO PRODUCE SEED

1. EXPERIMENTAL METHODS

a) Procedure

120 plants of the Ermelo strain of weeping lovegrass were grown from seed in pots in a temperature controlled glasshouse. The experimental conditions, design and procedure were the same as those described for the previous experiment.

In this experiment seed was sown directly into pots on 3 June 1972 and the harvesting of seedheads began approximately 15 weeks later on 16 September.

b) Treatments

Nitrogen was applied as nitrate in eight treatment combinations (Table 29). The times of application coincided with emergence of the first, third and fifth primary tillers. Each treatment received either a 'basal' or an 'increased' level of nitrogen at each time of application. The basal dressing (1N) supplied 0,06g N per pot and the increased level (4N) supplied 0,24g N per pot.

TABLE 29 The rate and time of nitrogen application for each treatment (Treatment no. 1 - control treatment)

Time of Nitrogen Application	Nitrogen Treatment Number							
	1	2	3	4	5	6	7	8
First primary tiller	1N	4N	1N	1N	4N	4N	1N	4N
Third primary tiller	1N	1N	4N	1N	4N	1N	4N	4N
Fifth primary tiller	1N	1N	1N	4N	1N	4N	4N	4N
Total Nitrogen Applied	3N	6N	6N	6N	9N	9N	9N	12N

The control treatment, treatment 1, received a basal dressing at each application while, at the other extreme, treatment 8 comprised 3 applications of the increased level of nitrogen. Consequently total

amounts of nitrogen supplied throughout the experiment ranged from 0,18g N to 0,72g N per pot.

c) Observations and Recordings

The same observations and recordings were made in this experiment as for the previous one.

The number of florets per spikelet and the capacity of these florets to set seed were recorded at selected primary branch positions within the inflorescence as described for the previous experiment. In addition, the positional effect of the spikelet on the selected basal primary branch on these two components of seed production was also analysed in this experiment. The basal, an intermediate and the penultimate spikelet from the basal primary branch were isolated from the remaining spikelets and each one analysed. This analysis was carried out on the basal primary branch only because of possible errors induced by shedding at the upper primary branch positions. Also the greater spikelet numbers on the basal primary branches, and so their greater contribution to seed yield, meant a greater chance of relating spikelet characteristics to seed yield.

Analysis of variance of this data was carried out and where F tests indicated significance (Appendix A, Tables 4-7) least significant difference (L.S.D.) tests were applied at both the 5 and 1 per cent levels of probability.

2. RESULTS

a) Inflorescence Development (Table 30)

The first secondary tiller emerged approximately 12 days after the first primary tiller and 32 days after the main shoot. Development to inflorescence initiation occurred at a much faster rate in the first secondary tiller than in either the first primary or main shoot tillers. The 32 day interval between emergence of the main shoot and first secondary tiller was reduced to about 24 days at inflorescence

initiation. In other words development of the main shoot to inflorescence initiation took 8-9 days longer than the first secondary tiller. This time interval was maintained throughout the development of both inflorescences. The rate of development of each labelled inflorescence appeared therefore to be similar.

TABLE 30 Time of inflorescence initiation and differentiation of the main shoot and labelled primary and secondary tillers (average for all nitrogen treatments)

	Labelled Tiller				
	Main Shoot	First Primary	Second Primary	First Secondary	Second Secondary
Days to tiller emergence from sowing	11,4	31,3	34,5	43,8	46,3
Days to inflorescence initiation from tiller emergence	40,7	37,2	*	32,0	*
Days to ear emergence from tiller emergence	50,4	46,4	40,5	41,8	40,0
Days to peak anthesis from tiller emergence	67,0	63,2	58,2	59,8	58,3
Days to peak anthesis from sowing	78,4	95,0	92,7	103,6	104,6

* not recorded

i. Time of ear emergence (Table 31). The influence of tiller position in the plant on the development of the tiller to ear emergence is shown further in Table 31. The average time taken by the main shoot to reach ear emergence was 4 days and 8 days longer than the time taken by the first primary and first secondary inflorescences respectively. The variation in the time interval to ear emergence between these three labelled inflorescences was highly significant ($p = 0,01$).

The average time taken for tillers to reach ear emergence was reduced when nitrogen was applied. However, a single dressing of nitrogen at either inflorescence initiation (treatment 2) or at initial anthesis (treatment 4) had no significant effect on development in

TABLE 31 Effect of nitrogen supply on time of ear emergence (as number of days from tiller emergence) in the main shoot and labelled primary and secondary tillers of weeping lovegrass

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main Shoot	50	51	49	50	50	51	48	52	50
1st primary	53	50	46	45	43	41	44	43	46
2nd primary	45	40	39	41	39	38	40	40	40
1st secondary	45	44	40	42	41	42	41	40	42
2nd secondary	44	39	39	40	41	39	41	37	40
N Treatment Mean	47	45	43	44	43	42	43	42	44

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 1,5	3,1	4,1
Between labelled tiller means	± 0,6	1,3	1,7
Between tillers at same nitrogen treatment	± 1,8	3,7	4,8
Between nitrogen treatments for same tiller	± 2,2	4,5	6,0

TABLE 32 Effect of tiller position in the plant and nitrogen supply on the length of stem (cm) of the weeping lovegrass culm

Labelled Tiller	Nitrogen Treatment Mean								Tiller Mean
	1	2	3	4	5	6	7	8	
Main Shoot	127,2	116,2	117,2	116,0	118,8	116,6	118,0	122,4	119,1
1st primary	136,4	125,0	123,8	130,4	127,8	126,2	132,8	128,0	128,8
2nd primary	139,2	129,4	129,0	128,2	132,0	125,8	131,4	128,0	130,4
1st secondary	133,2	134,2	128,2	137,8	138,0	128,8	131,8	128,2	132,5
2nd secondary	136,6	130,6	127,0	135,8	137,2	128,8	135,6	135,6	133,4
N Treatment Mean	134,5	127,1	125,0	129,6	130,8	125,2	129,9	128,4	128,8

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 3,05		
Between labelled tiller means	± 1,72	3,40	4,49
Between tillers at same nitrogen treatment	± 4,86	9,61	12,71
Between nitrogen treatments for same tiller	± 5,31		

individual tillers. The remaining treatments had a significant effect particularly treatment 6 and treatment 8 in which the average time taken for tillers to reach ear emergence was 5 days less than in the control treatment; this reduction in time was highly significant ($p = 0,01$).

Development of the main shoot to ear emergence was not affected by the application of nitrogen at any treatment. The first primary and second primary inflorescence emerged 12 days and 7 days earlier, respectively, in treatment 6 as compared with the time taken in the control treatment. These differences were highly significant ($p = 0,01$).

Nitrogen as applied in treatment 8 resulted in the fastest rate of development of the secondary tillers to ear emergence. This applied especially to the second secondary tiller whose inflorescence emerged 7 days earlier in this treatment than in the control treatment.

b) Culm Size

i. Stem length (Table 32). Stem length increased as the position of the tiller moved further away from the main shoot. The variation in stem length between the main shoot mean and the primary tiller means was highly significant ($p = 0,01$). There were no significant differences between either primary or secondary tiller means but the average length of the first primary stem was significantly shorter than that of the first secondary stem ($p = 0,05$).

The application of the increased level of nitrogen had no significant effect on stem length and any variation between treatment means was not significant.

ii. Stem mass (Table 33). The position of the tiller in the plant had much the same effect on stem mass as on stem length. The main shoot developed the lightest stem in each treatment and the heaviest recorded stem was generally that produced by the second secondary tiller. The main shoot mean was significantly lighter than

the primary and secondary tiller means (p = 0,01).

In most treatments the main shoot and primary tiller stems were consistently lighter than in the control treatment but this effect was not significant. On the other hand, more than one application of the high nitrogen level in a treatment increased the mass of the secondary tiller stems by as much as 400-500 mg. The greatest response was obtained in treatment 5 and treatment 7. The variation in stem mass of both secondary tillers between the control treatment and most nitrogen treatments was significant to at least the 5 per cent level of probability.

iii. Inflorescence length (Table 34). There was little variation in inflorescence length between the main shoot, first primary and second primary tiller means. However, the secondary inflorescences were, on average, 4-5 cm shorter than primary inflorescences and this difference was highly significant (p = 0,01).

Increasing nitrogen supply to the plant at any stage prior to inflorescence initiation had a significant effect on the length of inflorescence produced by the primary and secondary tillers (p = 0,01). The greatest response to nitrogen was obtained in the secondary inflorescences. A single dressing of the increased nitrogen level (treatments 2, 3 and 4) had a highly significant effect (p = 0,01) on the length of the second secondary inflorescence when compared with the control treatment. A double dressing of the increased level as applied in treatments 5, 6 and 7 had a greater effect so that the variation between single and double dressings of the increased nitrogen level was significant to at least the 5 per cent level of probability. The triple application of the high nitrogen level at treatment 8 was generally not as effective as the double dressing but still resulted in a significantly longer second secondary inflorescence than that obtained following a single application of the high nitrogen level (p = 0,05).

TABLE 33 Effect of tiller position in the plant and nitrogen supply on the stem dry mass (g) of the inflorescence culm of weeping lovegrass

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main Shoot	1,13	1,02	1,01	0,97	1,08	1,02	0,94	1,08	1,03
1st primary	1,39	1,24	1,28	1,29	1,37	1,28	1,41	1,25	1,31
2nd primary	1,43	1,33	1,31	1,35	1,45	1,38	1,43	1,32	1,38
1st secondary	1,09	1,41	1,24	1,38	1,56	1,38	1,58	1,23	1,36
2nd secondary	1,18	1,46	1,35	1,51	1,48	1,54	1,48	1,46	1,43
N Treatment Mean	1,24	1,29	1,24	1,30	1,39	1,32	1,37	1,27	1,30

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 0,086		
Between labelled tiller means	± 0,039	0,077	0,102
Between tillers at same nitrogen treatment	± 0,110	0,217	0,287
Between nitrogen treatments for same tiller	± 0,131	0,262	0,350

TABLE 34 Effect of tiller position in the plant and nitrogen supply on the length of inflorescence (cm) of weeping lovegrass

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	37,2	38,4	37,4	38,4	38,8	39,4	38,2	38,0	38,2
1st primary	34,2	39,0	38,6	39,2	41,2	39,4	41,2	40,8	39,2
2nd primary	32,2	39,2	36,4	39,8	40,6	40,4	41,8	41,2	39,0
1st secondary	22,0	34,4	34,4	32,4	39,8	35,6	38,4	38,2	34,4
2nd secondary	22,6	34,6	34,4	34,0	40,4	39,4	39,4	38,8	35,5
N Treatment Mean	29,6	37,1	36,2	36,8	40,2	38,8	39,8	39,4	37,2

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 1,47	3,01	4,07
Between labelled tiller means	± 0,53	1,05	1,39
Between tillers at same nitrogen treatment	± 1,50	2,97	3,93
Between nitrogen treatments for same tiller	± 1,99	4,02	5,37

An analysis of the treatment means shows that the longest inflorescence was obtained when the high level of nitrogen was applied at emergence of the first and the third primary tiller (treatment 5). In this treatment the average inflorescence was significantly longer than the inflorescence produced when a single dressing of the high nitrogen level was applied ($p = 0,01$).

c) Inflorescence Size

i. Number of primary branches per inflorescence (Table 35). Increased levels of nitrogen generally increased the number of primary branches on each inflorescence, particularly in the secondary inflorescences. However, the effect was usually small and not significant.

In each treatment the secondary inflorescences had more primary branches than the primary inflorescences which, in turn, had between 3 and 6 more branches than the main shoot inflorescence. The variation in primary branch numbers between the main shoot inflorescence and the primary inflorescences in each treatment was highly significant ($p = 0,01$).

ii. Number of spikelets per inflorescence (Table 36). The average main shoot inflorescence contained at least 150 spikelets fewer than the average primary and secondary inflorescences and this difference was highly significant ($p = 0,01$). There was no significant difference in the mean number of spikelets per inflorescence between primary and secondary inflorescences.

The application of nitrogen in treatments 5 and 8 had the greatest mean effect on spikelet production per inflorescence but the effect was not significantly greater than that recorded in treatments 6 and 7. The mean number of spikelets recorded per inflorescence when a single dressing of the increased nitrogen level was applied in treatments 2 and 3 was significantly lower than in treatments 5 and 8 ($p = 0,05$).

The increased nitrogen supply had little effect on spikelet production in the main shoot inflorescence. The number of spikelets in

TABLE 35 Effect of tiller position in the plant and nitrogen supply on the number of primary branches in the weeping lovegrass inflorescence

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	28,4	29,6	29,0	27,8	29,0	30,2	27,2	30,0	28,9
1st primary	32,2	33,4	33,6	33,4	34,8	33,0	33,8	35,8	33,8
2nd primary	33,4	33,4	33,0	34,8	35,2	33,4	34,8	35,2	34,2
1st secondary	32,8	35,6	35,0	34,8	36,0	36,4	35,8	37,2	35,6
2nd secondary	34,0	36,4	35,0	37,4	37,0	35,8	35,2	37,0	36,0
N Treatment Mean	32,4	33,7	33,1	33,6	34,4	33,8	33,4	35,0	33,7

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 0,84		
Between labelled tiller means	± 0,36	0,71	0,94
Between tillers at same nitrogen treatment	± 1,02	2,01	2,66
Between nitrogen treatments for same tiller	± 1,24		

TABLE 36 Effect of tiller position in the plant and nitrogen supply on the number of spikelets produced per inflorescence of weeping lovegrass

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	323	303	306	311	336	351	291	343	321
1st primary	448	465	431	502	504	438	499	491	472
2nd primary	476	484	452	507	533	493	511	522	497
1st secondary	323	458	478	459	568	498	533	575	487
2nd secondary	326	495	449	516	532	538	539	533	491
N Treatment Mean	379	441	423	459	494	464	475	493	453

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 25,6	52,4	70,7
Between labelled tiller means	± 12,6	24,9	32,9
Between tillers at same nitrogen treatment	± 35,5	70,4	93,0
Between nitrogen treatments for same tiller	± 40,8	81,9	109,1

the primary inflorescences was increased by a maximum of approximately 12 per cent when the higher nitrogen level was applied in treatment 5. However, the greatest response to nitrogen was recorded in the secondary inflorescences. In treatment 1 the secondary inflorescences contained about the same number of spikelets as the main shoot inflorescences and approximately 125 spikelets fewer than the primary inflorescences, a difference which was highly significant ($p = 0,01$). The application of the increased level of nitrogen resulted in a highly significant increase in the number of spikelets in the secondary inflorescences ($p = 0,01$). The maximum number of spikelets in the first secondary inflorescence was recorded in treatment 8, 80 per cent more than in treatment 1, and 84 spikelets more than in the first primary inflorescence in the same treatment; the difference between both inflorescences was significant ($p = 0,05$). The second secondary inflorescence contained approximately 60 per cent more spikelets in treatments 5 to 8 than in treatment 1.

iii. Number of florets per spikelet (Table 37). The position of the tiller in the plant had a marked effect on the number of florets in the spikelet. In each treatment, spikelets in the main shoot inflorescence contained consistently more florets than those spikelets in the primary inflorescences. The smallest spikelets were found in the secondary inflorescences. The variation in mean spikelet size between the main shoot, primary and secondary inflorescences was highly significant ($p = 0,01$).

Increasing the nitrogen rate increased spikelet size in each treatment, and the response to nitrogen increased from the main shoot inflorescence to the secondary inflorescences. However the variation in the number of florets per spikelet between treatments for each labelled inflorescence and between treatment means (including the control treatment) was not significant.

The position of the spikelet in the inflorescence influenced the

TABLE 37 Effect of tiller position in the plant and nitrogen supply on the number of florets produced per spikelet in the weeping lovegrass inflorescence

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	8,1	9,5	9,0	9,2	8,4	8,5	9,7	8,6	8,9
1st primary	6,2	6,9	6,7	6,1	7,3	7,6	7,9	6,8	6,9
2nd primary	5,6	6,8	7,1	6,2	6,7	7,9	7,3	7,1	6,8
1st secondary	4,1	5,7	5,6	5,7	6,0	5,9	6,3	5,3	5,6
2nd secondary	4,4	6,0	5,7	5,6	6,1	6,7	6,3	5,2	5,8
N Treatment Mean	5,7	7,0	6,8	6,6	6,9	7,3	7,5	6,6	6,8

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 0,59		
Between labelled tiller means	± 0,30	0,60	0,80
Between tillers at same nitrogen treatment	± 0,86	1,72	2,25
Between nitrogen treatments for same tiller	± 0,96		

TABLE 38 The number of florets per spikelet on basal, intermediate and upper primary branches of inflorescences produced by the main shoot and selected primary and secondary tillers of weeping lovegrass (average for all nitrogen treatments)

Primary Branch Position	Labelled Tiller					Primary Branch Mean
	Main Shoot	First Primary	Second Primary	First Secondary	Second Secondary	
Basal	8,9	6,6	6,6	5,5	5,9	6,7
Intermediate	9,3	7,3	7,3	5,9	6,0	7,2
Upper	8,5	6,9	6,6	5,4	5,5	6,6
Labelled Tiller Mean	8,9	6,9	6,8	5,6	5,8	6,8

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between labelled tiller means	± 0,30	0,60	0,80
Between primary branch means	± 0,22	0,44	0,60
Between primary branches for the same tiller	± 0,50		
Between tillers for the same primary branch	± 0,51	1,00	1,32

size of the spikelet as shown in Table 38. Within each labelled inflorescence the spikelets on the selected intermediate primary branch contained more florets than those spikelets on the upper and basal branches. The mean number of florets per spikelet on the intermediate primary branch was significantly greater than either the basal mean ($p = 0,05$) or upper branch mean ($p = 0,01$).

Nitrogen had no significant effect on spikelet size at each primary branch position in the inflorescence (Table 39).

On the basal primary branch the penultimate (upper) spikelet was smaller than either the intermediate or basal spikelets in all labelled inflorescences (Table 40). The variation in spikelet size between the upper spikelet and the two more basally located spikelets was highly significant ($p = 0,01$) in each inflorescence. Also, the decline in floret numbers in the basal, intermediate and penultimate spikelets from the main shoot inflorescence to the secondary inflorescences was similar at all three spikelet locations. The variation in spikelet size between the main shoot inflorescence, primary inflorescence and secondary inflorescence was highly significant at each spikelet location ($p = 0,01$).

The results in Table 41 show that the response to nitrogen was similar at each spikelet location on the basal primary branch. The greatest response at each location was obtained at treatments 6 and 7. However, all treatments to which the increased level of nitrogen was applied produced more florets per spikelet at each spikelet location, than the application of nitrogen in treatment 1. The variation in spikelet size between treatment 1 and all but one of the other treatments (4) was significant to at least the 5 per cent level of probability.

iv. Number of florets per inflorescence (Table 42). The primary inflorescences contained more florets than the main shoot inflorescence and secondary inflorescences in each treatment. Variation between the

TABLE 39 Effect of nitrogen supply on the number of florets per spikelet on basal, intermediate and upper primary branches of the weeping lovegrass inflorescence (average for all labelled tillers)

Primary Branch Position	Nitrogen Treatment Number								Branch Mean
	1	2	3	4	5	6	7	8	
Basal	5,5	6,8	6,7	6,3	6,9	7,2	7,6	6,6	6,7
Intermediate	6,1	7,4	7,2	7,0	7,1	7,7	7,9	6,9	7,2
Upper	5,4	6,8	6,6	6,5	6,8	7,0	7,1	6,4	6,6
N Treatment Mean	5,7	7,0	6,8	6,6	6,9	7,3	7,5	6,6	6,8

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 0,59		
Between primary branch means	± 0,22	0,44	0,60
Between primary branches at same nitrogen treatment	± 0,63		
Between nitrogen treatments for same primary branch	± 0,77	1,56	2,09

TABLE 40 The number of florets in basal, intermediate and upper spikelets of a basal primary branch of inflorescences produced by the main shoot and labelled primary and secondary tillers of weeping lovegrass (average for all nitrogen treatments)

Position of spikelet in basal primary branch	Labelled Tiller					Primary Branch Mean
	Main Shoot	First Primary	Second Primary	First Secondary	Second Secondary	
Basal	9,4	6,9	6,9	6,0	6,0	7,0
Intermediate	9,4	7,0	7,0	6,0	6,0	7,1
Upper	8,0	6,1	6,1	5,2	5,1	6,1
Labelled Tiller Mean	8,9	6,7	6,7	5,7	5,7	6,7

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between labelled tiller means	± 0,19	0,37	0,49
Between spikelet position means	± 0,06	0,12	0,16
Between spikelet positions for same tiller	± 0,14	0,27	0,36
Between tillers for same spikelet position	± 0,22	0,43	0,57

TABLE 41 Effect of nitrogen supply on the number of florets in basal, intermediate and upper spikelets of a basal primary branch of weeping lovegrass inflorescences (average for all labelled tillers)

Spikelet Position	Nitrogen Treatment Number								Spikelet Mean
	1	2	3	4	5	6	7	8	
Basal	5,6	7,0	7,0	6,4	7,1	7,7	8,3	7,2	7,0
Intermediate	5,8	7,3	7,2	6,3	7,1	7,7	8,1	7,0	7,1
Upper	5,1	6,4	6,5	5,5	6,0	6,7	6,7	5,8	6,1
N Treatment Mean	5,5	6,9	6,9	6,1	6,7	7,4	7,7	6,7	6,7

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 0,43	0,88	1,19
Between spikelet position means	± 0,06	0,12	0,16
Between spikelets at same nitrogen treatment	± 0,17	0,34	0,45
Between nitrogen treatments for same spikelet position	± 0,45	0,93	1,25

TABLE 42 Effect of tiller position in the plant and nitrogen supply on the number of florets produced per weeping lovegrass inflorescence

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	2642	2848	2710	2843	2823	3004	2837	2935	2830
1st primary	2810	3204	2895	3053	3708	3363	3938	3313	3285
2nd primary	2678	3260	3169	3125	3556	3848	3739	3682	3382
1st secondary	1340	2662	2646	2427	3396	2922	3392	3065	2731
2nd secondary	1456	2995	2539	2697	3231	3651	3472	2707	2844
N Treatment Mean	2185	2994	2792	2829	3343	3357	3476	3140	3014

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 271,5	556,1	750,2
Between labelled tiller means	± 92,5	183,1	242,1
Between tillers at same nitrogen treatment	± 261,6	518,0	684,6
Between nitrogen treatments for same tiller	± 358,4	723,7	968,2

three tiller groups varied according to the treatment but the primary inflorescence means were both significantly greater than the main shoot and both secondary inflorescence means ($p = 0,01$).

In treatment 1 the secondary inflorescences contained between 1166 and 1470 fewer florets than main shoot and primary inflorescences; these differences were highly significant ($p = 0,01$). When the increased level of nitrogen was applied in any treatment the variation between the main shoot inflorescence and secondary inflorescences failed to reach significance. This was due to a considerable increase in floret production in the secondary inflorescences.

The number of florets in the first and second secondary inflorescences was doubled when nitrogen was applied in treatments 2, 3 and 4 as compared with inflorescence size in treatment 1 (control). The variation in floret production of both secondary inflorescences between treatment 1 and all other treatments (2 to 8) was highly significant ($p = 0,01$). The higher level of nitrogen increased the number of florets in the main shoot inflorescence in each treatment but in this case the response was not significant.

The application of the increased nitrogen level at emergence of the third primary tiller and again at the fifth primary tiller stage of the plant (treatment 7) was responsible for the greatest number of florets per inflorescence. Treatment 7 was a virtual combination of treatments 3 and 4 at which a single application of the increased nitrogen level was given at emergence of the third primary tiller and the fifth primary tiller respectively. The mean number of florets per inflorescence at treatment 7 was significantly greater than at treatments 3 and 4 ($p = 0,05$).

Variation in inflorescence size between treatments 2, 3 and 4 and also between treatments 5, 6 and 7 was small and not significant. Therefore, it would appear that the rate of nitrogen applied prior to the onset of the reproductive phase was of greater consequence to

floret production per inflorescence than the actual time of application.

d) Seed Production per Inflorescence

i. Floret fertility (Table 43). The average fertility of florets in this experiment was only 33 per cent. The highest fertility was recorded in the main shoot inflorescences and there was a decline in the capacity of florets to set seed from the main shoot to the secondary inflorescences. Florets in the secondary inflorescences were, on average, 8-10 per cent less fertile than those florets in the primary inflorescences which were themselves 2-3 per cent less fertile than those of the main shoot inflorescence. The variation in floret fertility between the primary and secondary inflorescences was highly significant ($p = 0,01$).

Nitrogen had no significant effect on the capacity of florets to set seed. However, the position of the spikelet in the inflorescence had a great influence on fertility as recorded in Table 44. Although an analysis of primary branch means shows a highly significant decline in floret fertility from the upper primary branch to the basal branch ($p = 0,01$) the actual fertility gradient in each inflorescence depended on the position of the parent tiller in the plant. For example, the basal primary branch in the main shoot inflorescence was more fertile than the upper branch - the difference of 3 per cent was significant ($p = 0,05$). This fertility gradient was reversed in the primary and secondary inflorescences. Florets on the basal primary branch in the second secondary inflorescence were 7 per cent less fertile than those on the upper branch; the difference was highly significant ($p = 0,01$).

The 17 per cent decline in floret fertility from main shoot to second secondary inflorescence at the basal primary branch position was more than double that at the upper primary branch. The capacity of florets to set seed on the basal primary branch of the main shoot

TABLE 43 Effect of tiller position in the plant and nitrogen supply on the percentage fertility of florets in the weeping lovegrass inflorescence

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	38	36	44	38	39	37	36	42	39
1st primary	31	38	38	39	38	32	33	39	36
2nd primary	37	34	40	37	38	42	32	33	37
1st secondary	24	26	35	29	29	28	26	29	28
2nd secondary	23	23	28	28	29	25	30	29	27
N Treatment Mean	31	32	37	34	35	33	31	34	33

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 3,1		
Between labelled tiller means	± 1,4	2,7	3,6
Between tillers at same nitrogen treatment	± 3,9	7,7	10,2
Between nitrogen treatments for same tiller	± 4,7		

TABLE 44 The percentage fertility of florets in basal, intermediate and upper primary branches of inflorescences produced by the main shoot and labelled primary and secondary tillers of weeping lovegrass (average for all nitrogen treatments)

Primary Branch Position	Labelled Tiller					Primary Branch Mean
	Main Shoot	First Primary	Second Primary	First Secondary	Second Secondary	
Basal	40	34	35	25	23	31
Intermediate	39	37	38	29	28	34
Upper	37	37	38	31	30	35
Labelled Tiller Mean	39	36	37	28	27	33

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between labelled tiller means	± 1,4	2,7	3,6
Between primary branch means	± 0,6	1,1	1,5
Between primary branches for same tiller	± 1,3	2,5	3,4
Between tillers for same primary branch	± 1,7	3,4	4,5

inflorescence was in fact almost double that of florets at the same location in the second secondary inflorescence.

The influence of nitrogen on floret fertility at each primary branch position is shown in Table 45. The slight positive effect of increased nitrogen supply on floret fertility was similar at each position. However the variation in fertility between treatments was not significant.

An analysis of the capacity of florets to set seed in spikelets on the basal primary branch of the inflorescence is recorded in Table 46. The marked decline in fertility towards the base of the primary branch in the labelled primary and secondary inflorescences was such that the upper spikelets were significantly more fertile than the basal spikelets ($p = 0,01$). There was no fertility gradient between spikelets on the basal primary branch of the main shoot inflorescence.

Only 15-17 per cent of florets in basal spikelets on the basal primary branch of the secondary inflorescences set seed, compared with 40 per cent in those spikelets at the same location in the main shoot inflorescence. The average fertility of the basal primary branch in the secondary inflorescences was approximately half that of the equivalent primary branch of the main shoot inflorescence.

Increasing the rate of applied nitrogen had no significant effect on the capacity of florets to set seed in basal, intermediate or upper spikelets on the basal primary branch of the inflorescence (Table 47).

ii. 100 seed mass (Table 48). In each treatment the heaviest seed was produced by the main shoot inflorescence and the lightest by the secondary inflorescences. In treatment 1 the mass of 100 seeds developed in the main shoot inflorescence was 16,3 mg heavier than the 100 seed mass in the first secondary inflorescence. The difference in 100 seed mass between these inflorescences declined when the higher nitrogen level was applied until, in treatment 6, it was only 7,0 mg. However, in each treatment the variation in seed size between the main

TABLE 45 Effect of nitrogen supply on the percentage fertility of florets in basal, intermediate and upper primary branches of the weeping lovegrass inflorescence (average for all labelled tillers)

Primary Branch Position	Nitrogen Treatment Number								Branch Mean
	1	2	3	4	5	6	7	8	
Basal	29	29	34	34	33	31	29	32	31
Intermediate	30	33	39	36	35	33	32	35	34
Upper	32	33	39	34	36	35	33	35	35
N Treatment Mean	31	32	37	34	35	33	31	34	33

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 3,1		
Between primary branch means	± 0,6	1,1	1,5
Between primary branches at same nitrogen treatment	± 1,6	3,6	4,3
Between nitrogen treatments for same primary branch	± 3,4		

TABLE 46 The percentage fertility of florets in basal, intermediate and upper spikelets of a basal primary branch of inflorescences produced by the main shoot and labelled primary and secondary tillers of weeping lovegrass (average for all nitrogen treatments)

Position of Spikelet on Primary Branch	Labelled Tiller					Spikelet Position Mean
	Main Shoot	First Primary	Second Primary	First Secondary	Second Secondary	
Basal	40	29	31	15	17	26
Intermediate	43	32	36	18	18	29
Upper	40	36	38	23	24	32
Labelled Tiller Mean	41	32	35	19	20	29

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between labelled tiller means	± 2,5	4,9	6,5
Between spikelet position means	± 1,0	1,9	2,6
Between spikelet positions for same tiller	± 2,2	4,3	5,7
Between tillers for same spikelet position	± 3,1	6,2	8,3

TABLE 47 Effect of nitrogen supply on the percentage fertility of florets in basal, intermediate and upper spikelets of a basal primary branch in the weeping lovegrass inflorescence (average for all labelled tillers)

Spikelet Position	Nitrogen Treatment Number								Spikelet Mean
	1	2	3	4	5	6	7	8	
Basal	25	21	35	27	26	28	20	30	26
Intermediate	26	24	35	29	32	32	26	32	29
Upper	29	31	37	34	34	33	27	33	32
N Treatment Mean	27	25	36	30	31	31	24	32	29

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 5,4		
Between spikelet position means	± 1,0	1,9	2,6
Between spikelet positions at same nitrogen treatment	± 2,8	5,5	7,2
Between nitrogen treatments for same spikelet	± 5,9		

TABLE 48 Effect of tiller position in the plant and nitrogen supply on the mass of 100 seeds (mg) from the weeping lovegrass inflorescence

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	43,7	45,5	44,1	43,8	44,5	43,8	46,4	44,9	44,6
1st primary	36,6	39,7	37,4	37,4	41,4	40,0	42,9	39,3	39,3
2nd primary	36,1	40,1	37,4	37,1	41,0	41,7	39,9	40,0	39,2
1st secondary	27,4	35,6	34,5	35,5	36,0	36,8	34,9	38,1	34,8
2nd secondary	30,7	36,5	34,2	35,4	36,4	36,9	33,4	36,3	35,0
N Treatment Mean	34,9	39,5	37,5	37,8	39,9	39,8	39,5	39,7	38,6

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 1,35	2,77	3,74
Between labelled tiller means	± 0,64	1,27	1,68
Between tillers at same nitrogen treatment	± 1,81	3,59	4,74
Between nitrogen treatments for same tiller	± 2,11	4,24	5,65

shoot and first secondary inflorescences was highly significant ($p = 0,01$).

The increased level of nitrogen had a marked overall effect on seed size. All treatments in which the increased level of nitrogen was applied, except treatment 3, increased the 100 seed mass mean significantly to at least the 5 per cent level of probability as compared with the average mass of 100 seeds in treatment 1. There were no significant differences between the 100 seed mass means of treatments 2 to 8 inclusive.

Seed carried in the secondary inflorescences showed the greatest response to increased nitrogen supply as compared with the response in the main shoot and primary inflorescences. The mass of 100 seeds in the first secondary inflorescence in treatments 2 to 8 inclusive was significantly greater than the 100 seed mass in the control treatment ($p = 0,01$). Seed size in the main shoot inflorescence was not increased significantly when the increased level of nitrogen was applied.

Within each inflorescence seed size varied considerably as shown in Table 49. Seed was of uniform size in the main shoot inflorescence. In the labelled primary and secondary inflorescences the heaviest seed was recorded on the upper primary branch and there was a decline in seed size down the inflorescence. In these inflorescences the variation in seed size between the basal, intermediate and upper primary branches was significant to at least the 5 per cent level of probability.

The greatest decline in 100 seed mass from main shoot to secondary inflorescence was recorded on the basal primary branch. The difference in 100 seed mass between the main shoot inflorescence and second secondary inflorescence at the basal, intermediate and upper primary branches was 10,7 mg, 9,8 mg and 8,5 mg respectively.

The results presented in Table 50 indicate that seed on the upper

TABLE 49 The mass of 100 seeds (mg) from basal, intermediate and upper primary branches of inflorescences produced by the main shoot and labelled primary and secondary tillers of weeping lovegrass (average for all nitrogen treatments)

Primary Branch Position	Labelled Tiller					Primary Branch Mean
	Main Shoot	First Primary	Second Primary	First Secondary	Second Secondary	
Basal	44,0	37,5	37,5	32,7	33,3	37,0
Intermediate	44,7	39,5	39,4	34,8	34,9	38,7
Upper	45,1	40,9	40,6	37,0	36,6	40,1
Labelled Tiller Mean	44,6	39,3	39,2	34,8	35,0	38,6

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between labelled tiller means	± 0,64	1,27	1,68
Between primary branch means	± 0,23	0,46	0,61
Between primary branches of same tiller	± 0,52	1,03	1,37
Between tillers for same primary branch	± 0,77	1,52	2,01

TABLE 50 Effect of nitrogen supply on the mass of 100 seeds (mg) from basal, intermediate and upper primary branches of the weeping lovegrass inflorescence (average for all labelled tillers)

Primary Branch Position	Nitrogen Treatment Number								Branch Mean
	1	2	3	4	5	6	7	8	
Basal	33,8	37,9	36,1	36,2	37,6	38,5	38,0	38,2	37,0
Intermediate	35,4	39,7	37,6	37,5	40,0	39,6	39,6	40,0	38,7
Upper	35,5	40,9	39,0	39,9	42,0	41,3	41,0	40,9	40,1
N Treatment Mean	34,9	39,5	37,5	37,8	39,9	39,8	39,5	39,7	38,6

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 1,35	2,77	3,74
Between primary branch means	± 0,23	0,46	0,61
Between primary branches at same nitrogen treatment	± 0,66	1,31	1,73
Between nitrogen treatments for same primary branch	± 1,46	2,97	4,00

primary branch of the inflorescence showed the greatest response to increased nitrogen nutrition as compared with seed developing on the more basal primary branches. The heaviest seed was obtained in treatment 5, and the mass of 100 seeds taken from the basal, intermediate and upper primary branches was 3,8 mg, 4,6 mg and 6,5 mg heavier respectively than on equivalent primary branches in treatment 1. This represents an 18,3 per cent increase in the upper branch and an 11,2 per cent increase in seed size in the basal primary branch.

iii. Seed mass per inflorescence (Table 51). The heaviest mean seed mass was recorded in the main shoot and second primary inflorescences. These inflorescences produced, on average, approximately 200 mg of seed more than both secondary inflorescences, and this variation in seed mass was highly significant ($p = 0,01$).

TABLE 51 Effect of tiller position in the plant and nitrogen supply on seed mass per inflorescence (mg) of weeping lovegrass

Labelled Tiller	Nitrogen Treatment Number								Tiller Mean
	1	2	3	4	5	6	7	8	
Main shoot	414	461	509	440	482	497	465	533	475
1st primary	311	445	407	430	562	451	550	482	455
2nd primary	338	408	460	424	534	658	439	484	474
1st secondary	96	241	310	256	347	299	325	352	278
2nd secondary	106	236	233	269	333	355	345	282	270
N Treatment Mean	253	358	384	364	451	452	435	427	390

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between nitrogen treatment means	± 48,7	99,8	134,7
Between labelled tiller means	± 22,6	44,7	59,0
Between tillers at same nitrogen treatment	± 63,8	126,3	167,0
Between nitrogen treatments for same tiller	± 75,1	150,8	201,0

In treatment 1 the mass of seed produced by the main shoot inflorescence was approximately four times that of the secondary inflorescence. The increased level of nitrogen had a considerable effect on

seed mass in the secondary inflorescences and reduced this difference by approximately 50 per cent. However, the yield of seed from the main shoot inflorescence remained significantly greater than the seed yield of the secondary inflorescences in each treatment ($p = 0,01$).

The greatest response to increased nitrogen supply was obtained in the secondary inflorescences. The mass of seed produced in both secondary inflorescences was increased significantly, to at least the 5 per cent level of probability, when nitrogen was applied in most treatments. The heaviest seed mass in the first and second secondary inflorescences was recorded in treatments 5 and 6 respectively. The highest seed yield from the first and second primary inflorescences was also obtained at treatments 5 and 6 respectively. In both these treatments the yield of seed was significantly greater, to at least the 5 per cent level of probability, than the yield obtained from the equivalent inflorescences in the control treatment.

The actual time of application of the increased nitrogen level was of little consequence to seed yield per inflorescence, for the variation in mean seed mass per inflorescence between treatments 2 to 8 inclusive was not significant.

The maximum mean seed mass per inflorescence was recorded when the increased level of nitrogen was applied at emergence of the first and either the third (treatment 5) or fifth primary tiller (treatment 6). The mean seed mass in these two treatments and also in treatments 7 and 8 was significantly greater than the mean recorded in treatment 1 ($p = 0,01$). Treatments 2, 3 and 4 outyielded treatment 1 by an average 119 mg per inflorescence and this difference was significant ($p = 0,05$).

e) Correlation Coefficients between Certain Characters

The correlation coefficients between seven yield components with each other and with seed yield per inflorescence presented in Table 52 were obtained from the combined data of all labelled inflorescences. For ease of interpretation the number of each character as it appears

in the table is given in brackets.

In this experiment all characters studied, except the number of primary branches (2) and number of spikelets per inflorescence (3), showed a high positive correlation with seed yield per inflorescence (8). The number of primary branches in the inflorescence showed a high positive correlation ($p = 0,01$) with spikelet numbers per inflorescence and both these characters showed a significantly negative correlation with spikelet size (4) and with floret fertility (6).

All characters except floret fertility showed a high positive correlation with floret number per inflorescence (5). The number of spikelets per inflorescence had a greater effect on the number of florets produced per inflorescence than did spikelet size or the number of primary branches per inflorescence.

Spikelet size (4) showed a high positive correlation with fertility (6) while both these characters and the number of florets per inflorescence (5) showed a high positive correlation ($p = 0,01$) with seed size (7).

The interrelationship between the seven characters and seed yield in each labelled inflorescence is shown in Table 53. In all inflorescences the number of florets per inflorescence (5), floret fertility (6) and seed size (7) showed a highly significant positive correlation ($p = 0,01$) with seed yield per inflorescence (8). Apart from the second primary inflorescence, the number of spikelets per inflorescence (3) showed a high positive correlation with seed yield ($p = 0,01$). In the primary and secondary inflorescences spikelet size (4) was also highly correlated with seed yield per inflorescence ($p = 0,01$).

Seed size (7) showed an unexpectedly high positive correlation with the number of florets per inflorescence (5) in all labelled inflorescences. Floret fertility generally had little association with the remaining six characters.

TABLE 52 Correlation coefficients between seven characters with each other and with yield of seed in the weeping lovegrass inflorescence (analysis from data of all labelled inflorescences)

	2	3	4	5	6	7	8
1. Inflorescence length (cm)	+0,038	+0,396**	+0,345**	+0,760**	+0,243*	+0,503**	+0,596**
2. Primary branches/ inflorescence		+0,744**	-0,486**	+0,242*	-0,391**	-0,447**	-0,203
3. Spikelets per inflorescence			-0,348**	+0,625**	-0,195*	-0,171	+0,140
4. Florets per spikelet				+0,317**	+0,335**	+0,572**	+0,498**
5. Florets per inflorescence					+0,152	+0,388**	+0,697**
6. Floret fertility (%)						+0,454**	+0,741**
7. 100 seed mass (mg)							+0,702**
8. Yield of seed/ inflorescence (mg)							-

* Significant at 5% level

** Significant at 1% level

Multiple correlation coefficient

r = 0,977** (198 d.f.)

TABLE 53 Correlation coefficients between seven characters with each other and with yield of seed in labelled inflorescences
(a) Main shoot inflorescence

	2	3	4	5	6	7	8
1. Inflorescence length (cm)	+0,347*	+0,442**	+0,073	+0,510**	-0,201	+0,014	+0,236
2. Primary branches/ inflorescence		+0,804**	-0,386*	+0,491**	+0,060	+0,059	+0,403**
3. Spikelets per inflorescence			-0,394*	+0,691**	+0,096	+0,178	+0,581**
4. Florets per spikelet				+0,383*	-0,077	+0,247	+0,243
5. Florets per inflorescence					+0,020	+0,368*	+0,763**
6. Floret fertility (%)						+0,058	+0,574**
7. 100 seed mass (mg)							+0,551**
8. Seed yield per inflorescence (mg)							-

* Significant at 5% level

** Significant at 1% level

Multiple correlation coefficient

r = 0,983** (38 d.f.)

TABLE 53 (b) First primary inflorescence

	2	3	4	5	6	7	8
1. Inflorescence length (cm)	+0,332*	+0,541**	+0,564**	+0,736**	-0,005	+0,374*	+0,503**
2. Primary branches/ inflorescence		+0,543**	+0,055	+0,396*	+0,102	+0,226	+0,330*
3. Spikelets per inflorescence			+0,079	+0,700**	-0,057	+0,145	+0,388*
4. Florets per spikelet				+0,759**	+0,124	+0,595**	+0,665**
5. Florets per inflorescence					+0,026	+0,531**	+0,721**
6. Floret fertility (%)						+0,092	+0,657**
7. 100 seed mass (mg)							+0,585**
8. Seed yield per inflorescence (mg)							-

* Significant at 5% level

** Significant at 1% level

Multiple correlation coefficient

r = 0,982** (38 d.f.)

TABLE 53 (c) Second primary inflorescence

	2	3	4	5	6	7	8
1. Inflorescence length (cm)	+0,183	+0,375*	+0,510**	+0,663**	-0,160	+0,636**	+0,425**
2. Primary branches/ inflorescence		+0,624**	-0,082	+0,376*	-0,421**	+0,131	-0,004
3. Spikelets per inflorescence			-0,136	+0,556**	-0,326*	+0,281	+0,171
4. Florets per spikelet				+0,741**	+0,134	+0,526**	+0,706**
5. Florets per inflorescence					-0,115	+0,636**	+0,711**
6. Floret fertility (%)						-0,148	+0,565**
7. 100 seed mass (mg)							+0,561**
8. Seed yield per inflorescence (mg)							-

* Significant at 5% level

** Significant at 1% level

Multiple correlation coefficient

r = 0,989** (38 d.f.)

TABLE 53 (d) First secondary inflorescence

	2	3	4	5	6	7	8
1. Inflorescence length (cm)	+0,436**	+0,771**	+0,099	+0,854**	+0,264	+0,599**	+0,702**
2. Primary branches/ inflorescence		+0,511**	-0,023	+0,439**	-0,222	+0,125	+0,150
3. Spikelets per inflorescence			-0,055	+0,874**	+0,227	+0,587**	+0,759**
4. Florets per spikelet				+0,111	+0,082	+0,178	+0,089
5. Florets per inflorescence					+0,184	+0,566**	+0,786**
6. Floret fertility (%)						+0,499**	+0,686**
7. 100 seed mass (mg)							+0,785**
8. Seed yield per inflorescence (mg)							-

* Significant at 5% level
** Significant at 1% level

Multiple correlation coefficient
r = 0,980** (38 d.f.)

TABLE 53 (e) Second secondary inflorescence

1. Inflorescence length (cm)	+0,533**	+0,741**	+0,645**	+0,770**	+0,181	+0,422**	+0,533**
2. Primary branches/ inflorescence		+0,617**	+0,131	+0,404*	-0,013	+0,385*	+0,259
3. Spikelets per inflorescence			+0,441**	+0,834**	+0,154	+0,446**	+0,666**
4. Florets per spikelet				+0,851**	+0,104	+0,245	+0,634**
5. Florets per inflorescence					+0,159	+0,387*	+0,783**
6. Floret fertility (%)						+0,261	+0,644**
7. 100 seed mass (mg)							+0,550**
8. Seed yield per inflorescence (mg)							-

* Significant at 5% level
** Significant at 1% level

Multiple correlation coefficient
r = 0,963** (38 d.f.)

The relationship between spikelet size (4) and the number of spikelets per inflorescence (3) changed depending on the inflorescence. In the main shoot inflorescence they were negatively correlated ($p = 0,05$). In both primary inflorescences and the first secondary inflorescence the relationship between them was not significant. However, the second secondary inflorescence showed a high positive correlation ($p = 0,01$) of spikelet size with spikelet number per inflorescence.

f) Plant Growth and Development (Table 54)

The number of inflorescences per plant was doubled when the total nitrogen supply to the plant was doubled (cf. treatments 2, 3 and 4 and treatment 1); this increase was highly significant ($p = 0,01$).

TABLE 54 Effect of nitrogen, applied at different physiological stages of vegetative growth on plant growth and development of weeping lovegrass

Nitrogen Treatment Number	Growth and Development per Plant				
	No. inflorescences	No. veg. tillers	Total No. Tillers	% tillers fertile	Herbage dry matter (g)
1	8,8	46,2	55,0	16,0	8,5
2	16,4	74,0	90,4	18,2	15,6
3	16,6	70,8	87,4	19,0	15,2
4	18,8	68,0	86,8	21,7	14,5
5	17,8	90,8	108,6	16,4	23,3
6	17,8	96,6	114,4	15,6	26,3
7	19,4	126,6	136,0	14,3	28,6
8	19,8	127,8	147,6	13,6	31,0
Between Treatments:					
S.E.	± 1,53	± 8,89	± 19,69		± 1,86
L.S.D. 5%	3,12	18,12	40,12		3,80
L.S.D. 1%	4,11	23,86	52,84		5,00

A further increase in total nitrogen supply had little effect on fertile tiller production until the supply was doubled in treatment 8 as compared with treatments 2, 3 and 4. The mean number of seedheads per

plant in treatment 8 was significantly greater than in treatments 2 and 3 ($p = 0,05$).

The mean fertility of florets ranged from 13,6 per cent to 21,7 per cent. The percentage of fertile tillers per plant in treatments 5 to 8 was reduced apparently as a consequence of the increased production of vegetative tillers in each plant in these treatments.

The quantity of vegetative dry matter produced per plant was dependent on the rate of nitrogen applied. A four-fold increase in total nitrogen supply, as obtained in treatment 8 compared with treatment 1, resulted in an equivalent increase in forage production per plant.

3. DISCUSSION

The aims of this experiment were similar to those in Experiment 2. A detailed study was made of the physiology of seed production in the weeping lovegrass inflorescence as influenced by the position of the tiller in the plant. In addition the effect of increasing the level of nitrogen nutrition prior to inflorescence initiation was recorded and has shown that nitrogen is an important prerequisite to the production of seed in the inflorescence.

a) Tiller Position in Relation to Inflorescence Size and Seed Yield

i. Inflorescence size. Inflorescences developed on primary tillers contained the greatest number of florets while the main shoot inflorescence was approximately the same size as the secondary inflorescences (Table 42). An analysis of the distribution of florets along each inflorescence showed that increases in both the number of primary branches and in the number of spikelets per inflorescence were accompanied by a decline in spikelet size with increasing order of succession of tillers from the main shoot. Similar trends between tiller orders were observed in the previous experiment and therefore the high negative correlation between the size of the spikelet and

number of spikelets in the inflorescence (Table 52) appears to be a characteristic of the weeping lovegrass inflorescence.

The reduced ability of the main shoot inflorescence to develop a large number of spikelets, as compared with the primary and secondary inflorescences (Table 36) was largely responsible for the reduced size of this inflorescence. Ear size in this experiment was more closely related to the number of spikelets in the inflorescence (Table 52) and not to the number of florets per spikelet as in the previous experiment. Consequently the number of spikelets in the primary inflorescences was largely responsible for the increased size of these inflorescences. The larger spikelet developed on the main shoot (Table 37) was unable to compensate for the reduced number of spikelets.

In each inflorescence developed by the labelled tillers the largest spikelets, containing the greater number of florets, were recorded on the intermediate primary branch (Table 38) while on the basal primary branch the basal spikelets were the largest and the outer ones the smallest (Table 40). Anslow (1963) found in perennial ryegrass that the intermediate spikelets in the inflorescence were larger than either the basal or upper spikelets. The decline in spikelet size from main shoot to secondary inflorescence in the present experiment was similar at each primary branch location with the spikelets developed in the second secondary inflorescence containing 3 florets fewer than those spikelets in the main shoot inflorescence.

As noted in the previous experiment the second tiller to emerge in each order developed a larger inflorescence than the first tiller (Table 42). Within the experimental conditions of both experiments the first tiller appeared incapable of producing a larger inflorescence.

ii. Seed yield per inflorescence. Only an average 33 per cent of all florets developed in the five inflorescences were fertile and had set seed at harvest (Table 43). The highest fertility was recorded in

the main shoot inflorescence and it declined with increasing order of succession of tillers. The florets of secondary inflorescences were 11-12 per cent less fertile than those of the main shoot inflorescences. In addition, the fertility decline from main shoot inflorescene to the secondary inflorescences in spikelets on the basal primary branches was more than double that in spikelets on the upper primary branch (Table 44). Also, the fertility decline through the tiller orders of basal spikelets on the selected basal primary branch was greater than that in the upper spikelets of the same primary branch (Table 46).

The experimental conditions have been regarded as the main cause of the reduced fertility obtained in this experiment. However, the gradations in fertility are in accordance with those obtained in the previous experiment and underline the influence of the position of the spikelet in the inflorescence and also the position of the fertile tiller in the plant.

From the combined data of all five labelled inflorescences the number of florets per spikelet, floret fertility and inflorescence size all showed a high positive correlation with seed size, shown as 100 seed mass (Table 52). The positive correlation between seed size and inflorescence size was consistently high in each inflorescence (Table 53).

The heaviest seed was produced in the main shoot inflorescence and the lightest in the secondary inflorescences (Table 48). In each inflorescence the heaviest seed was found in spikelets on the upper primary branches and seed size declined down the inflorescence (Table 49). This meant that the more fertile spikelets were also those containing the heavier seed. In the previous experiment there was a high negative correlation between fertility and seed size, but the heaviest seed developed in the upper spikelets of each inflorescence. While spikelet size may not have had any influence on the final mass

of individual seeds in this present experiment, competition for assimilates between spikelets on the basal primary branches was still presumably more intense than between spikelets on the upper branches.

Despite the reduced number of florets, the mass of seed in the main shoot inflorescence was similar to that obtained in the primary inflorescences (Table 51). The higher fertility of florets in the main shoot and the heavier seed produced in these florets compensated for the reduced number of florets.

Seed production in the secondary inflorescences was significantly reduced, obviously due to the low fertility of florets recorded in these inflorescences and also, but to a much lesser extent, due to the production of lighter seed.

b) Nitrogen Supply, Inflorescence Size and Seed Yield

In this experiment the total level of nitrogen applied varied between treatments (Table 29) and, apart from the time of application, differed from the previous experiment in which the same total level of nitrogen was applied at each treatment. In general, increased levels of nitrogen applied prior to reproductive growth in single plants of weeping lovegrass increased the seed productivity of selected tillers and the effect became greater in the lower order tillers.

The increased level of nitrogen was responsible for earlier ear emergence in the primary and secondary tillers but had no effect on the rate of development in the main shoot (Table 31). The actual time of application prior to inflorescence initiation was of little consequence although an increase in the total amount of applied nitrogen resulted in slightly earlier emergence. Wilson (1959) found that high levels of nitrogen supply resulted in earlier floret initiation and ear emergence in four temperate grasses. In timothy a deficiency in the nitrogen supply delayed the onset of reproductive growth and ear emergence particularly in the younger tillers (Ryle, 1963a).

Increasing the nitrogen supply prior to inflorescence initiation

had no significant effect on the number of primary branches produced in the weeping lovegrass inflorescence (Table 35) and had little effect on the number of florets developed in the spikelet (Table 37). Floret fertility was also little affected by nitrogen supply (Table 43). However, both the number of spikelets per inflorescence and the mass of seed produced in the inflorescence were significantly affected by the increased nitrogen supply.

Nitrogen had little effect however, on the number of spikelets developed in the main shoot and primary inflorescences. The marked response to nitrogen was virtually restricted to spikelet production in the secondary inflorescences (Table 36). The increasing response to nitrogen supply with increasing tiller order suggests that the main shoot and labelled primary tillers were not able to benefit fully from the increased availability of nutrients, or had already reached a ceiling level for the number of spikelets that could be produced in the inflorescence.

The final application of nitrogen occurred at emergence of the fifth primary tiller, 49 days after sowing and therefore only 3 days prior to inflorescence initiation in the main shoot and 5 days prior to emergence of the first secondary tiller (Table 30). The secondary tillers emerged therefore at a time when mineral nutrients were readily available.

In four of the seven treatments in which the high level of nitrogen was applied spikelet production was actually lower in the main shoot inflorescence than in the same inflorescence in the control treatment (Table 36). Reduced spikelet production also occurred in the primary inflorescences, particularly when the high level of nitrogen was applied in the early stages of vegetative growth. It would appear therefore that high levels of nitrogen applied at this time may have had an inhibiting effect on reproductive growth in the main shoot and primary tillers.

The other component of seed yield significantly influenced by the application of high levels of nitrogen prior to reproductive growth was the final size an individual seed attained (Table 48). Again, the response to nitrogen increased with increasing order of succession of the tillers. Seed in the main shoot inflorescence was little affected by nitrogen supply. However, in the later-emerging secondary inflorescences the size of seed developed was significantly increased.

The actual time of application of the high nitrogen level was of little consequence and the mass of seed was only slightly increased when the high level was applied more than once in the same treatment. That nitrogen applied prior to inflorescence initiation should have a marked positive effect on seed size even if only in the later-emerging tillers shows a tendency not normally obtained in the field. In the glasshouse, where conditions approach an optimum for growth, development occurs at a rate which cannot be compared with that in the field and so a residual effect of applied nitrogen is perhaps to be expected to a far greater degree in pot experiments in the glasshouse than in experiments conducted in the field.

GENERAL DISCUSSION OF EXPERIMENTS 2 AND 3

Both experiments were carried out specifically to gain some knowledge of (a) the physiology of seed production in the weeping lovegrass inflorescence; (b) the influence of tiller position (and possibly tiller age) on production of seed per inflorescence, and (c) the effect of nitrogen applied during and prior to inflorescence development on the capacity of the inflorescence to produce seed. Although results from both experiments cannot be compared directly, because of possible differences in growing conditions, several conclusions pertinent to both experiments can be drawn.

While day and night temperatures, photoperiod and humidity conditions in the glasshouse were the same for both experiments it is noted that the main shoot and the two labelled primary tillers in plants in Experiment 2 (Table 9) grew and developed at a faster rate than the equivalent tillers in Experiment 3 (Table 30). Experiment 2 was carried out in autumn while Experiment 3 continued throughout the winter when temperatures were generally lower. It is possible therefore that night temperatures in the glasshouse in winter may, on occasions, have been lower than the required 24^{o} C. This would occur whenever outside temperatures became too low for the glasshouse heating system to fully counteract. It is further suggested that because of the shorter natural winter daylength, daily light energy levels were lower for Experiment 3 than for Experiment 2. This factor and the lower night temperatures may have had some influence on the reduced growth rate of tillers in Experiment 3.

Another factor which may have attributed to the reduced rate of growth of tillers in Experiment 3 was the application of the increased level of nitrogen to the young weeping lovegrass plant, particularly at emergence of the first primary tiller. It is possible that this level of nitrogen was excessive when applied at this time, and, as a

consequence, was detrimental to normal plant growth. Growth and development of secondary tillers was not affected to the same extent because these tillers emerged at a later stage when the plant was larger.

It would appear that the early-emerged tillers were not able to recover fully from this initial setback in growth. In Experiment 3 the main shoot inflorescence and, to a lesser extent, the primary inflorescences contained fewer spikelets in those treatments when the increased level of nitrogen was applied as compared with equivalent inflorescences produced in the control treatment (Table 36). The number of spikelets produced in each inflorescence is dependent largely on the size of the apical meristem at inflorescence initiation (Ryle, 1966) which infers therefore that the high level of nitrogen applied in Experiment 3 was responsible for a reduction in the size of the apical meristem in early-emerged tillers. Presumably the smaller apical meristem was a consequence of the depressed rate of growth in the young weeping lovegrass plant brought about by the application of excessive amounts of nitrogen.

In both Experiments 2 and 3 increased spikelet production with increasing order of succession of tillers was a characteristic of weeping lovegrass in the experimental conditions imposed on the plants. In Experiment 2, however, spikelet size (Table 15) more than compensated for reduced spikelet number in the main shoot inflorescence. In Experiment 3, the largest spikelets were recorded in the main shoot inflorescence (Table 37) but they could only partially compensate for lower spikelet numbers. In both experiments there was a high negative correlation between spikelet size and spikelet number in the inflorescence suggesting that there was indeed some compensatory mechanism, probably competition for assimilates, in action within the weeping lovegrass inflorescence.

In both experiments, but particularly in Experiment 2 (Table 25),

the main shoot inflorescence produced, on average, a greater mass of seed than either the primary or secondary inflorescences. Seed yield per inflorescence declined therefore, with increasing order of tillers. In Experiment 3 the main shoot inflorescence yielded as well as the primary inflorescences (Table 51) despite producing significantly ($p = 0,01$) fewer florets (Table 42). However, the higher fertility of florets and the heavier seed compensated for lower floret numbers in the main shoot inflorescence.

The overall effect of increasing nitrogen nutrition, either prior to or during reproductive growth, was to increase considerably the mass of seed produced in the weeping lovegrass inflorescence. In general, nitrogen increased the number of florets produced in the inflorescence and was also responsible for the production of heavier seed. The nitrogen status of the shoot at inflorescence initiation appeared to determine the manner in which floret production was increased in the inflorescence. Nitrogen applied during inflorescence development in Experiment 2 significantly increased the number of florets developed per spikelet but had no significant effect on spikelet production. However, the application of nitrogen prior to inflorescence initiation (Experiment 2) generally resulted in a marked increase in the number of spikelets per inflorescence and had little effect on spikelet size. The results of these two experiments provide an interesting illustration of how increased nitrogen nutrition increased floret numbers via diverse pathways, depending on time of nitrogen application.

Increasing the level of nitrogen had no significant effect on floret fertility and the actual time of application was of little consequence. In Paspalum plicatulum Chadhokar and Humphreys (1970) found that nitrogen nutrition had little influence on seed production after ear emergence and concluded that seed yield was already determined before the external appearances of inflorescence. In Experiment

2 nitrogen applied as late as initial anthesis in weeping lovegrass increased seed yield per inflorescence largely by increasing seed size. However, it is noted that the optimum time of application in Experiment 2 was at inflorescence initiation. In Experiment 3 time of application prior to inflorescence initiation was of little consequence. It does appear therefore, that nitrogen must be applied at or prior to the onset of reproductive growth in order to maximise seed production and utilise applied nitrogen as efficiently as possible.

SECTION 3 SEED DEVELOPMENT

INTRODUCTION

The fertilisation of florets and subsequent development of seed are as important as components of seed yield as tiller fertility and inflorescence size. If the potential yield of the seed crop is to be realised a high proportion of florets must be fertilised and set seed, and ultimately attain the necessary seed mass.

Although little attention has been paid to the effect of pollination and fertilisation on seed production in herbage grasses the efficiency of the flowering process is reflected to a large extent in the proportion of florets which set seed (Anslow, 1963). In many perennial grasses this proportion seldom exceeds 70 per cent (Ryle, 1966). For example, in perennial ryegrass (Lolium perenne) 65 per cent of florets set seed (Anslow, 1963). A similar figure has been recorded for bromegrass (Bromus inermis) and species of wheatgrass (Agropyron spp.) (Knowles and Baenziger, 1962). The proportion of florets setting seed in timothy (Phleum pratense) and cocksfoot (Dactylis glomerata) has been found to range between 26 and 65 per cent (Johnston, 1960; Hill and Hovin, 1964) while inflorescences of meadow fescue (Festuca pratensis) contain florets of which approximately 40 per cent set seed (Lewis, 1963).

In several strains and hybrids of Bermudagrass (Cynodon dactylon) Ahring, Taliaferro and Morrison (1974) found seed set to range from approximately 1 to 67 per cent. This evidence suggested that seed set is a major component determining seed yield.

In perennial ryegrass (Anslow, 1963), wheatgrass and bromegrass (Knowles and Baenziger, 1962) the ability of a floret to set seed depends on its location in the inflorescence. A slight decrease in floret fertility has been recorded in the upper spikelets of the inflorescence when compared with those in the middle and at the base,

and a marked reduction in fertility was recorded in the outer florets of each spikelet. In addition, the proportion of florets setting seed was found to be lower in late-emerging inflorescences than in earlier groups in timothy and perennial ryegrass crops (Stoddart, 1959; Anslow, 1963).

While the proportion of florets capable of setting seed may be genetically controlled (Johnston, 1960; Knowles and Baenziger, 1962) the environment appears to have some influence (Jones and Brown, 1951; Dotzenko and Stegmeier, 1959; Knowles and Baenziger, 1962).

The development and maturity of seed in crops of herbage grasses has received considerable attention in recent years because of the importance of crop ripeness and time of harvest on maximum seed yields. Ripeness has been defined in terms of the external appearance of seedheads, the time from ear emergence or anthesis to ripeness, and the degree of shedding (Roberts, 1969). Endosperm consistency has been used to determine crop ripeness (Evans, 1960). Taken collectively these definitions have been useful general criteria whereby seed ripeness may be detected under field conditions. Nevertheless, a more specific criterion of ripeness is required. Research has been directed towards a study of biochemical changes that take place in the seed during the maturation process so that it is possible to detect and characterise physiological ripeness in metabolic as well as purely physical terms (Stoddart, 1964a; 1964b; 1964c). However, most attention has been given to the relationship of moisture content to seed mass as a measure of ripeness (Griffith and Harrison, 1954; Grabe, 1956; Hyde, McLeary and Harris, 1959; Nellist and Rees, 1967; 1968; Roberts, 1969; 1971). Klein and Harmond (1971) found that the moisture content of the standing seed crop of seven forage species was the only property of maturing seed that correlated well with time of harvest for maximum yields.

Seed viability itself is neither a reliable criterion of ripeness nor is it a limiting factor for optimum time of harvest (Stoddart, 1964a; Nellist and Rees, 1968; Roberts, 1969; 1971). Research has shown that maximum viability is reached in seeds of many herbage species at an early stage in the ripening process (Hyde et al., 1959; Roberts, 1969). Griffiths et al. (1967) suggested that the point at which maximum viability is attained is of practical importance in estimating the earliest safe harvest date. However, seed harvested at this stage is not in a suitable physical condition for harvesting (Roberts, 1969). It has a low mass, a fluid endosperm and a high moisture content (Hyde et al., 1959). Its storage life is very limited (McAlister, 1943) and seedlings possess little vigour on germination (Hyde et al., 1959) because of inadequate food supplies (Stoddart, 1964a).

Seed development proceeds in three distinct phases: growth, reserve food accumulation and ripening (Hyde et al., 1959; Roberts, 1971). Seed is defined as being mature when it has relatively stable mass and constant moisture content (Griffiths et al., 1967). Anslow (1964) found that the seed ripening process in the inflorescence is reflected to a considerable extent in the moisture content of succeeding spikelets. The seed in the upper spikelets of the inflorescence was drier than in the lower ones. In addition the loss of moisture occurred earliest in the older heads and at a faster rate than in later-emerging heads.

The final size attained by the individual seed is also influenced by the location of the floret in the inflorescence. In perennial ryegrass inflorescences the basal spikelets develop heavier seed than the upper ones while the basal florets in each spikelet produce heavier seed than the terminal florets (Anslow, 1964). Anslow (1964) also found that early-emerging seedheads produced seed 67 per cent heavier than those in late-emerging heads. A similar observation has

been recorded in timothy seed crops (Stoddart, 1959).

Physiologically mature seed is generally over-ripe in terms of optimum time of harvest and one of the principle sources of loss in yield in grasses is the ease with which ripe seed is shed from the inflorescence (Anslow, 1964). Seed losses due to shedding have been reported as high as 40 per cent (Griffiths, Lewis and Bean, 1966) while a survey conducted in the United States of America has revealed losses of up to 47 per cent due to shedding and unsatisfactory harvesting techniques (Klein and Harmond, 1971). Shedding can be particularly severe in many tropical species (Boonman, 1973).

The onset of shedding can be correlated with seed moisture content in many grasses (Nellist and Rees, 1967; Roberts, 1969; 1971) although seed retention in the inflorescence appears to be genetically controlled (Bonin and Goplen, 1963; McWilliam, 1963). In inflorescences of perennial ryegrass Anslow (1964) found that shedding began before seed reached maximum dry mass and continued at a constant rate. However, seed losses became progressively more important during the latter stages of seed development since the proportion of seed shed increased and the mass of these seeds became greater (Anslow, 1964).

According to Klein and Harmond (1971) the optimum time of harvest is the result of a balance between crop mass and germination gains, and shedding and combining losses. Roberts (1969) stated that at this time seed had acquired its maximum mass, losses through shedding were minimal and the moisture content of the seed had fallen to an acceptable level so that the physical condition of the seed was not adversely affected by threshing.

An accurate assessment of the optimum time of harvest is an essential requirement for herbage seed production. While more reliable techniques for evaluating the optimum stage of maturity of seedheads may assist in minimising seed losses the problem of uneven ripening between and within seedheads remains a complicating factor in most

perennial grasses of temperate (Stoddart, 1959; Anslow, 1964) and tropical origin (Boonman, 1971).

The wide range of maturity among inflorescences has been ascribed to age differences (Colombus-Jones, 1959) and therefore to time of emergence of the seedheads (Anslow, 1964) and to the influence of climate and to genetic characteristics (Evans, 1960). Individual seeds within the inflorescence vary in degree of ripeness because of differences in the timing of anther exertion, pollination and seed maturation in each floret (Anslow, 1963). These factors are dependent on the position of the floret in the inflorescence (Anslow, 1964).

The selected date of harvest must be an informed compromise between seed loss due to under- or over-ripeness. The seed producer must be able to correlate crop ripeness with a stage in the development of the individual seed in the inflorescence and also assess the relative contributions to total yield of the different inflorescence age groups in the population (Griffiths et al., 1967).

The available evidence suggests that seed yields might be considerably increased if greater attention is given to the pattern of seed set and maturation in the crop (Ryle, 1966). The present study is therefore an attempt to trace seed development to maturity in weeping lovegrass grown in the field under local conditions. Variation in the ability of florets to set seed that is likely in the seed crop is analysed and the change in seed mass, the final size of seeds obtained and their capacity for germination in seedheads emerging at different times, are studied.

EXPERIMENT 4 A STUDY OF THE PHYSIOLOGY OF SEED DEVELOPMENT AND CROP MATURITY IN WEEPING LOVEGRASS

1. EXPERIMENTAL METHODS

a) Procedure

During August 1972 six plots, each measuring 1 metre square and spaced 1 metre apart, were marked out in an established sward of weeping lovegrass (Ermelo strain) growing in the Kamberg district of Natal. The sward which had been sown in 15 cm drill rows at a seeding rate of approximately 8 kg/ha was 7 years old and managed for hay and seed production. In September the trial site received a single dressing of limestone ammonium nitrate supplying the equivalent of 90 kgN/ha.

Head emergence began in the first week of November 1972 and on 9 November all emerged heads in each plot were tagged with red plastic rings, cut from PVC sleeving 6 mm in diameter. This precedure was repeated on 15 November when all heads emerging after 9 November were tagged with yellow rings. Seedheads which emerged after 15 November were left untagged. The seedhead population in the six plots was thus divided into three groups according to time of emergence (Table 55).

TABLE 55 Time of emergence of early-, intermediate- and late-emerged seedheads of weeping lovegrass

Emergence Group	Date seedheads emerged	
	1972	1973
Early	Before 9 November	Before 4 November
Intermediate	9 Nov. to 15 Nov.	4 Nov. to 10 Nov.
Late	After 15 November	After 10 November

The initial emergence of anthers was taken as the datum line in measuring the subsequent growth of seeds. In a number of investigations peak anthesis has been taken as a datum line (Baltensperger and Kalton, 1959; Hyde et al., 1959; Anslow, 1964) while time of ear

emergence has also been used (Roberts, 1971). Peak anthesis in weeping lovegrass was difficult to define and, in addition, initial anthesis was considered to be a more practical stage from which to measure subsequent growth and development of seeds. In 1972 anther exertion in weeping lovegrass began on 16 November.

On 8 December, 22 days after initial anthesis, the first plot was harvested. Harvesting continued every 4 days until 28 December 1972. One plot was harvested on each occasion. At each harvest the culms were cut, separated into early-, intermediate- and late-emerged groups according to the tag, counted and removed to the laboratory for analysis.

Immediately on reaching the laboratory 20 heads were randomly withdrawn from each of the three emergence groups; 10 of these were used to determine the dry matter content of the seed, the other 10 to determine the germination capacity of the fresh seed. A further 10 heads from each emergence group were subsequently removed to measure seed set and size of inflorescence produced.

The experiment was repeated in 1973 mainly due to unfavourable weather conditions during the spring in 1972 (Table 56). An additional two plots were marked out in September 1973 and all received the same quantity of nitrogen fertiliser as applied in 1972.

The seedheads were tagged using the same procedure as in 1972. Early-emerged heads were tagged on 3 November 1973, intermediate heads emerged between 4 and 10 November and late-emerged heads after 10 November 1973 (Table 55). Anthesis began in the early heads on 12 November 1973 and the first plot was harvested 24 days later on 6 December. The eighth and last plot was harvested on 3 January 1974.

b) Observations and Recordings

i. Seed set and inflorescence size. On one group of 10 culms, removed at random from each emergence group, stems and inflorescences were measured and a count was taken of the number of spikelets on

each inflorescence. A basal, an intermediate and an upper primary branch were removed from the inflorescence ¼, ½ and ¾ along the central axis, respectively. Further reference to 'basal', 'intermediate' and 'upper' primary branches implies that they occupied the same relative positions on the inflorescence. From each selected primary branch three centrally situated spikelets were removed, their contents separated into fertile and sterile florets and their numbers recorded.

In 1973 the three spikelets dissected in each primary branch were taken from each of a basal, an intermediate and an upper position. On each inflorescence there were thus 3 primary branch locations and 9 spikelet locations in which the ability of florets to set seed was determined.

ii. Maturation of seed. Immediately after the harvested heads reached the laboratory the dry matter content of seeds was determined in those spikelets taken from basal, intermediate and upper primary branches of 10 inflorescences from each emergence group. The bulked contents of the spikelets from each primary branch were weighed, dried to constant mass at 90° C and reweighed.

Once the dry mass of seeds had been determined a further 10 seed-heads were taken from each emergence group, the contents of three spikelets from each of the three selected primary branches were bulked and tested for germinating capacity. The fresh seed was placed in covered petri-dishes on 3 thicknesses of filter paper dampened with a 0,2 per cent and 0,02 per cent solution of potassium nitrate and captan, respectively. The germinating cabinets were maintained at 35° C day and 20° C night temperatures with an 8 hour photoperiod. Seed viability was determined after 10 days.

After each harvest a note was made of the external appearances of the crop and individual inflorescences. Changes in seed-coat pigmentation and the consistency of the endosperm were also noted.

iii. Shedding. After the dissection of inflorescences and the

separation of fertile and sterile florets, as described in (i), the number of seeds shed from spikelets was recorded in the same material. Empty florets from which seed had shed were distinguished from sterile florets by the characteristic appearance of palea and lemma, the appearance of the rachilla and the presence of degenerate ovaries in the floret.

2. CLIMATIC DATA

Experimental data collected in 1973 have been recorded separately from data obtained in 1972 because of the marked climatic differences between the two years. Fluctuations in the seed maturing process are doubtless connected with climate, and particularly with rainfall. Rainfall figures during the period of study in 1972 and 1973 are presented in Table 56, together with seasonal figures.

TABLE 56 (a) Monthly rainfall (mm) at the experimental site in 1972 and 1973

	Sept	Oct	Nov	Dec	Total
1972	0	35	132	61	228
1973	94	59	193	130	476

(b) Rainfall (mm) recorded every four days at the experimental site during the period under study in 1972 and 1973

1972: Dec	8-11	12-15	16-19	20-23	24-28	Total
	28	0	11	6	13	58

1973: Dec	6-9	10-13	14-17	18-21	22-25	26-29	30-3 Jan	Total
	15	8	41	19	33	8	60	184

A combination of an extremely dry spring in 1972 and a very wet early summer in 1973 meant that seasonal rainfall in 1973 was more than double that in 1972. In addition the rainfall during the interval studied in 1972 was half that over the equivalent period in 1973. The

probable implications of the variation in rainfall on seed ripening is discussed further.

3. RESULTS

a) Seedhead Characteristics

The main anatomical and physiological differences between heads, based on time of emergence are shown in Table 57.

TABLE 57 Characteristics of early-, intermediate- and late-emerged seedheads of weeping lovegrass

Seedhead Characteristic	Time of Seedhead Emergence					
	1972			1973		
	Early	Interm.	Late	Early	Interm.	Late
No. of seedheads/metre^2	63	222	318	104	373	402
% contribution to seedhead population	10,4	36,8	52,8	11,8	42,4	45,8
Mean inflorescence length (cm)	22,9	20,6	18,9	21,7	20,4	18,1
Mean culm length (cm)	105,0	103,8	97,2	103,0	101,3	95,7
Mean no. spikelets per inflorescence	250	233	199	176	172	161
Mean no. florets/spikelet	5,0	4,8	4,7	7,1	6,5	5,8
Mean no. florets per inflorescence	1275	1095	935	1250	1101	918
% seed set	54,8	55,5	46,7	50,9	47,7	45,0
100 seed mass (mg) at 12,5% moisture	27,2	28,3	28,3	35,4	33,7	31,8

i. The seedhead population. The mean number of early, intermediate and late heads per square metre and the percentage contribution of each group to the seedhead population present at harvest in 1972 and in 1973 are recorded in Table 57. The increase in the number of seedheads in 1973 was due largely to a 68 per cent increase in intermediate heads. In 1972 the majority of heads were late-emerging but in 1973 there was little difference between the contributions from intermediate and late heads. Early-emerged heads contributed about 10 per cent to the total seedhead population in both years.

ii. Inflorescence size. Inflorescences decreased in size as heads emerged later (Table 57). Inflorescence length, number of spikelets per inflorescence and number of florets per inflorescence were all greatest in the early heads and smallest in late heads. In both years the early heads contained approximately 300 florets more than the late heads.

In both years the mean number of florets per spikelet declined as heads emerged later (Table 57). The size of the spikelet also varied within the inflorescence (Table 58). There was little difference between primary branch positions in early, intermediate and late heads in 1972. However, in 1973 the largest spikelets were recorded on the upper primary branch in heads in each emergence group.

TABLE 58 The mean number of florets per spikelet on basal, intermediate and upper primary branches of early-, intermediate- and late-emerged seedheads of weeping lovegrass (average of all harvests)

Primary Branch Position	Time of Seedhead Emergence 1972		
	Early	Intermed.	Late
Basal	4,9 ± 0,8	4,7 ± 0,7	4,6 ± 1,1
Intermediate	5,0 ± 1,1	4,8 ± 0,8	4,7 ± 0,6
Upper	5,0 ± 1,0	4,8 ± 0,9	4,9 ± 0,8

Primary Branch Position	Time of Seedhead Emergence 1973		
	Early	Intermed.	Late
Basal	6,9 ± 1,6	6,2 ± 1,6	5,6 ± 1,3
Intermediate	7,2 ± 1,5	6,6 ± 1,4	5,8 ± 1,4
Upper	7,3 ± 1,6	6,8 ± 1,5	6,0 ± 1,4

iii. The fertility of florets. Seed set also varied according to time of ear emergence (Table 57). Florets in early-emerged heads were considerably more fertile than those in late-emerged heads.

The effect of spikelet location in the inflorescence on the capacity of florets to set seed is shown in Table 59.

TABLE 59 The mean percentage of florets setting seed on basal, intermediate and upper primary branches of early-, intermediate- and late-emerged seedheads of weeping lovegrass (average of all harvests)

Primary Branch Position	Time of Seedhead Emergence 1972		
	Early	Intermed.	Late
Basal	53,2 ± 7,4	54,3 ± 8,8	43,0 ± 8,3
Intermediate	56,2 ± 8,3	55,6 ±10,8	48,1 ±10,0
Upper	54,9 ± 9,9	56,5 ± 8,7	49,0 ±11,0

Primary Branch Position	Time of Seedhead Emergence 1973		
	Early	Intermed.	Late
Basal	47,0 ± 9,8	44,0 ±10,0	41,5 ± 8,9
Intermediate	49,5 ±11,0	48,1 ±11,2	44,0 ± 9,5
Upper	55,9 ±13,4	51,3 ±10,9	49,6 ±10,4

In each emergence group, in both years, the percentage of florets which set seed declined as the position of the primary branch in the inflorescence became more basal. In 1973, spikelets on the upper primary branch were 9 per cent more fertile than those on the basal branch in early and late heads.

In 1973 the variation in floret fertility between primary branches in the inflorescence was generally greater than that between spikelets on the same primary branch. This is illustrated in Figure 1. The upper spikelets on each selected primary branch in inflorescences of each emergence group were more fertile than the basal spikelets. The fertility difference between the upper and basal spikelets varied between 1 and 9 per cent.

iv. Seed size. The final size which seed attained was strongly influenced by the date of emergence of the inflorescence (Table 57) and also by the location of the spikelet in the inflorescence (Table 60). The mass of 100 seeds at uniform moisture content declined as heads emerged later. In each emergence group in 1973, seeds on the upper

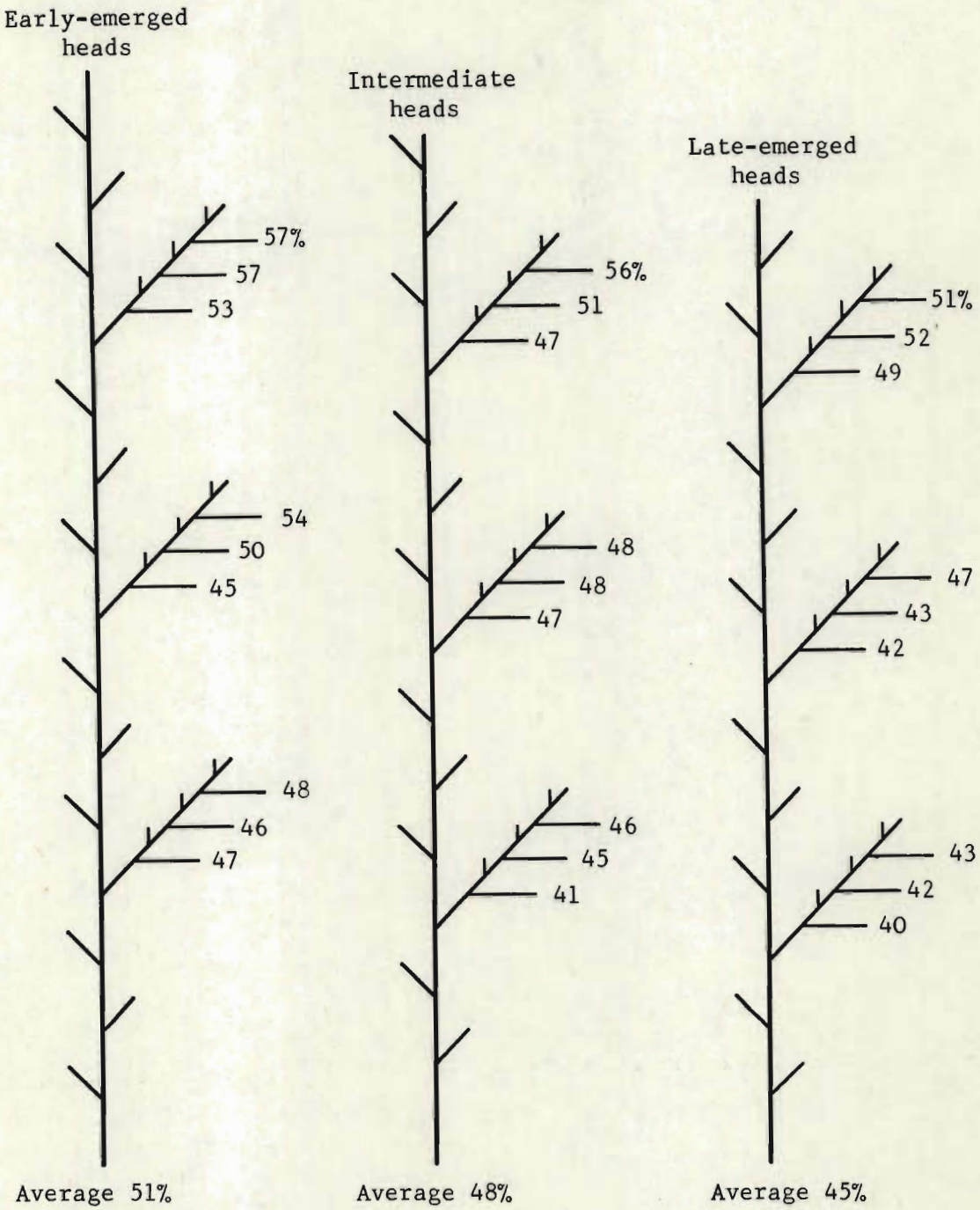

FIGURE 1 The percentage of florets setting seed in basal, intermediate and upper spikelets of basal, intermediate and upper primary branches in early-, intermediate- and late-emerged seedheads of weeping lovegrass in 1973

primary branch were larger than those on the intermediate and basal primary branches. In addition seed size declined as the spikelet position became more basal on the basal primary branch; the decline became greater as heads emerged later.

TABLE 60 The mass of 100 seeds (mg), weighed at 12,5% moisture content, from basal, intermediate and upper primary branches of early-, intermediate- and late-emerged seedheads of weeping lovegrass in 1973 (average of all harvests)

Primary Branch	Spikelet location	Time of Head Emergence		
		Early	Intermed.	Late
Basal	Basal	33,1 ± 2,2	29,7 ± 5,6	28,6 ± 4,8
	Interm.	35,2 ± 0,9	33,1 ± 6,5	31,4 ± 3,2
	Upper	36,7 ± 0,6	34,1 ± 5,1	33,0 ± 4,6
	Mean	35,0 ± 2,0	32,3 ± 5,6	31,0 ± 4,7
Intermediate		35,4 ± 1,1	33,4 ± 4,1	32,0 ± 3,9
Upper		36,1 ± 1,1	35,5 ± 3,0	32,3 ± 2,7
Mean		35,8	33,7	31,8

b) Maturation of Seed

i. Seed mass. Variation in seed fresh mass and dry mass between heads of the three emergence groups in 1972 is shown in Figure 2.

The maximum fresh mass of seed in early heads was reached 26 days after initial anthesis and approximately 12 days prior to the peak fresh mass of seed in intermediate and late heads.

The maximum dry mass of seed in early and intermediate heads was reached after 34 and 38 days respectively. Seed in late-emerged heads continued to increase in dry mass throughout the period studied although the maximum value appeared to be reached soon after the 38th day.

In early heads, seed on the upper primary branch had a consist-

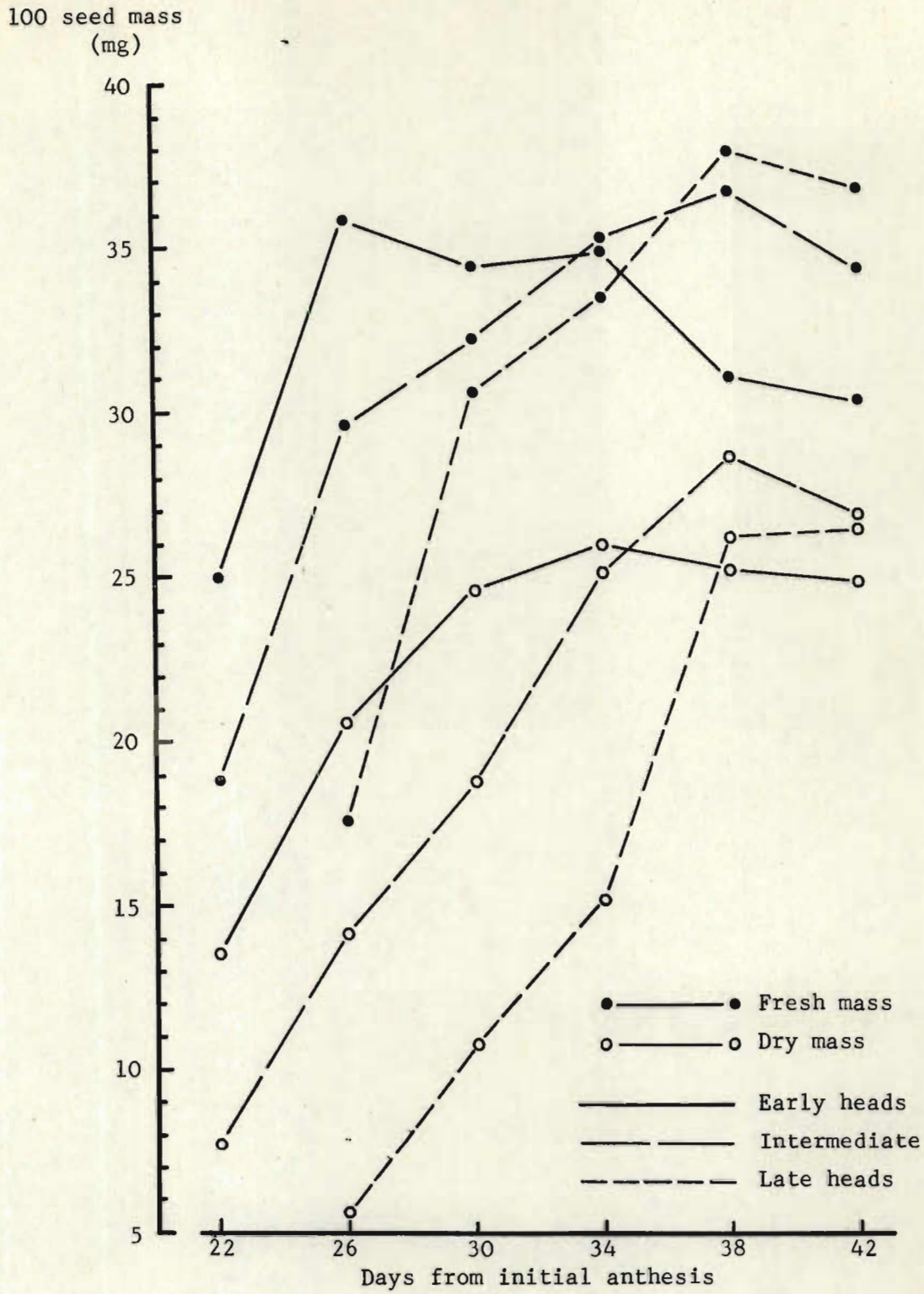

FIGURE 2 Changes in fresh mass (mg) and dry mass (mg) of 100 seeds from early-, intermediate- and late-emerged heads of weeping lovegrass with increasing crop maturity in 1972

ently lower fresh mass than those on lower primary branches (Figure 3). In intermediate and late heads the situation was reversed at least to a stage 34 days after the initial anthesis. In both early and intermediate heads, seed on the intermediate primary branches had the greatest maximum fresh mass. Seed on the basal primary branch in late heads had the greatest maximum fresh mass although seed on the intermediate branch was still increasing in size at the end of the recording period.

Figure 4 shows that the variation in seed dry mass between basal, intermediate and upper primary branches of early-emerged heads was generally much smaller than in the intermediate- and late-emerged heads at any time during the period studied in 1972. In late heads, seed on the upper primary branch had a consistently greater dry mass during maturation compared with seed on lower primary branches. Maximum dry mass values at each primary branch position were reached at the same time in intermediate heads and within a 4-day period in early- and late-emerged heads.

The change in the mass of individual seeds in early, intermediate and late heads with increasing maturity in 1973 is shown in Figure 5. Maximum fresh mass of seed in early heads was reached 36 days after initial anthesis and maximum dry mass was achieved 4 days later. Maximum values of the fresh and dry mass of seed in intermediate heads were reached at the same time, about 44 days after initial anthesis. Seed in the late heads continued to increase in fresh mass and dry mass throughout the period studied.

The variation in fresh mass between primary branches in each emergence group in 1973 (Figure 6) was very similar to that in 1972 (Figure 3). A comparison of maximum values in each emergence group showed that the heaviest seed developed on the basal primary branches.

The variation in dry mass between primary branches was reasonably consistent in time in each emergence group (Figure 7). Seed on the

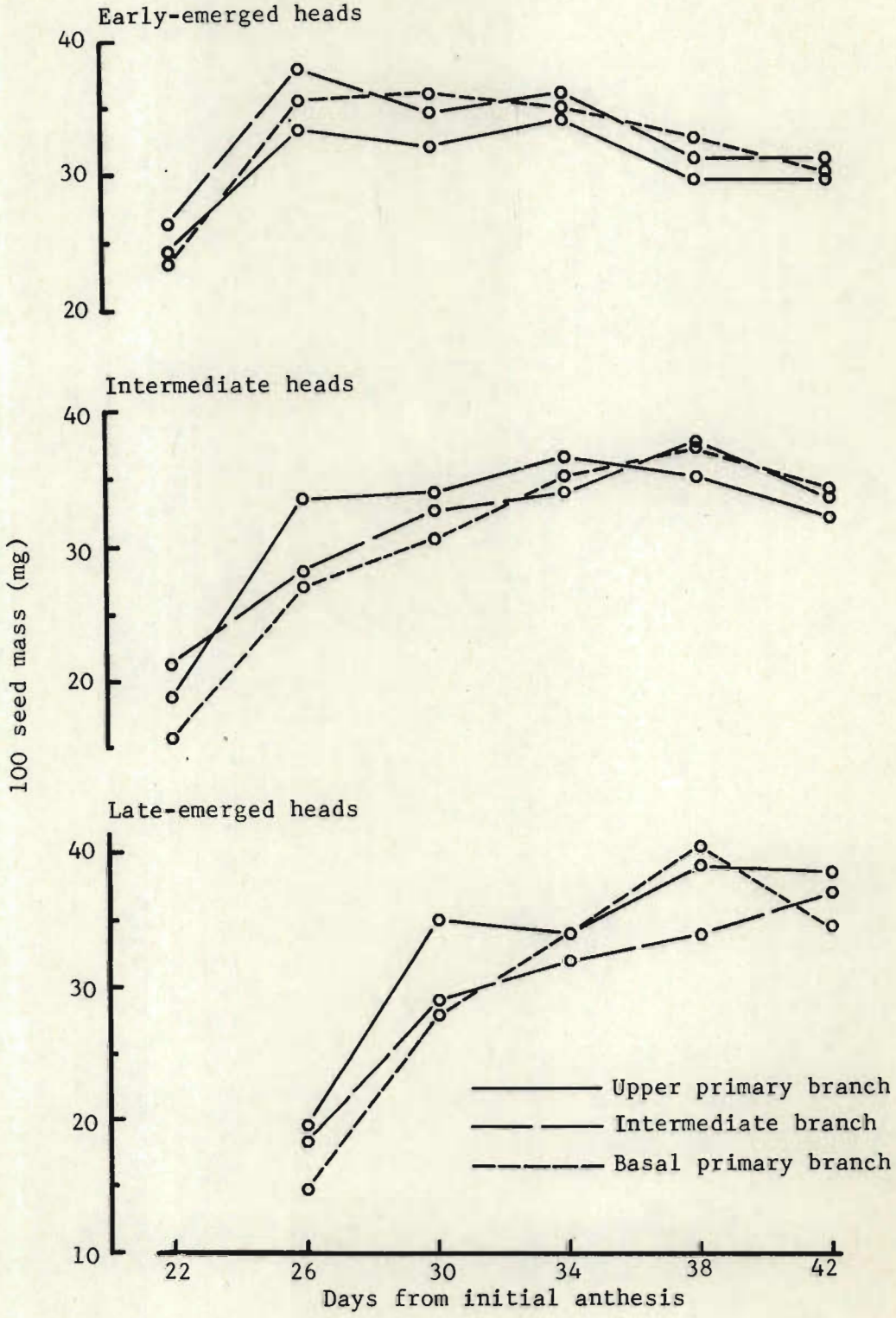

FIGURE 3 Changes in fresh mass of 100 seeds (mg) from basal, intermediate and upper primary branches of early-, intermediate- and late-emerged heads of weeping lovegrass in 1972

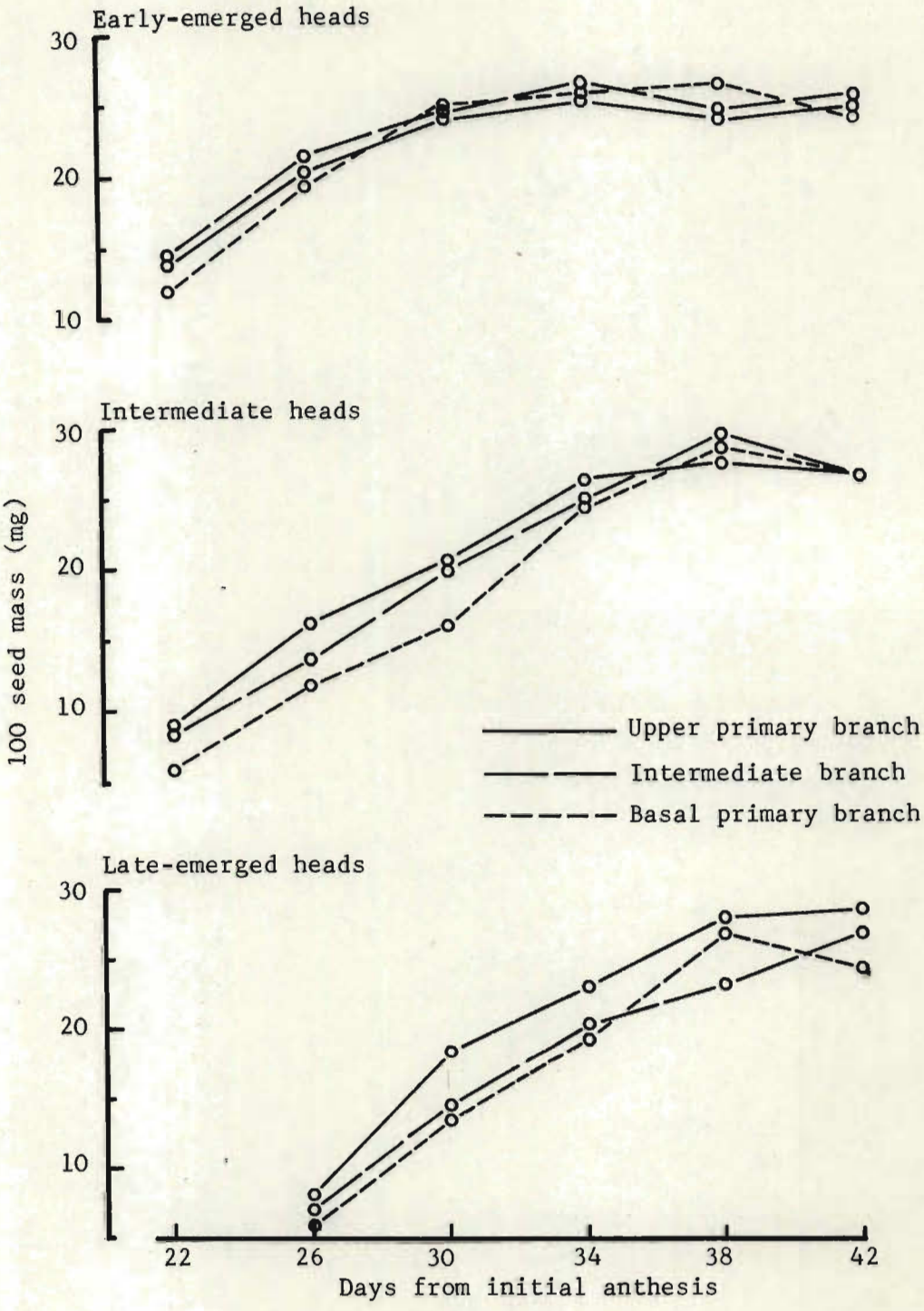

FIGURE 4 Changes in dry mass of 100 seeds (mg) from basal, intermediate and upper primary branches of early-, intermediate- and early-emerged heads of weeping lovegrass in 1972

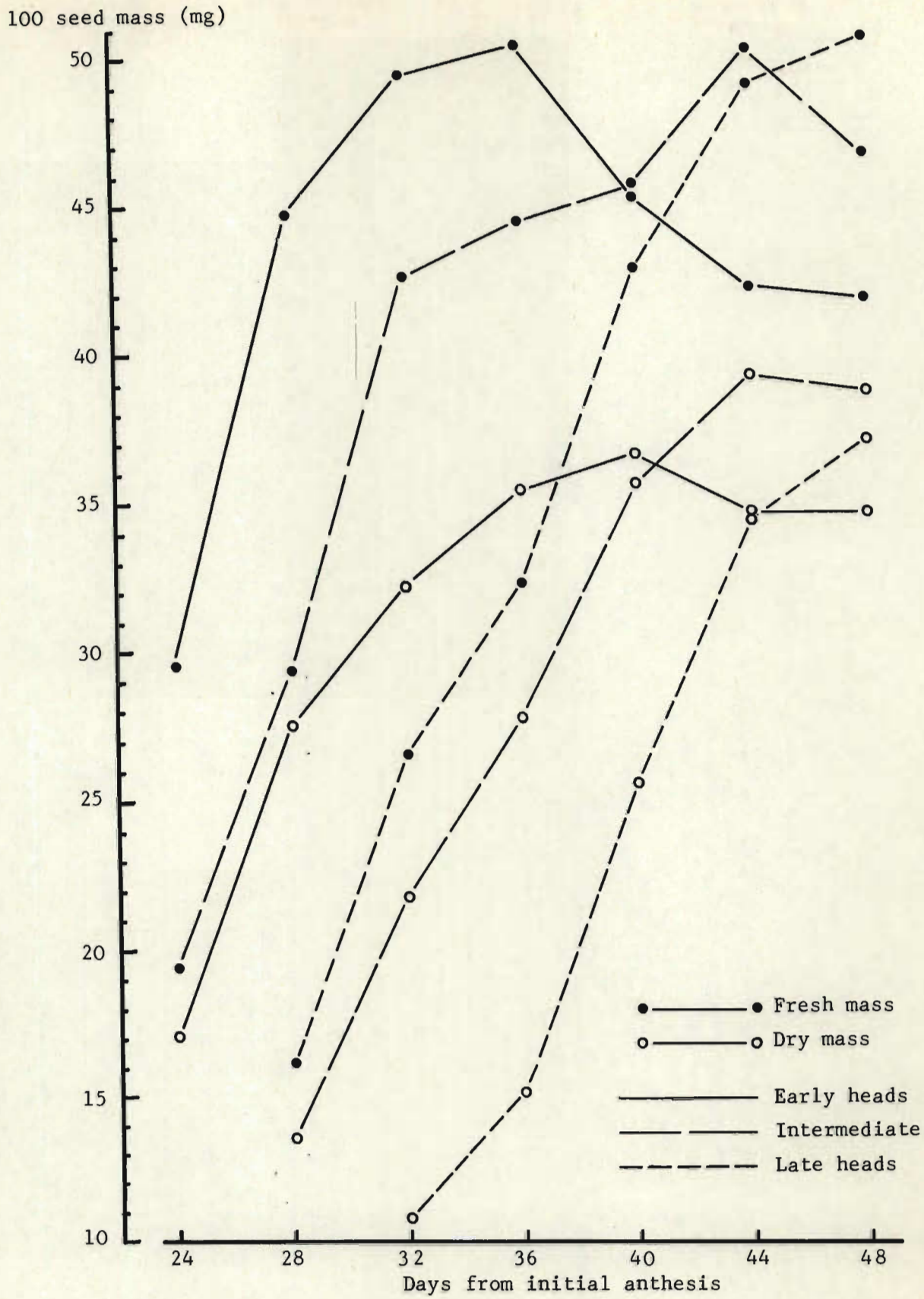

FIGURE 5 Change in fresh mass (mg) and dry mass (mg) of 100 seeds in early-, intermediate- and late-emerged heads of weeping lovegrass with increasing crop maturity in 1973

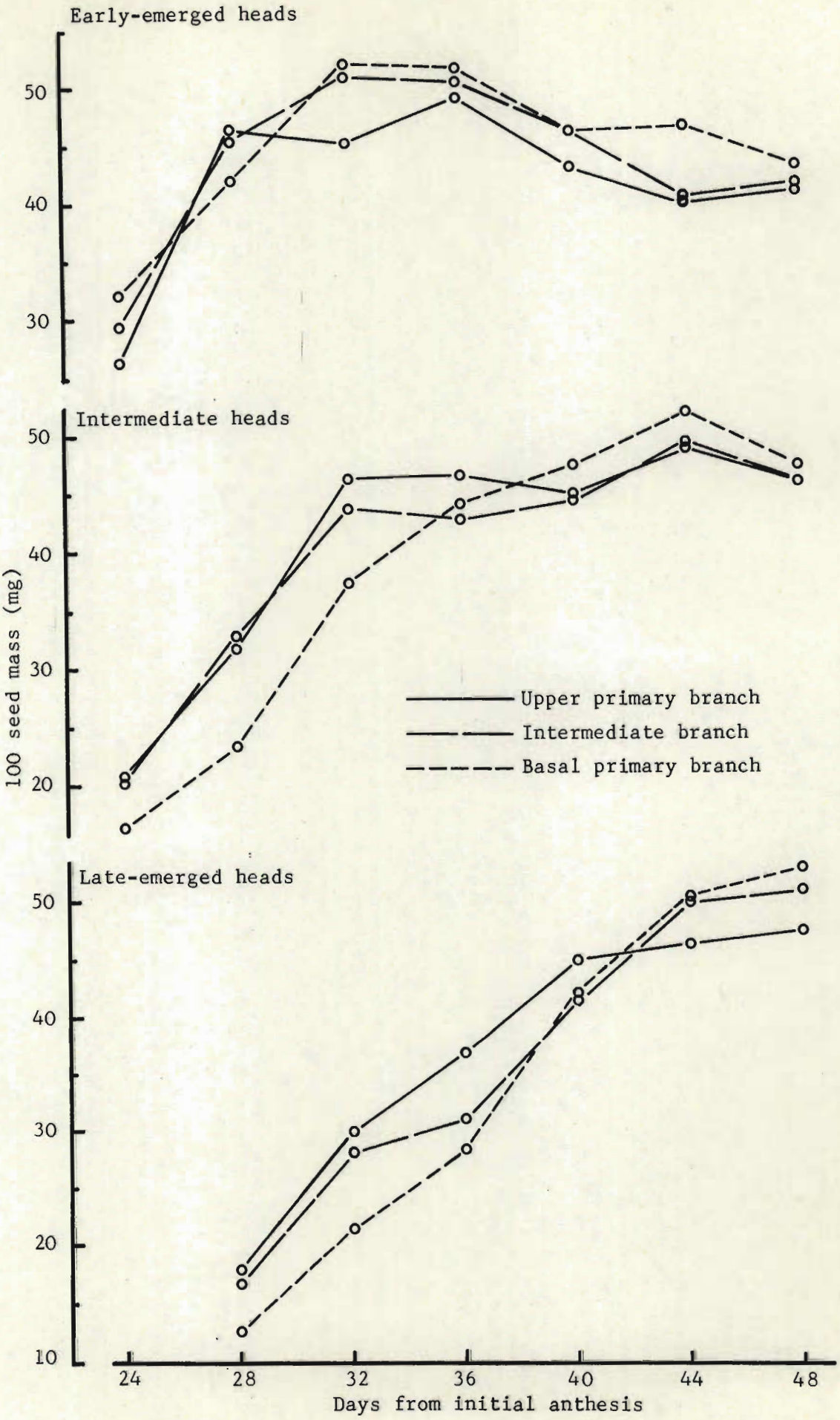

FIGURE 6 Changes in fresh mass of 100 seeds (mg) from basal, intermediate and upper primary branches of early-,

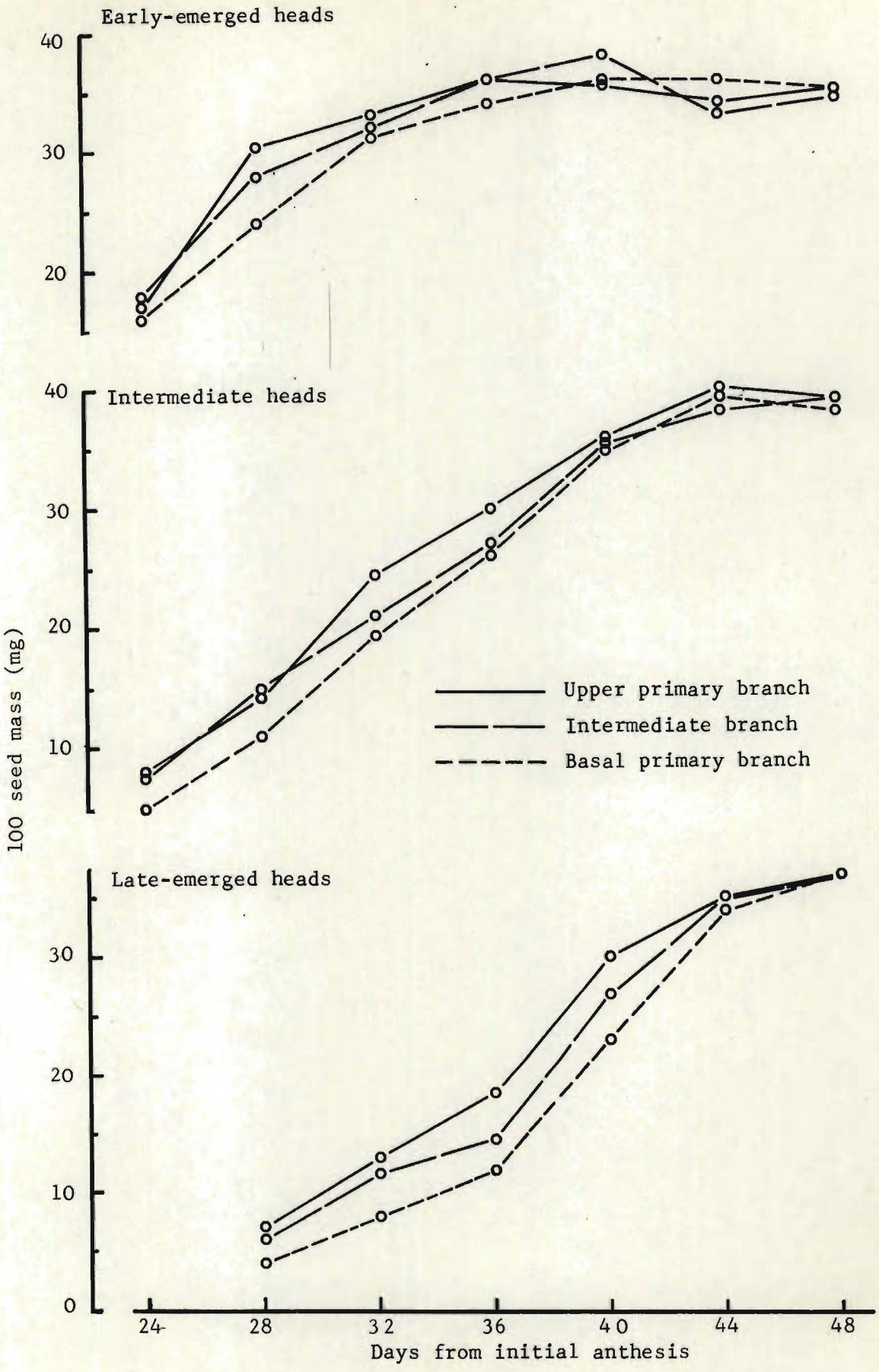

FIGURE 7 Changes in dry mass of 100 seeds (mg) from basal, intermediate and upper primary branches of early-, intermediate- and late-emerged heads of weeping lovegrass in 1973

upper primary branch generally had the greater dry mass than seed on lower primary branches at any time during the period studied, particularly in the intermediate- and late-emerged heads.

ii. Moisture content. Figure 8 shows the reduction in moisture content of seed in early, intermediate and late heads with increasing maturity. The early heads carried drier seed throughout the interval studied in both years. The rate of drying appeared to be greater in intermediate heads than in the early-emerged heads. At the final harvest the moisture content in late heads was approximately 10 per cent greater than in early and intermediate heads.

The variation between primary branches in 1972 is shown in Figure 9. The rate of moisture loss was similar at each primary branch position, and seed on the upper primary branch was consistently drier than on the lower branches.

The variation in percentage moisture content between primary branches was greater in 1973 than in 1972 (Figure 10). However, the drier seed on the upper primary branch and the increase in moisture content down the inflorescence in each emergence group and throughout the period studied is in accord with the findings of the previous year.

In 1973 the rate of loss of moisture from seeds in intermediate-emerged heads was approximately double the rate in early heads. For example the rate of loss from seed on the intermediate primary branch of early heads was 1,0 per cent per day compared with 2,2 per cent per day in intermediate heads during the period from the 24th to the 48th day after initial anthesis. The rate of loss of moisture from seed on the intermediate primary branch in late-emerged heads from the 28th to the 48th day was 1,9 per cent per day. However, seed on the intermediate and upper primary branches in early heads reached a relatively constant moisture level of 17 per cent 40 days after initial anthesis and at least 8 days prior to the attainment of a

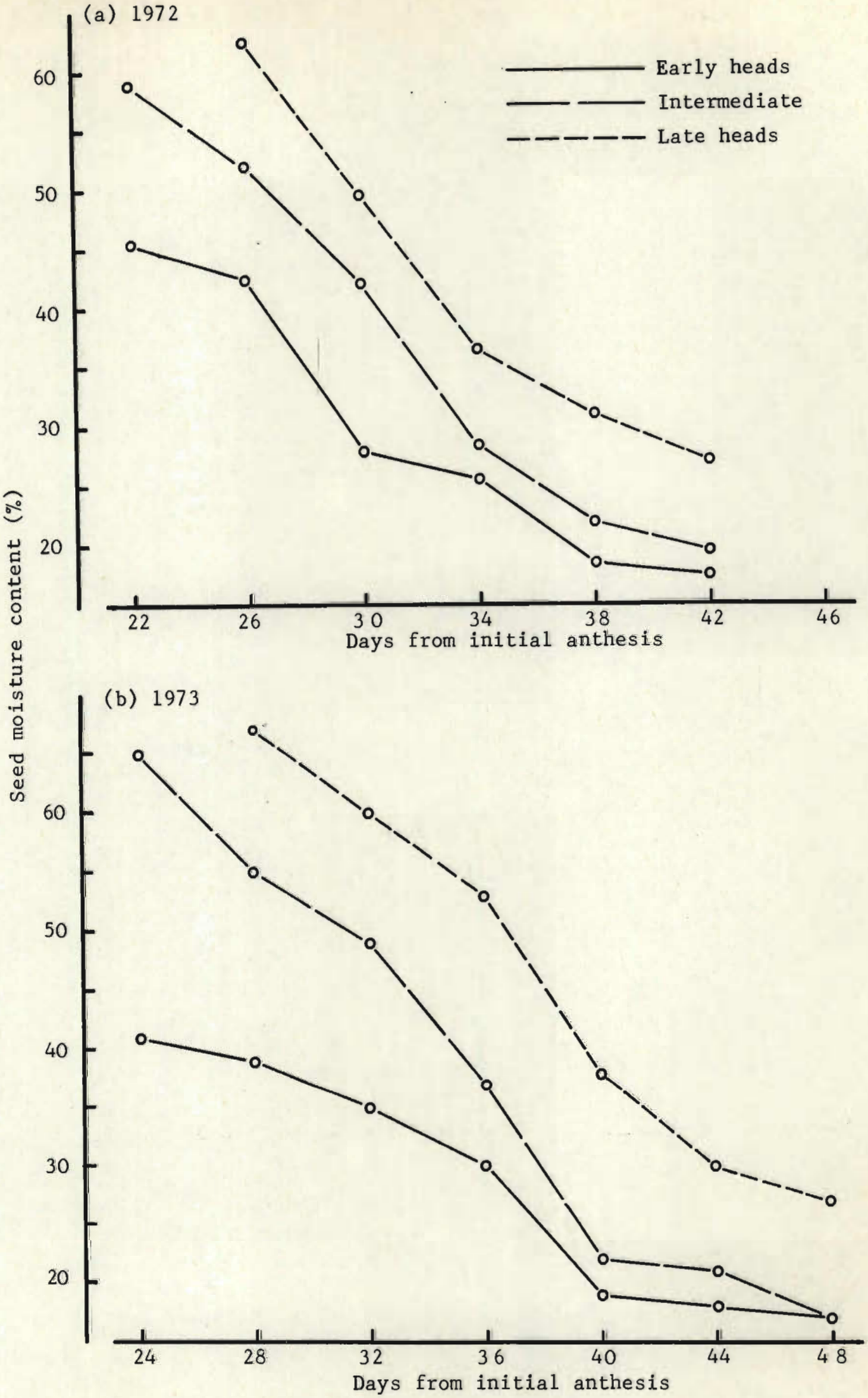

FIGURE 8 Change in moisture content (%) of seed from early-, intermediate- and late-emerged heads of weeping lovegrass with increasing crop maturity in (a) 1972 and (b) 1973

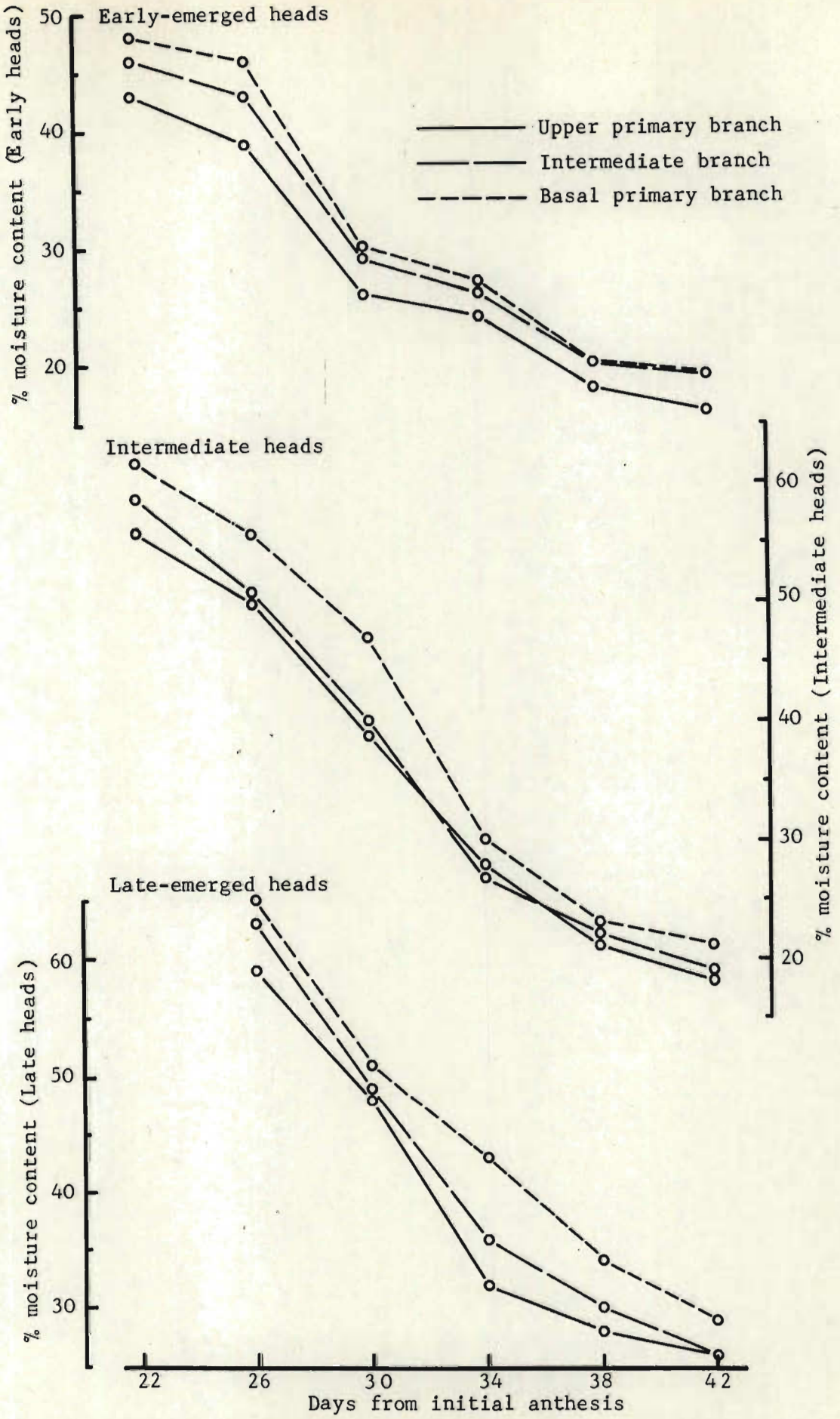

FIGURE 9 Changes in moisture content (%) of seed from basal, intermediate and upper primary branches of early-, intermediate- and late-emerged heads of weeping lovegrass in 1972

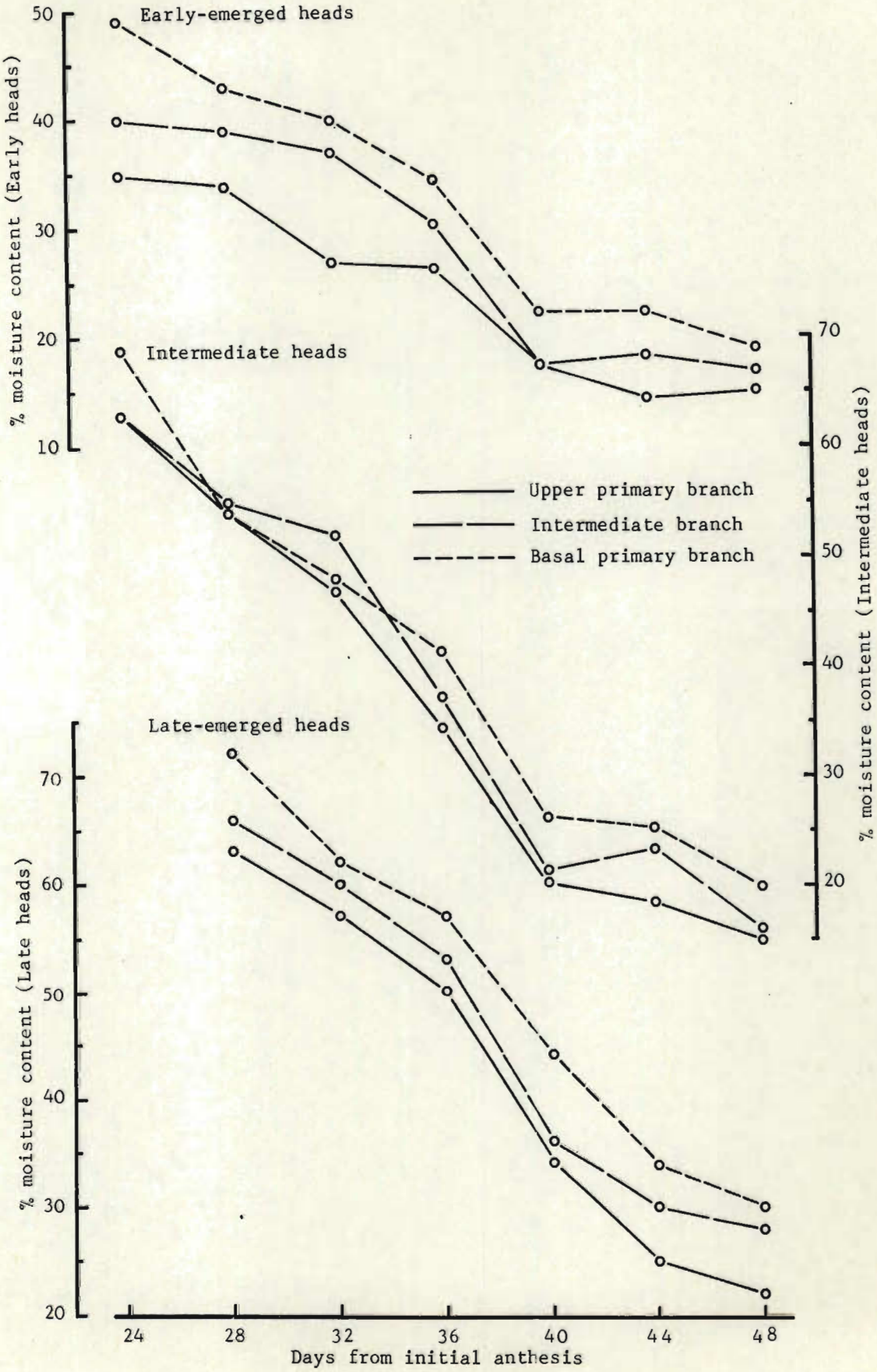

FIGURE 10 Changes in moisture content (%) of seed from basal, intermediate and upper primary branches of early-, intermediate- and late-emerged heads of weeping lovegrass in 1973

similar level in heads which emerged at a later date.

According to the results shown in Figure 11, seed not only had a lower moisture content in spikelets on the upper primary branches but was also drier in ascending order along each primary branch. The variation was greatest on primary branches in late-emerged heads and was as much as 8 per cent between basal and upper spikelets. Also, the variation from the basal spikelets on the basal primary branch to the upper spikelet on the upper branch was of the order of 11 per cent in early and intermediate heads and 15 per cent in late-emerged heads. At this stage, 36 days after initial anthesis, the early heads carried seed 7 per cent and 23 per cent drier than intermediate and late heads respectively.

iii. Germination. The increase in germinating capacity of seed from early, intermediate and late heads with increasing maturity, in 1972 and 1973, is shown in Figure 12. The maximum germination of the 1972 crop was approximately 85 per cent. Seed in the early heads had reached 85 per cent germination approximately 26 days after initial anthesis. The maximum germination of seed in intermediate heads, 87 per cent, was achieved after 34 days. The germination capacity of seeds in the late-emerged heads continued to increase throughout the period studied.

Maximum germination of seed from all three germination groups in 1973 was about 98 per cent. Seed in early, intermediate and late heads had reached this value 32, 40 and 44 days respectively after initial anthesis. At the time when the maximum value was obtained in the early heads, the germination capacity of seed in intermediate and late heads was 71 per cent and 30 per cent respectively. Four days later the values recorded were 91 per cent and 76 per cent respectively.

Figure 13 shows the variation in germination capacity of seed on basal, intermediate and upper primary branches of inflorescences in

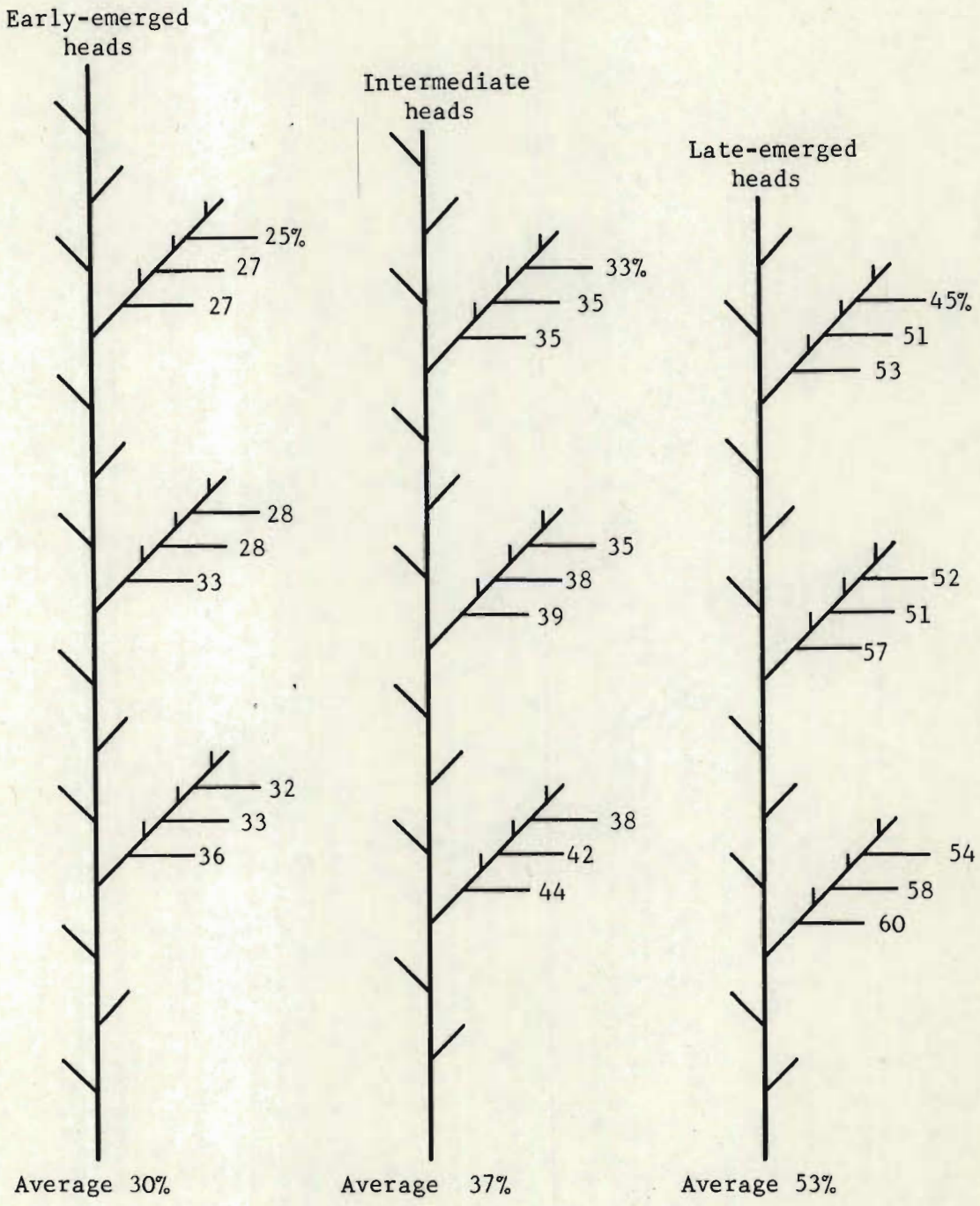

FIGURE 11 The moisture content (%) of seeds from basal, intermediate and upper spikelets in basal, intermediate and upper primary branches of early-, intermediate- and late-emerged heads of weeping lovegrass, 36 days after initial anthesis in 1973

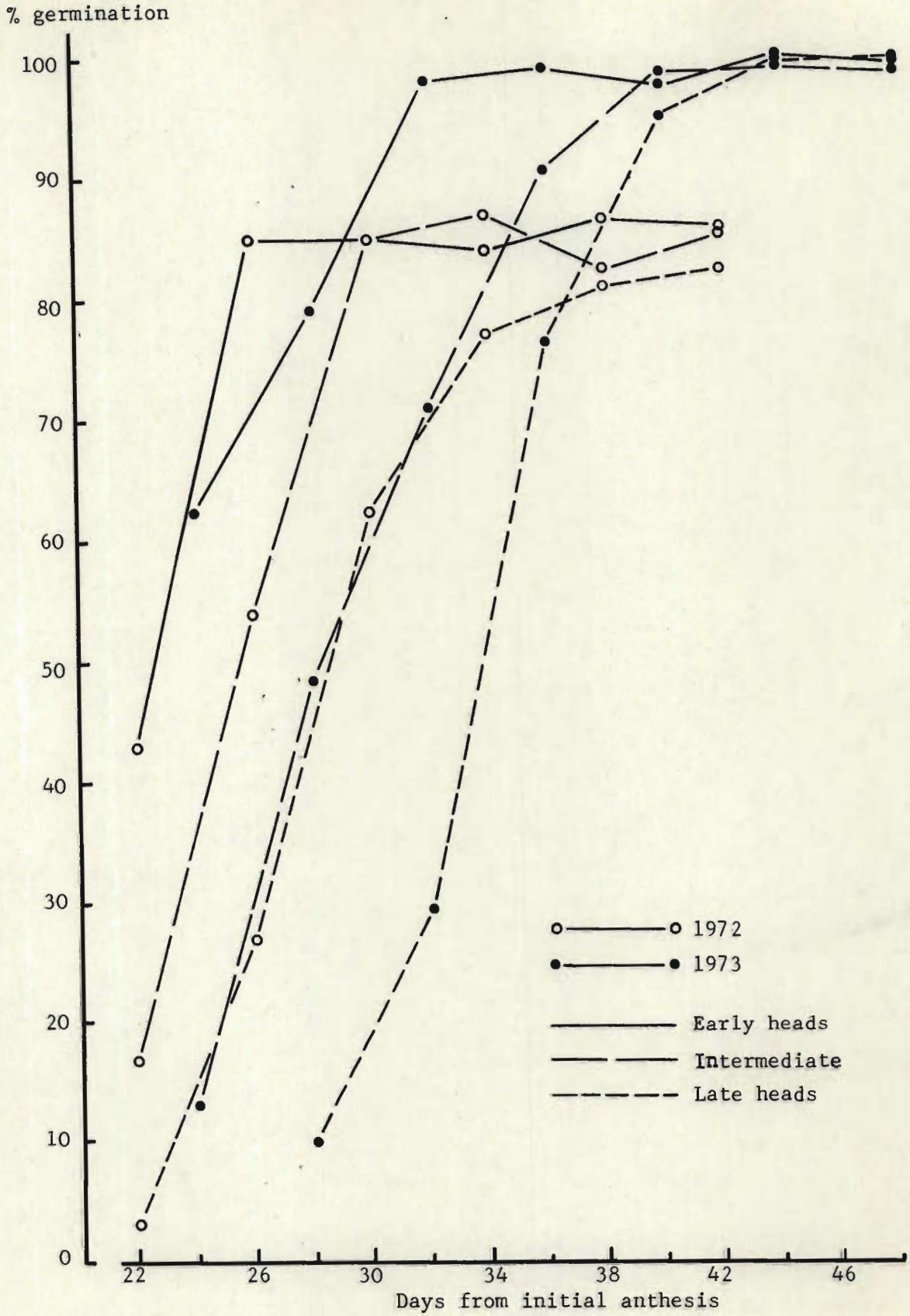

FIGURE 12 Changes in germination (%) of seed from early-, intermediate- and late-emerged heads of weeping lovegrass with increasing crop maturity in 1972 and 1973

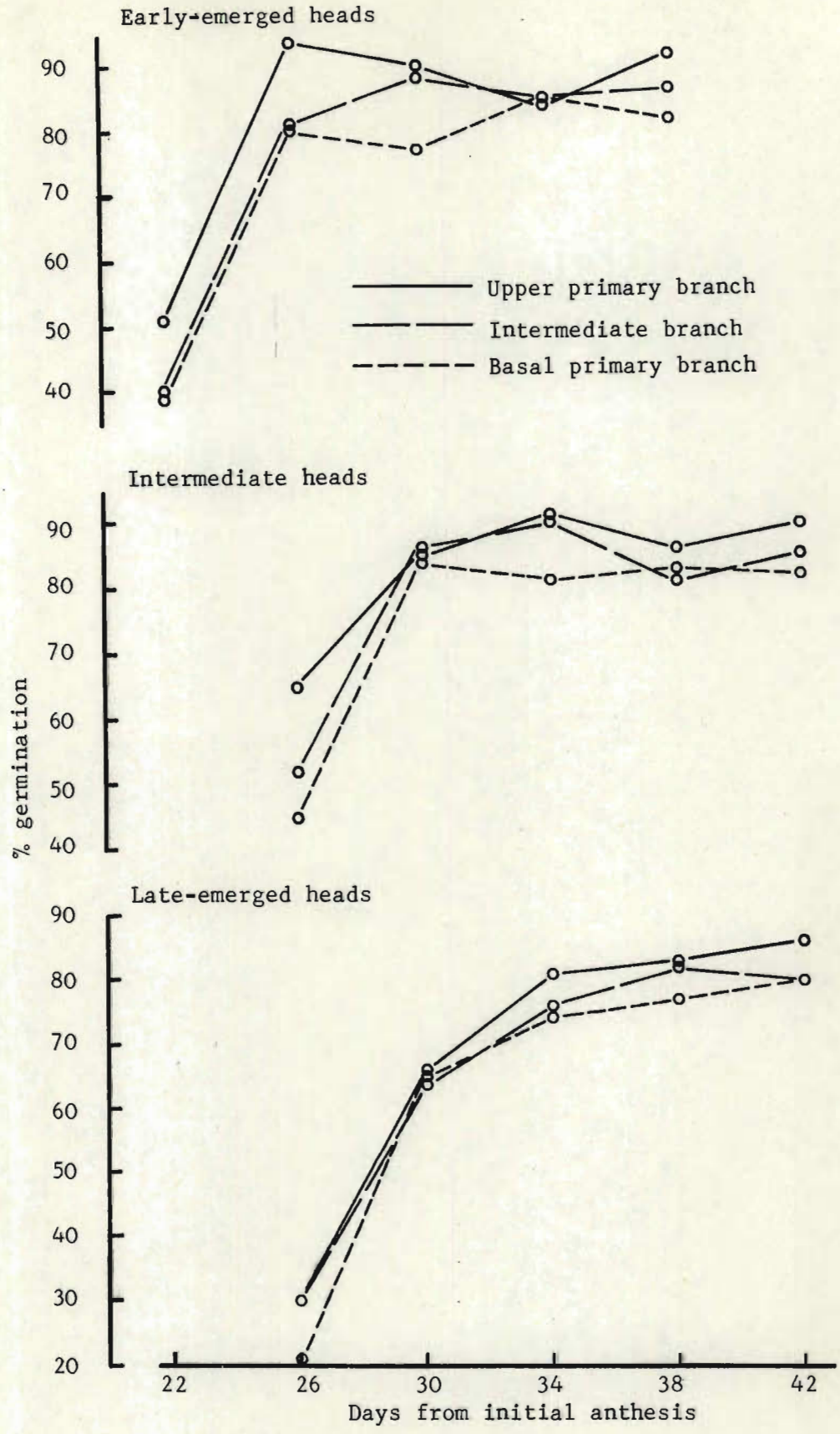

FIGURE 13 Changes in % germination of seed from basal, intermediate and upper primary branches of early-, intermediate- and late-emerged heads of weeping lovegrass in 1972

each emergence group in 1972. Seed on the upper primary branch in each group was the most viable throughout the period studied. The lowest germination percentage was generally associated with seed on the basal primary branch.

Variation between primary branches in 1973 was only apparent in the initial stages of the maturation period studied (Figure 14). The rate of increase in viability increased in descending order of primary branches in the inflorescence. For example, the germination capacity of seed on the upper primary branch in the early-emerged head increased from 75 per cent to 99 per cent over an eight-day period, 24 to 32 days after initial anthesis. The viability of seed on the basal branch of the same head increased from 49 per cent to 97 per cent over the same period.

Figure 15 shows that the germination capacity 32 days after initial anthesis was much lower on average in late heads, that seed on the upper primary branch gave the highest germination percentage, and that the outer spikelets on each primary branch generally contained seeds of greater viability than the basal spikelets. The increase in germination capacity from basal to upper spikelets on the upper primary branch of intermediate and late heads was of the order of 25 per cent. The range in germination capacity in the late heads was 5 per cent to 65 per cent, and that of the crop as a whole was 5 per cent to 100 per cent at this stage of maturity.

c) Shedding

The loss of seed following anthesis is recorded in Figure 16. In 1972 shedding began 30 days after initial anthesis in early heads and after 34 days in intermediate and late heads. At the conclusion of the study, 42 days after initial anthesis, recorded percentage seed losses from spikelets in early, intermediate and late heads were 64 per cent, 33 per cent and 20 per cent respectively.

In 1973 shedding was recorded initially 32 days after initial

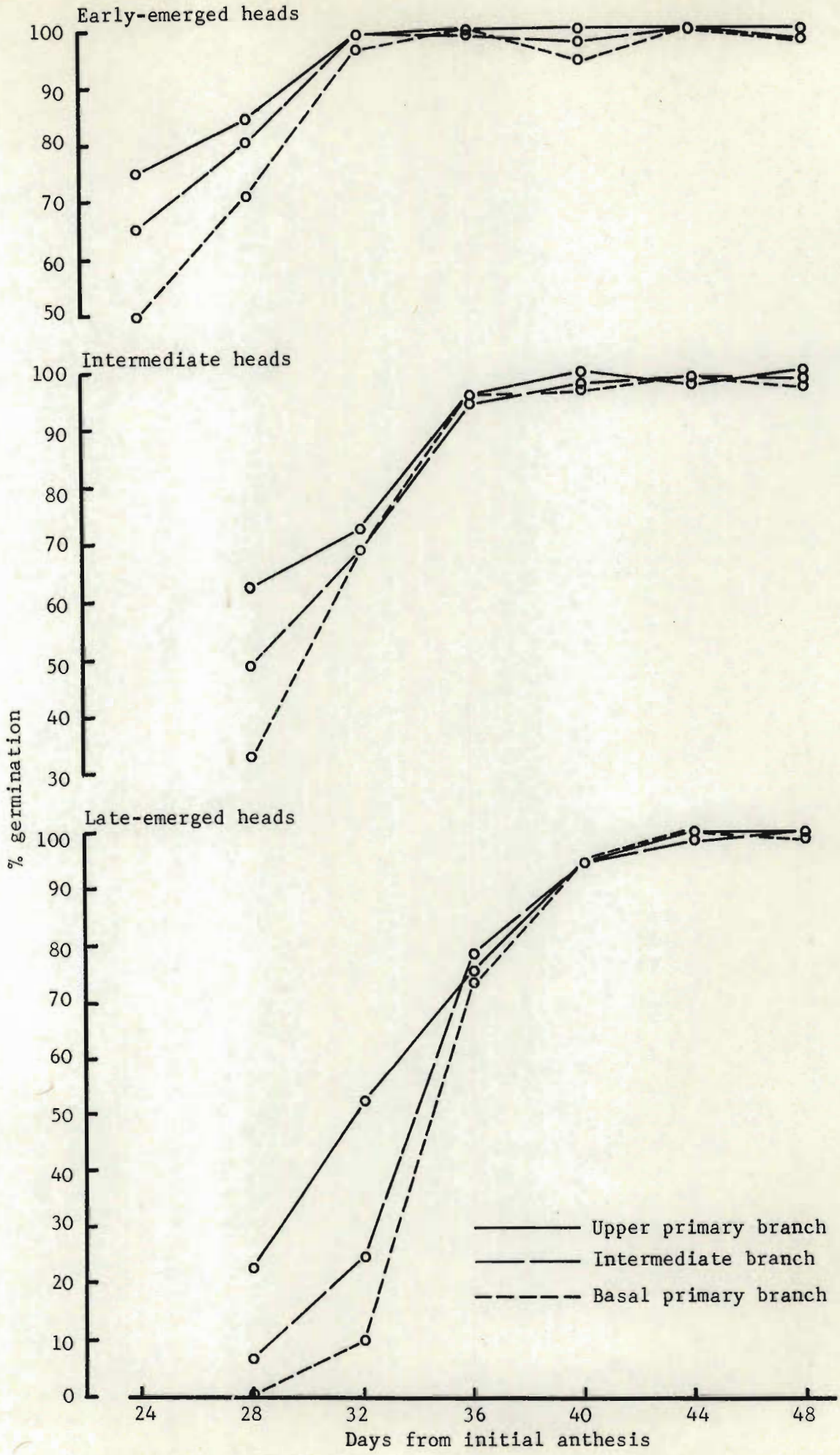

FIGURE 14 Changes in the % germination of seed from basal, intermediate and upper primary branches of early-, intermediate- and late-

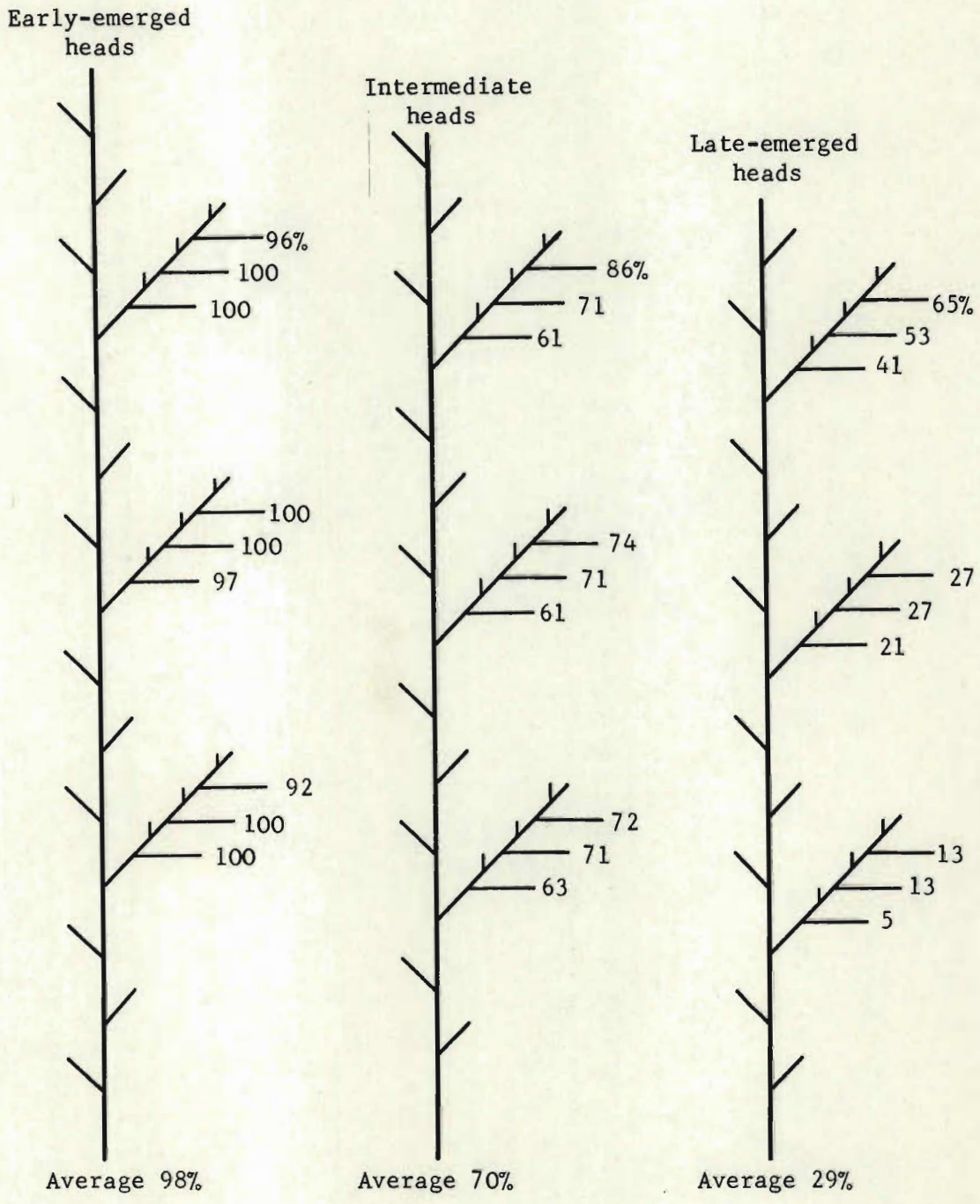

FIGURE 15 The % germination of seed from basal, intermediate and upper spikelets in basal, intermediate and upper primary branches of early-, intermediate- and late-emerged heads, 32 days from initial anthesis in 1973

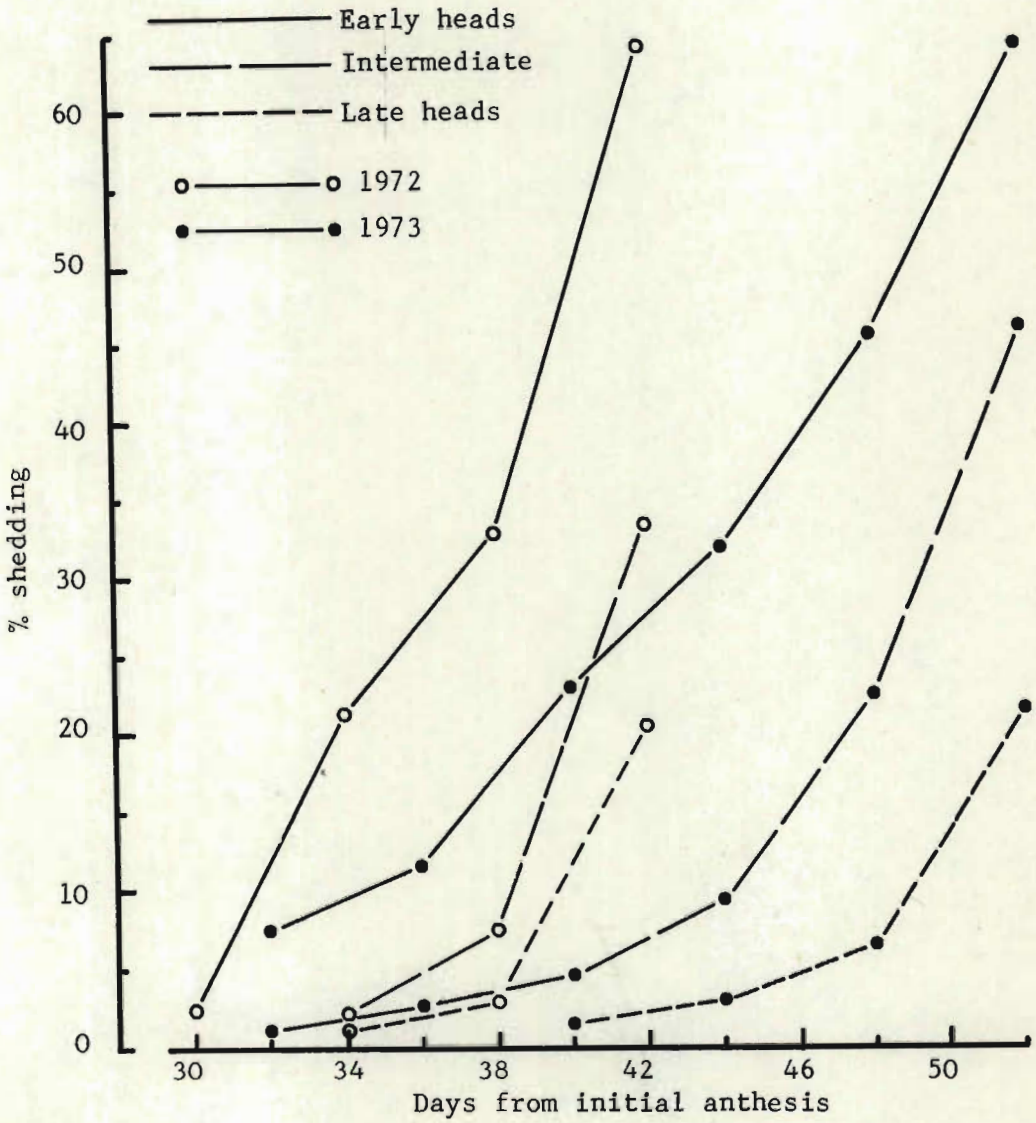

FIGURE 16 Increase in shedding loss (%) of seed from early-, intermediate- and late-emerged heads of weeping lovegrass with increasing crop maturity in 1972 and 1973

anthesis in early and intermediate heads and after 36 days in late heads. At the last harvest date, 52 days after initial anthesis, the shedding percentage in early, intermediate and late heads was 64 per cent, 46 per cent and 22 per cent respectively.

The rate of seed less appeared to be greater in 1972 than in the following year. The maximum recorded shedding loss in early-emerged heads, the same in both years, occurred 12 days after shedding was first recorded in 1972 and after 20 days in 1973.

Seed loss from spikelets on basal, intermediate and upper primary branches, with increasing maturity, is shown in Figures 17 and 18 for succeeding years. The pattern of shedding was similar in each emergence group and in both years. Shedding from the upper primary branch was consistently greater than from intermediate and basal primary branches. In addition, the date of onset of shedding was earlier in the upper primary branch than in intermediate and basal branches.

d) Yield of Viable Seed during Maturation

From measurements made throughout this study of seed (and crop) growth and development an estimate can be made of variations in the mass per unit area of viable seed from early, intermediate and late heads during maturation. A combination of yields from the three emergence groups will allow an estimation of expected 'crop yield' during the maturation period studied.

The changes which took place after anthesis in the yield of viable seed from early, intermediate and late heads in 1972 are shown in Figure 19, and in 1973, in Figure 20. In both years the yield of seed in each emergence group increased after anthesis as a result of an increase in the mass of each seed and an increase in germinating capacity. A maximum yield was obtained which then decreased as a consequence of increased shedding losses. In both years maximum seed yield in early heads was reached approximately 8 days before the

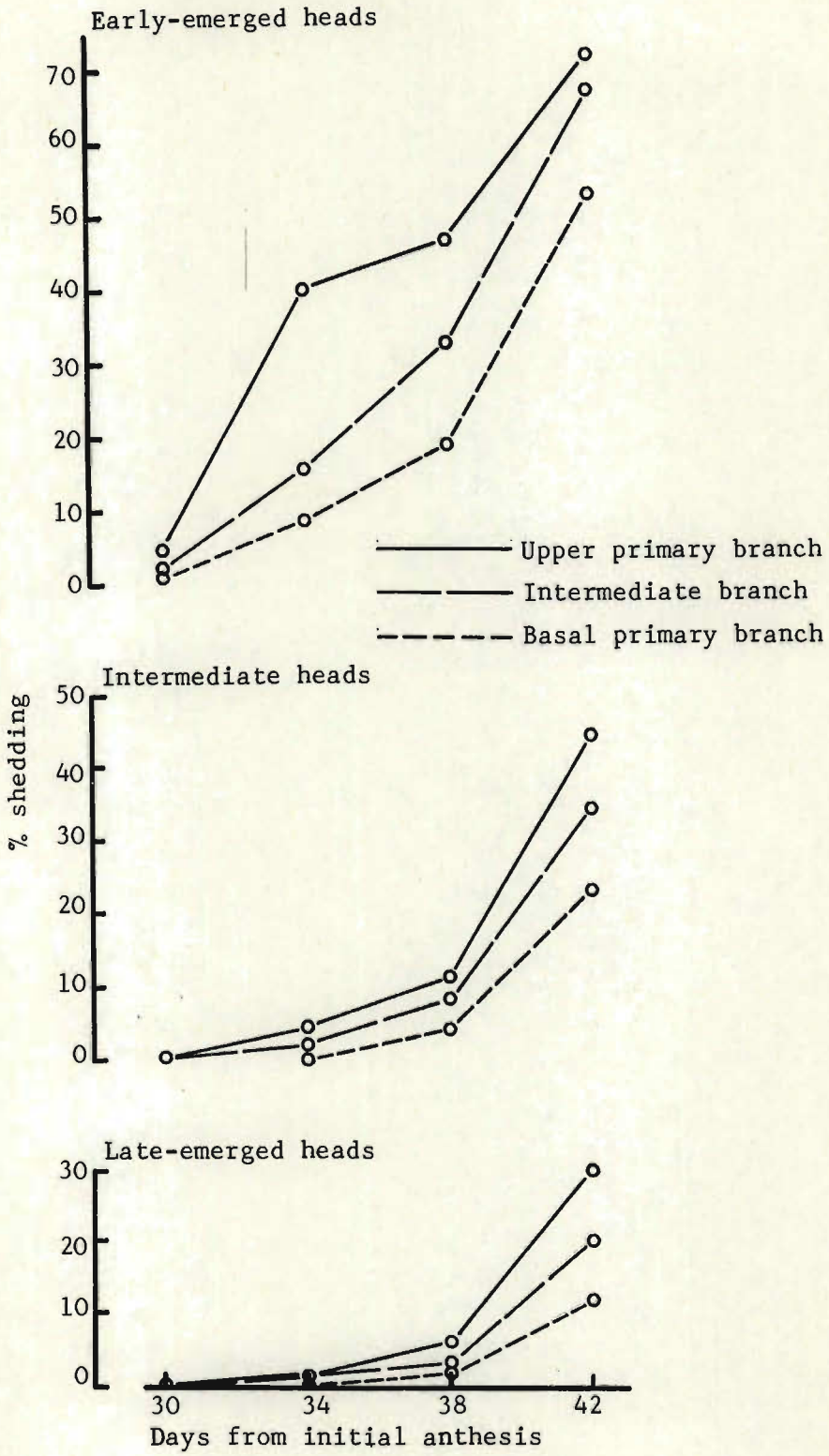

FIGURE 17 Increase in % shedding loss from basal, intermediate and upper primary branches of early-, intermediate- and late-emerged heads of weeping lovegrass in 1972

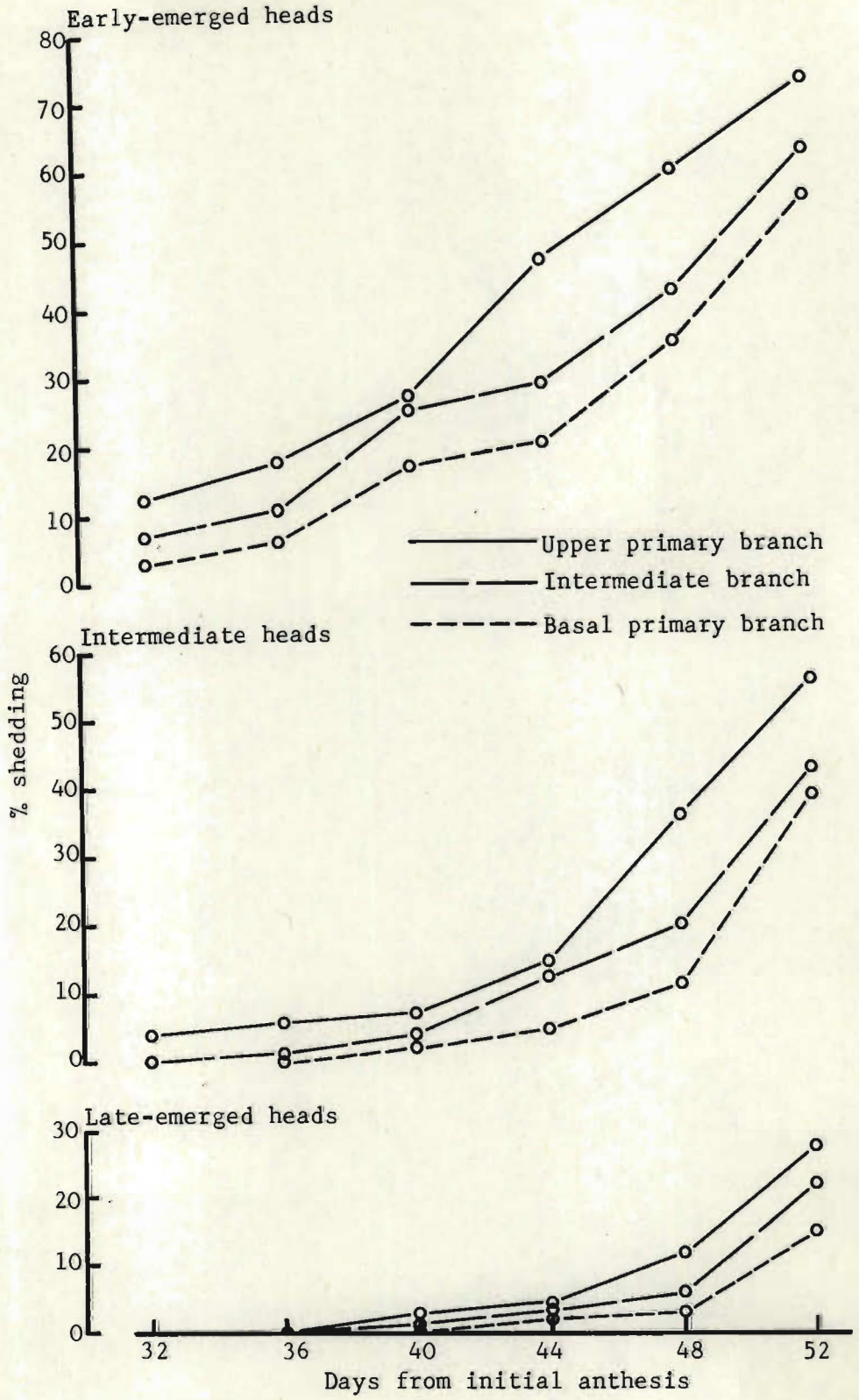

FIGURE 18 Increase in % shedding loss from basal, intermediate and upper primary branches of early-, intermediate- and late-emerged heads of weeping lovegrass in 1973

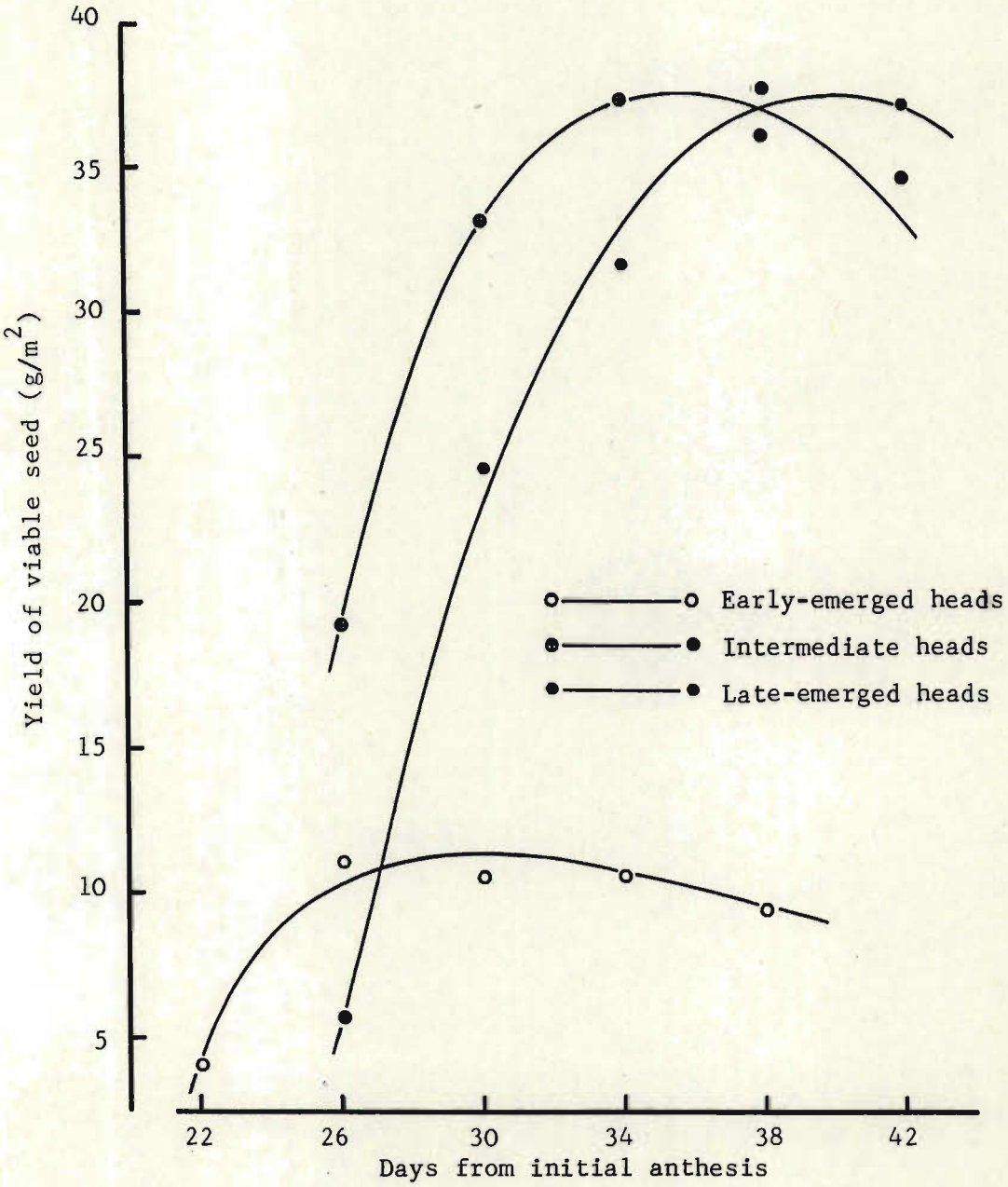

FIGURE 19 Change in yield of viable seed (g/m^2) from early-, intermediate- and late-emerged heads of weeping lovegrass with increasing crop maturity in 1972

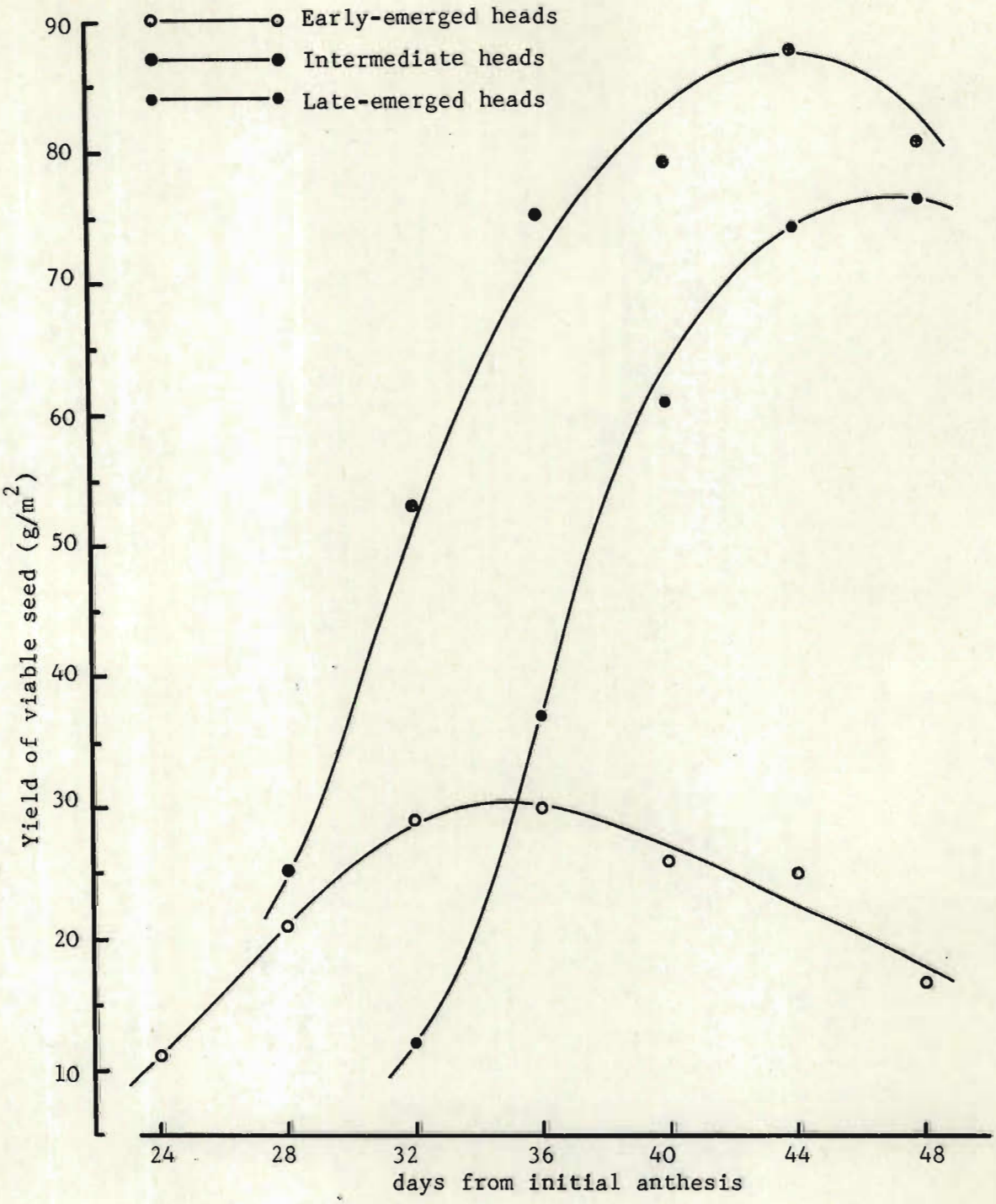

FIGURE 20 Change in yield of viable seed (g/m^2) from early-, intermediate- and late-emerged heads of weeping lovegrass with increasing crop maturity in 1973

maximum in intermediate heads and 12 days before that in late heads. In 1972 it is assumed that maximum seed yield in the late emergence group had been reached 42 days after initial anthesis.

The combined yields from the three emergence groups for 1972 and 1973 are shown in Figure 21. In 1972 the maximum crop yield of approximately 80 g/m^2 was obtained about 38 days after initial anthesis. The early, intermediate and late-emerged heads contributed 11 per cent, 43 per cent and 48 per cent respectively to this maximum yield. In 1973 the maximum crop yield was 180 g/m^2, 125 per cent greater than that of the previous year, and was obtained about 44 days after initial anthesis. The intermediate heads were the main contributors to this yield with 47 per cent, the early and late heads contributing 13 per cent and 40 per cent respectively.

4. DISCUSSION

a) The Seedhead Population and Inflorescence Size

The change in pattern of head emergence with a greater proportion of intermediate heads in 1973 compared with 1972 (Table 57) would appear to indicate greater uniformity in time of head emergence. In comparison with emergence groups in 1972, the early and intermediate head populations in 1973 were larger by more than 40 per cent while the number of heads in the late-emerged groups increased by only 8 per cent. There can be little doubt that the increase in seedheads which emerged earlier coupled with the 25 per cent increase in head numbers per unit area in 1973 can be attributed to improved climatic conditions which prevailed during the spring of that year (Table 56). In 1972 a delay in the first (reliable) rains of the season until early November (Table 56) not only appeared responsible for a reduced seedhead population but also delayed time of emergence of the seed crop so that the majority of heads emerged late (Table 57).

The decline in inflorescence size with increasing lateness of

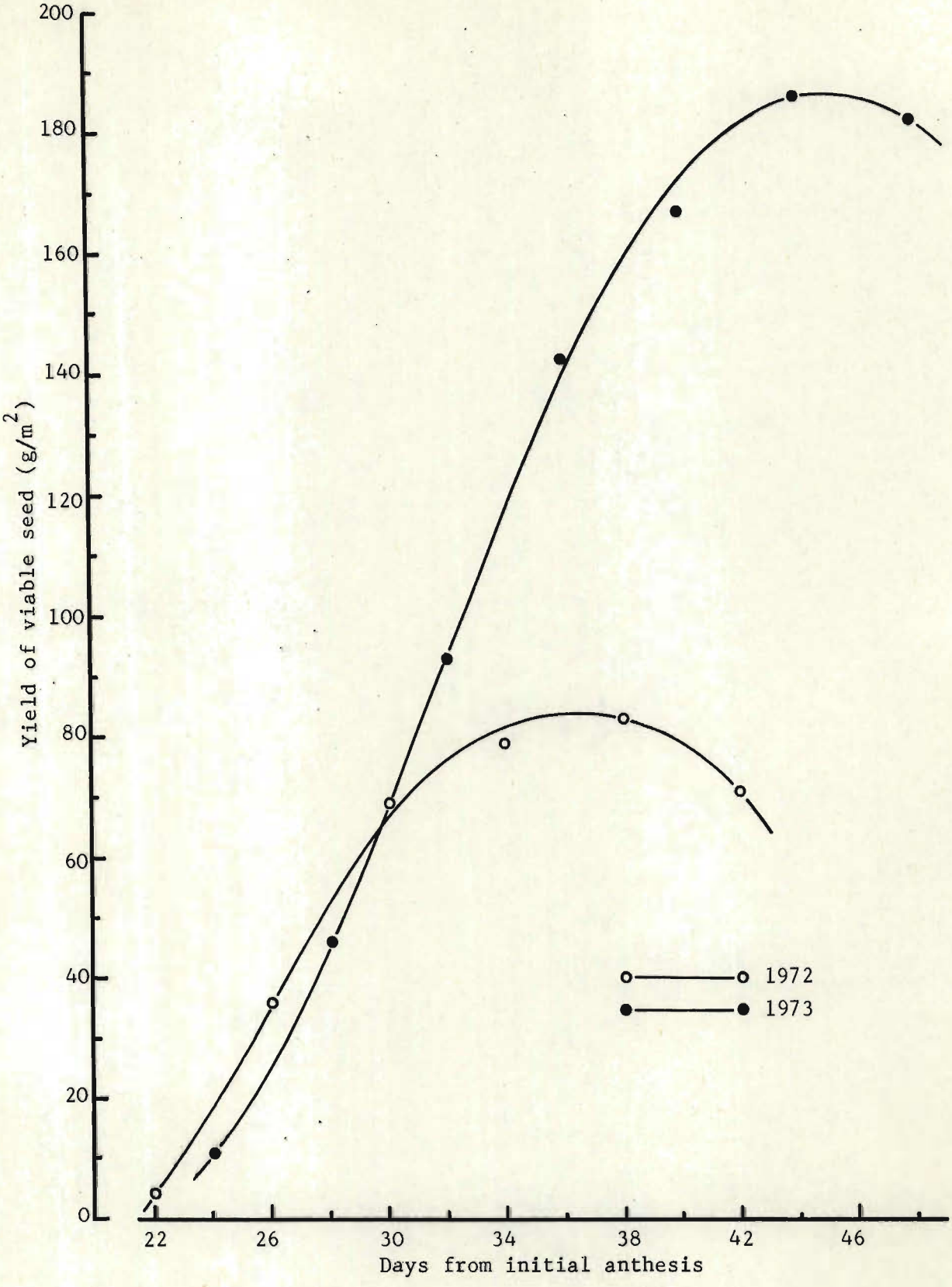

FIGURE 21 Change in total yield of viable seed (g/m^2) from weeping lovegrass with increasing crop maturity in 1972 and 1973

seedhead emergence obtained in the weeping lovegrass crop in both years (Table 57) is in accord with the results obtained by Anslow (1963) who worked with perennial ryegrass and found that the earliest heads to emerge had a larger number of spikelets and more florets per spikelet than those heads which emerged later. From this work and also that of Langer (1956), Wilson (1959), Ryle (1963b) and Ryle and Langer (1963b), Anslow (1963) postulated that the earliest heads to emerge were from tillers formed at an earlier stage in the life history of the plant than those which emerged subsequently.

This postulation has been substantiated in these studies on seed production in weeping lovegrass. In Experiment 1 (Section 1) early-formed tillers were found to produce the largest inflorescences and there was a decline in ear size with decreasing age of the tiller. In the glasshouse studies (Experiments 2 and 3, Section 2) inflorescences from earliest-formed tillers in weeping lovegrass emerged earlier and were larger than those inflorescences from later-formed tillers. Therefore although the division of inflorescences in the crop into three groups was arbitrary, it would appear that the early-emerged heads were physiologically superior to those heads which emerged later.

b) The Fertility of Florets

The capacity of florets to set seed was influenced by time of emergence of the inflorescence and by the location of the floret in the inflorescence. In 1972 time of ear emergence appeared to have a greater effect than floret location in the inflorescence although the reverse was true the following year (Table 59).

The average fertility of early and intermediate heads in 1972 was about 8-9 per cent higher than that of the late heads. In 1973 the fertility of florets ranged from 45 per cent in late heads to 51 per cent in the early-emerged heads. This smaller range in 1973 may be further evidence of greater uniformity between emergence groups in 1973.

The lower fertility of florets in late-emerged heads has been attributed to microclimatic differences within the crop (Anslow, 1963). In weeping lovegrass late-emerged heads were shorter and developed on shorter stems than older inflorescences (Table 57) and may have developed under conditions of increased shading and greater humidity than the taller heads. These conditions are not conducive to efficient floret-opening, anthesis, stigma-exertion and fertilisation (Jones and Brown, 1951; Anslow, 1963) and consequently the capacity of the floret in late heads to set seed was reduced.

Lodging may have had a marked detrimental effect on fertility. In both years the crop lodged prior to seed harvest and lodging was particularly severe in 1973. The larger seedhead population and the damper conditions induced early lodging in 1973, prior to anthesis in the late heads. Increased humidity and reduced air circulation in the lodged crop would no doubt restrict pollen shedding and movement through the crop particularly in the late-emerged heads.

The possible causes of reduced fertility in late-emerged heads could apply also to reduced fertility of florets in basal spikelets in inflorescences of each emergence group (Table 59). In 1973, upper primary branches were 8-9 per cent more fertile than the basal primary branches, and upper spikelets 1-9 per cent more fertile than basal spikelets on each primary branch (Figure 1). The maximum percentage of florets setting seed in the 1973 seed crop was of the order of 57 per cent in the upper and central spikelets on the upper primary branch in early-emerged heads. The lowest percentage was recorded in the basal spikelet on the basal primary branch in late-emerged heads, 17 per cent lower than the crop maximum.

The average fertility of florets in weeping lovegrass seed crops was low at approximately 50 per cent. It might, however, be possible to improve the fertility of florets in the weeping lovegrass crop by applying cultural conditions which reduce lodging or which increase

the proportion of early-emerged heads. Weeping lovegrass is a heavy pollen producer (Jones and Brown, 1951) and therefore it is doubtful whether the efficiency of the pollination and seed set mechanism can be improved by selection and other breeding methods.

It is suggested that unfavourable climatic conditions prevailing at the time of anthesis was the main cause of the low fertility of florets in weeping lovegrass at the experimental site. In both years, the highest rainfall occurred in November, the month during which the crop flowered. Cloudy, dull conditions also predominated, particularly in 1972. High humidity and cloudiness are two important factors affecting floret fertility (Hyde and Williams, 1945; Jones and Brown, 1951). The higher average fertility of the 1972 crop, 52,4 per cent compared with 47,7 per cent in 1973, can be attributed to the drier conditions and the reduced seedhead population, which meant that the crop was more open and the degree of lodging was therefore reduced.

The fact that half of the florets produced in this crop failed to set seed obviously imposes limitation to the yield of seed attainable. Johnston (1960) has described the seed set mechanism in herbage grasses as 'the most significant factor in reducing seed yields'. Little attention has been paid to this aspect of seed production in herbage grasses. An investigation of seed set in weeping lovegrass and the factors causing reduced efficiency of the mechanism is doubtless warranted.

c) Maturation of Seed

i. Seed mass. The final size which an individual seed attained was influenced strongly by the time of emergence of the inflorescence which carried it (Table 60). Anslow (1964) found that seed size varied within the inflorescence and between inflorescences which emerged at different times in the perennial ryegrass seed crop. Stoddart (1959) worked with timothy and reported that 1000 seed mass

decreased as heads emerged later.

Seed mass, at a uniform moisture content, declined from the upper to the basal primary branch and declined from the upper spikelet to the basal spikelet on the primary branch (Table 60). This is in direct contrast to the results obtained by Anslow (1964) in perennial ryegrass where the largest seed was found in basal spikelets in the inflorescence. However, the results obtained in this experiment are in accord with those of the glasshouse experiments (Section 2). As discussed in the previous section the size which an individual seed finally attained appeared to be influenced by the competition for assimilates between spikelets. Competition was presumably more intense in the basal primary branches, because of the considerably greater number of spikelets and developing seeds on these branches than on the upper primary branches and hence the reduced seed size in the basal parts of the inflorescence.

In addition, variability in seed mass between basal and upper spikelets in the inflorescence may have been influenced by competition for light and the products of photosynthesis. It is suggested that the spikelets on the basal primary branch were shaded by the upper portion of the inflorescence, particularly when the crop had lodged. Even prior to lodging the number of seedheads per unit area was high, especially in 1973, and light penetrating to the base of inflorescences would certainly be only a fraction of full sunlight. As the seedheads remained green well after the seed was physiologically mature it may be assumed that the ear itself photosynthesises actively and may be an important contributor to the assimilate requirements of the developing seed. Thorne (1965) has shown that in terms of total carbohydrate entering the wheat ear, 17 per cent appeared to come from ear photosynthesis. On the same basis, 60 per cent of the ear carbohydrate in barley was attributed to ear photosynthesis. This source of carbodrate could become important if the remainder of the shoot is severely

shaded. Therefore, if the weeping lovegrass inflorescence actively photosynthesises and the basal regions are shaded the developing seed in the upper parts of the inflorescence would benefit from the products of photosynthesis in this region.

The variability in seed size between inflorescences which emerged at different times has been attributed mainly to competition for light (Anslow, 1964). The last heads to emerge were presumably shaded by the earlier and taller heads. The shading effect must have intensified as the crop lodged. Consequently the ability of these smaller heads to assimilate would have been reduced and seed size would have been less than that possible in full daylight.

Competition for moisture and nutrients between inflorescences and between parent tillers prior to reproductive growth and development can have a major influence on the variability in seed size (Donald, 1954). The late heads were morphologically and physiologically smaller than those which emerged earlier, largely the result of smaller (later forming) parent tillers at inflorescence initiation (Langer, 1956; Ryle, 1964) and the resulting decreased ability of these tillers and subsequently of the developing inflorescences to compete for assimilates.

Comparison of Figures 2 and 5 shows that larger seed was produced in 1973 than in 1972. The smaller seed in 1972 was undoubtedly due to the dry conditions prevailing immediately prior to flowering. In 1972 the heavier seed came from inflorescences which emerged late. The moister conditions in November may have been of greater benefit to seed development in these seedheads.

Perhaps one further effect of the contrasting moisture conditions was the slower rate of maturity in the seed crop in 1973. Seed in early and intermediate heads took 6 days longer to reach maximum dry mass in 1973 (Figure 5) than in the previous year (Figure 2). Seed in late heads had reached maximum dry mass approximately 38 days after

initial anthesis in 1972, but in 1973 dry mass continued to increase after 48 days.

ii. Moisture content. In this experiment (Figures 8, 9 and 10) the loss of moisture occurred earliest in the older heads and proceeded from the upper regions of the panicle downwards. In both years seed dry mass in all emergence groups reached a maximum at moisture contents between 20 and 25 per cent. Moisture content values were a little higher in 1972, particularly in the early heads. In 1972 maximum dry mass of seed in early heads occurred when the moisture content of the seed was 25 per cent; in 1973 the equivalent moisture content was 19 per cent. The moisture content of seed in intermediate heads at maximum dry mass was 22 per cent and 21 per cent in 1972 and 1973 respectively.

Hyde et al. (1959) and Anslow (1964) reported that dry matter accumulation in perennial ryegrass seed was complete when the moisture content of the seed was approximately 40 per cent. Grabe (1956) recorded moisture contents of 57 per cent and 47 per cent in two years when maximum dry mass of bromegrass seed was attained. The seed of both these species is much larger than weeping lovegrass seed and has a much larger endosperm. Therefore the higher moisture content of these seeds at maximum dry mass is expected.

The rate of moisture loss from seeds in 1972 was reasonably constant during the interval studied, although there appeared to be a more gradual decline in drying from 34 days after initial anthesis to the conclusion of the experiment (Figure 8). In 1973, there was a distinct increase in the rate of moisture loss from seed in each emergence group between days 36 and 40. This period coincided with the calendar dates of 18-22 December and during this period there was a marked decline in rainfall compared with the preceding and succeeding 4-day periods (Table 56).

As previously indicated the moisture content of seed at maximum

dry mass in early-emerged heads was greater in 1972, a drier year, than in 1973. Despite this anomaly, the rate of seed drying was greater in 1972 than 1973. The average seed moisture content in early, intermediate and late heads 36 days after initial anthesis in 1972 was approximately 22 per cent, 25 per cent and 34 per cent respectively. In the second year (1973) with the higher rainfall during the maturation period, the corresponding average seed moisture contents 36 days after initial anthesis were approximately 30 per cent, 37 per cent and 53 per cent respectively. This variation between the two years stresses the influence of weather on the rate and also on the extent of seed drying in the crop.

The pattern of maturation in the crop is reflected to a considerable extent in the moisture content of seed in inflorescences which make up the seedhead population. The range in seed moisture content values at any one time in the maturation process as illustrated in Figure 11 shows clearly the great variation in seed maturity within the seed crop, not only between inflorescences but also within the individual inflorescence.

iii. Germinating capacity. Seed in early and intermediate heads in 1972 achieved maximum germination 26 days and 30 days respectively after initial anthesis (Figure 12), or approximately 8 days prior to the attainment of maximum seed dry mass in both emergence groups. Seed in late-emerged heads did not reach maximum germination capacity until 42 days (Figure 12) and at a stage when seed dry mass appeared to be also at a maximum.

In 1973 (Figure 12) maximum germination of seed in early and intermediate heads was reached 8 days and 4 days respectively before the attainment of maximum seed dry mass. Seed in late-emerged heads in 1973 achieved maximum germination after 44 days. At this stage maximum dry mass of the seed had still not been reached.

It appears therefore that if seed is harvested as near to its

maximum mass as possible viability should not be a limiting factor of yield at this time. This is in accord with results obtained in perennial ryegrass (Anslow, 1964; Hyde et al., 1959; Nellist and Rees, 1968) and timothy (Roberts, 1969).

All seed in the crop in 1973 had attained maximum viability approximately 44 days after initial anthesis (Figure 12). In 1972 seed from early and intermediate heads had reached maximum viability after 30 days. However, the maximum germination capacity of seed in late heads was not obtained until approximately 38 days after anthesis (Figure 12).

The tremendous range in viability in the seed crop, 5 per cent to 100 per cent at the time at which seed in the early heads achieved maximum viability (Figure 15) is sufficient evidence of the necessity to delay crop harvest until all seeds in the intermediate heads are viable. In 1973 this stage was reached 40 days after anthesis, at which stage the average germination percentage of seed in the late-emerged heads had increased to 95 per cent.

The lower germination capacity of seeds in the crop in 1972 can also be attributed to the drier weather conditions of that year, which resulted in the development of smaller, lighter seed. In many herbage species it has been shown that germination capacity is directly related to seed mass, the larger seeds having the greater capacity to germinate than smaller seeds (Kneebone, 1960; Kittock and Patterson, 1962; ten Hove and Kleinendorst, 1962).

d) Seed Shedding

Loss of seed from maturing inflorescences is common in grasses and constitutes a serious economic problem in many species. In weeping lovegrass the present study showed that seed was retained within the spikelet and not susceptible to shedding until reasonably mature. Shedding increased markedly when the seed had reached or was close to its maximum mass and its moisture content had decreased to a value

below 30 per cent. Consequently only 10 per cent of seed had shed from early, intermediate and late heads 32 days, 38 days and 40 days respectively after initial anthesis in 1972. The same level of shedding in early, intermediate and late heads in 1973 was reached 34, 44 and 48 days respectively (Figure 16).

In perennial ryegrass, Anslow (1964) found that shedding of florets occurred at any early stage of maturity. Shedding began when seed had a moisture content of between 45 per cent and 55 per cent, depending on date of emergence of the inflorescence, and when the mass was less than the maximum. Work carried out by Nellist and Rees (1967) and Roberts (1969) showed that shedding of timothy seed began at 41 per cent moisture content.

As seeds in upper spikelets in weeping lovegrass inflorescences were more mature than seeds in basal spikelets and attained a heavier final mass, it is inevitable that they should shed first and to a greater extent than those more basally located. This occurred in 1972 (Figure 17) and 1973 (Figure 18). As the maturity of inflorescences increased the rate of seed loss between primary branch positions became similar, especially in 1973.

e) Crop Yield and Optimum Harvest Time

The maximum quantity of viable seed produced per unit area was obtained approximately 38 and 44 days after initial anthesis in 1972 (Figure 19) and 1973 (Figure 20) respectively. The maximum yield of seed in the field would be expected over a period of time, and in weeping lovegrass it appears that this plateau may extend for at least 3-4 days. This will depend on climatic conditions and other factors, such as the final proportion of each emergence group in the crop.

At maximum crop yield in 1972 (Figure 21) the contribution made by intermediate and late heads was very close to the maximum yield of seed attained in each group. The contribution from early-emerged heads at this time was approximately 14 per cent lower than the maximum yield

of seed produced by this group approximately 26 days after initial anthesis (Figure 19). In 1973, the respective contributions to maximum crop yield by each emergence group was very similar to those obtained in 1972. The contribution from the early heads at this time was only 72 per cent of the maximum value achieved by this group, 8 days prior to the attainment of maximum crop yield (Figure 20). Maximum crop yield corresponded with the maximum yield in the intermediate emergence group, the largest contributor to total yield.

The attainment of maximum crop yield signifies the optimum harvest time. Therefore, the optimum time of harvest of the weeping lovegrass seed crop in 1973 was 44 days after initial anthesis. The variation in seed maturity within and between inflorescences at this time is illustrated in Figure 22.

The average moisture contents of seed in early, intermediate and late heads at optimum harvest time were 19 per cent, 22 per cent and 31 per cent respectively. The crop range was from 14 per cent to 34 per cent.

The heaviest seed at this time was recorded in late-emerged heads. Mean losses due to shedding were 33 per cent, 11 per cent and 3 per cent in early-, intermediate and late-emerged heads respectively. No shedding had occurred in the basal spikelets on the basal primary branch in late heads. However, more than half of the seeds developed in upper spikelets on the upper primary branch in early heads had shed at this time.

All seed in the crop had achieved maximum viability at optimum harvest time.

From research observations of the appearance of heads at each sampling date, the visible signs of ripeness when maximum crop yield was obtained can be described. The early heads were generally a rusty-brown colour, the spikelets on these heads were brown and dry, and shedding was severe in the upper spikelets. Seeds from the upper

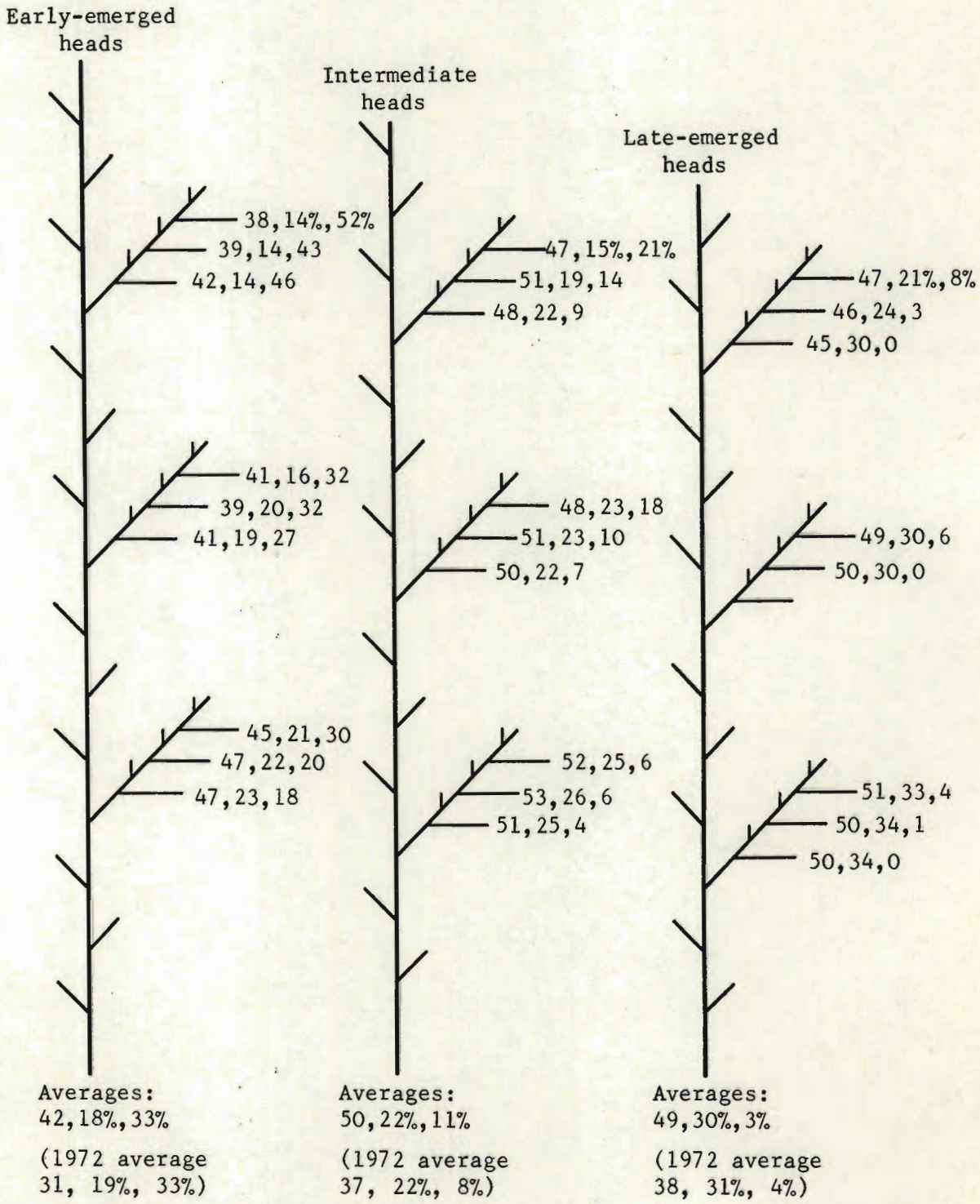

FIGURE 22 The fresh mass of 100 seeds (mg), % moisture content and % shedding of seeds from early-, intermediate- and late-emerged heads of weeping lovegrass at the 'optimum' time of harvest in 1973, 44 days after initial anthesis

spikelets were fully mature and had taken on the characteristic golden amber colour. Seeds in the basal spikelets were at the hard dough stage but had not attained the amber colour. They were pale brown in colour.

The intermediate heads were a green-brown colour. The central axis at the base of the panicle was in many cases still green. The spikelets on the basal primary branches were also green and the seeds in these spikelets were at a medium-hard dough stage and grey-brown in colour. The seed in the upper spikelets was light brown and at the hard dough stage.

In late heads, which were green but brittle, seed was generally at the medium-hard dough stage. Seeds in the basal spikelets were generally at a soft-dough stage and a dirty-white colour. Shedding in the late heads was not evident.

The optimum time of harvest is therefore a compromise. At one extreme seed is lost due to severe shedding and at the other extreme, seed is not considered sufficiently mature for harvest, even though it is physiologically mature, and therefore is also lost to final seed yield. The balance between these two maturity extremes obviously depends on maximum crop yield, which however, does not take into consideration losses due to harvesting techniques.

In the field an estimation of optimum harvest time can be made from the combination of a measure of the number of days after initial anthesis, the visual estimation of stage of ripeness and the moisture content of seeds in the inflorescences. From the difference between results in each of the two years it can be seen that the relationship between seed mass and seed moisture content is the most reliable and the more consistent index to optimum harvest time. Although rate of moisture loss in the standing crop can vary according to environmental conditions, the average seed moisture content of the crop lay between 22 per cent and 30 per cent at time of maximum crop yield in 1972 and

1973 (Figure 22).

Klein and Harmond (1971) established a good correlation between time of obtaining maximum yield of pure live seed and the moisture content of the standing crop for a number of crops. Seed moisture content curves were established for each crop, related to changes in yield in time, and used to predict the optimum harvest time. Despite the variation in physiological maturity of seed in weeping lovegrass it is considered that a seed drying curve could be used in this crop and would be the most useful factor to decide on the correct time for harvesting.

CHAPTER IV

EXPERIMENTAL. CULTURAL TECHNIQUES FOR INCREASING SEED YIELD IN AN ESTABLISHED STAND OF *Eragrostis curvula*

EXPERIMENT 5 THE EFFECT OF RATE AND TIMING OF NITROGEN APPLICATIONS ON SEED PRODUCTION IN WEEPING LOVEGRASS

1. INTRODUCTION

Many published reports of research on grass seed production have shown the beneficial effect of nitrogen fertilisation on seed yield. Most research has indicated that production of seed is dependent on nitrogen fertilisation more than on any other cultural practice as long as levels of other nutrients, particularly phosphorus and potassium, are adequate and soil moisture is not limiting. In most crops there can be little doubt that nitrogen is the most limiting production factor other than water.

The actual quantity of nitrogen required for maximum production of seed is a critical factor. When nitrogen is limiting seed production is severely restricted. On the other hand excess nitrogen produces excess vegetative growth, inducing early lodging in the crop and consequently restricting seed set and seed development (Griffiths *et al.*, 1967). In terms of optimum nitrogen requirements for seed production a compromise must be reached somewhere between these two extreme situations of nitrogen being either in seriously short supply or available in excess quantities.

In addition, other environmental and cultural factors have some influence on optimum rates of nitrogen for seed production. These include the species or cultivar grown, the age and density of the stand and the climatic conditions prevailing during seed crop development each year. The soil type and availability of soil nitrates or residual

nitrogen are also important factors. Soil moisture conditions and whether production is under irrigated or dryland conditions have a strong influence on optimum requirements. Utilisation of forage in the seed crop prior to reproductive growth may also affect total nitrogen requirements (this is discussed at length in Experiment 6). Of necessity therefore, recommendations for various species and cultivars must be highly arbitrary because of these important variables.

The influence of nitrogen on seed production in weeping lovegrass has been studied over a period of time in the seed-producing regions of the United States of America. Murphy, Staten and Elder (1947) reported responses that ranged from 0,4 to 2,2 kg seed for each kilogram of applied nitrogen when between 50 and 54 kg/ha of nitrogen was applied to weeping lovegrass. Denman, Elder and Holler (1953) increased seed yield of weeping lovegrass from 50 to 266 kg/ha by applying 100 kgN/ha in early spring. Dalrymple (1969) has recommended an application of between 55 and 110 kgN/ha in early spring for maximum seed production in weeping lovegrass. Nitrogen applied at a rate of 65 kg/ha was considered sufficient for good seed production in Morpa weeping lovegrass (Ahring et al., 1971).

Published reports of research on the influence of nitrogen fertilisation on seed production in weeping lovegrass grown in South Africa are totally lacking. However, Kerr (1961) has recommended that 100 kgN/ha be applied to weeping lovegrass seed crops in Rhodesia as a single dressing on heavy soils and as a split dressing on light free-draining soils.

Weeping lovegrass generally produces one good seed crop in the summer of each year. A second lighter crop is often produced in the autumn and this may be harvested if environmental conditions have been suitable for seed production (Ahring, 1970). A review of published data shows that other subtropical and tropical grasses, which produce more than one crop per year, respond to nitrogen in much the same way

as weeping lovegrass. Additions of between 45 and 90 kgN/ha appeared to be optimum for seed production in switchgrass (Panicum virgatum) (Harlan and Kneebone, 1953), side oats grama (Bouteloua curtipendula) (Smika and Newell, 1965), blue grama (B. gracilis) (Kneebone, 1953) and 'Plains' bluestem (Bothriochloa ischaemum) (Ahring, Taliaferro and Morrill, 1973). However the optimum level of nitrogen for seed production in many tropical species can be higher (Boonman, 1972a; 1972b; Cameron and Mullaly, 1969; Haggar, 1966; Stickland, 1971).

The effect of nitrogen fertilisation on seed production in temperate grasses has been reviewed by Garrison (1960), Anslow (1962) and Griffiths et al. (1967). Seed yields of these grasses are generally increased by annual applications of between 30 and 130 kgN/ha. Increasing rates of nitrogen generally show a diminishing response (Evans, 1953; Canode, 1965; Roberts, 1966) and excessive amounts may reduce yields (Lewis, 1969; Sharp, 1965).

The demands of the grass seed crop for nutrients are linked with the seasonal growth pattern of the crop and also with crop requirements during reproductive development. Therefore, while total nitrogen requirements are important the timing of the application and the availability of nitrogen at critical growth periods are equally important.

In weeping lovegrass Dalrymple (1969) and Ahring et al. (1971) have recommended that nitrogen fertiliser be applied as a single dressing in early spring for the main summer crop. Similar recommendations have been made for other warm-season grasses (Hacker and Jones, 1971; Boonman, 1972c; Ahring et al., 1973). However, Harlan and Kneebone (1953) obtained maximum seed yields of switchgrass when nitrogen was applied in early spring and again at the onset of reproductive growth in late spring.

Studies have shown that the best time to apply nitrogen for seed production in most temperate grasses is in early spring (Anslow, 1962;

Griffiths et al., 1967). The actual time of application depends on the time of flowering (Griffiths et al., 1967) and there are instances when the best results in early flowering species and cultivars are obtained by applying all the nitrogen not in the spring but in the previous autumn or at least by applying half in autumn and the remainder in early spring (Davies and Edwards, 1953; Evans, 1954; Rampton and Jackson, 1969; Garrison, 1960; Griffiths et al., 1967).

According to Griffiths et al. (1967) the effect of time of nitrogen application is related to the stage of physiological growth of the crop when the nitrogen is applied. The major purpose of nitrogen applied in autumn and in early spring, several weeks prior to inflorescence differentiation, is to stimulate tillering and so increase the number of fertile tillers produced in the seed crop (Evans, 1954; Stoddart, 1961; Lambert, 1963b; Lewis, 1968). Spring applications at the onset of reproductive growth also provide further nutrients for the continued development of each tiller so that a well developed inflorescence is ultimately produced (Griffiths et al., 1967). In temperate species spring-applied nitrogen increases the size of the seedhead by increasing the number of florets which develop (Lambert, 1967), increases the capacity of florets to set seed (Evans, 1954; Lambert, 1956b; Carlson, 1964) and also has a considerable effect on seed size (Lambert, 1956a; Evans, 1959; Anslow, 1962; Lewis, 1969; Rampton and Jackson, 1969).

Because of the absence of published research in South Africa, information available to the seed producer on the use of nitrogen to increase seed yields is lacking. The level of nitrogen applied and the time of application are generally based on the producer's own experience or on recommendations made for weeping lovegrass seed crops grown in the United States of America.

The most reliable guide from which to develop recommendations is obtained through experimentation over a number of years in different

(climatic) areas. The present study was undertaken as a preliminary investigation of the effect of nitrogen on the seed productivity of an established stand of weeping lovegrass growing in a high rainfall area of Natal. In South Africa, and particularly in Natal, few stands are established in wide rows for specialised seed production. Most seed is produced from denser, narrow-rowed multipurpose stands in which grazing or mowing is generally deferred until after the summer (December) crop has been harvested. The autumn (March/April) seed crop is normally too small to be economically harvested for seed, and is cut for hay. The primary aim of this present experiment therefore, was to study the influence of different levels of nitrogen applied at different times on the productivity of the first and main seed crop of the season.

2. EXPERIMENTAL METHODS

a) Experimental Site

The experiment was conducted on a farm in the Kamberg district. This district is in a region that has been agro-ecologically described as 'Highland Sourveld' (Pentz, 1945), but which has been designated 'Group 4' in a recent classification of bioclimatic areas in the Natal region (Phillips, 1969).

Bioclimatic Group 4 occupies 20,5 per cent of the region and is the most extensive group. Lying between an altitude of 1 400 m and 1 950 m, Group 4 enjoys a predominantly mild climate. The average mean temperature in January is about 18° C and in July is 7° C; mean annual temperatures are between 13° C and 15° C. In general, there are one or two warm summer months with occasional hot days (30° C) and two cool winter months with regular moderate to severe frosts (-7,2° C). Snow is often experienced locally. The annual rainfall is between 800 mm and 1 500 mm with an average of 920 mm. Nearly half of the normal precipitation falls in the three summer months (December to February)

and more than 80 per cent in the summer half-year. Hail storms may occur at irregular intervals during the summer months.

Unfortunately climatic data for the area surrounding the experimental site were not available. The nearest meterorological station was situated on the Tabamhlope Research Farm of the Department of Agricultural and Technical Services but daily recording only began there in 1974. However, daily rainfall figures were taken in close proximity to the experimental site (Table 56).

The experiment was carried out in a six-year-old weeping lovegrass stand established to 15 cm drill rows, sown at a rate of 6 kg/ha and managed almost exclusively for hay production. However, since 1971 the stand has been managed for seed production from early spring and yields of between 100 and 200 kg/ha recorded. In autumn 1972, the stand was in excellent condition, vigorous and weed free. However, during the winter dormant period, winter weeds, notably Helichrysum spp. and Bromus spp. were evident.

The soil at the experimental site was classified as a Farningham soil of the Hutton form and was typically acidic and free draining. Soil tests of the upper 15 cm showed that at the beginning of the experiment phosphorus and potassium were in low supply (Table 61).

TABLE 61 Summary of chemical analyses on ten soil samples taken from the upper 15 cm of soil at the experimental site in February 1972

KCl pH	Element (kg/ha)				
	P	K	Al	Ca	Mg
4,2	25	96	240	768	163

b) Treatments and Experimental Design

The trial was arranged in randomised blocks, replicated four times with 2 m wide pathways between each block. Each plot was 12 m long and 9 m wide.

Two rates of nitrogen, the higher rate twice the lower, were applied by hand as limestone ammonium nitrate (30% N) in single dressings in autumn, in early spring and in late spring and as split dressings in factorial combinations of these times of application. A control treatment was included in which no nitrogen was applied. There were therefore 15 treatments in the experiment; 2 rates of nitrogen, 7 times of application and 1 control, which are presented in Table 62.

TABLE 62 Nitrogen treatments: the rate of nitrogen applied (kg N/ha) at each time of application

Treatment Number	Time Nitrogen Application			Total Nitrogen Applied (kg/ha)
	Autumn	Early Spring	Late Spring	
1	120	0	0	120
2	0	120	0	120
3	0	0	120	120
4	60	60	0	120
5	60	0	60	120
6	0	60	60	120
7	40	40	40	120
8	240	0	0	240
9	0	240	0	240
10	0	0	240	240
11	120	120	0	240
12	120	0	120	240
13	0	120	120	240
14	80	80	80	240
15	0	0	0	Control

Autumn nitrogen was applied after the plots had been cut (for hay) in March. Early spring nitrogen was applied soon after the resumption of growth in spring and following the first reliable spring rains. Nitrogen was applied in late spring during stem elongation, otherwise known as the 'boot' stage. The developing inflorescence at this stage

was still basally located in the shoot but was above ground level.

c) Procedure

The experimental area was mown on 12 March 1972 and two days later autumn nitrogen was applied. On 22 March basal dressings of phosphorus and potassium were applied, each at the rate of 80 kg/ha. This rate was based on the soil tests and took into consideration the high rate of nitrogen applied.

The first good spring rain was recorded during the first week of October 1972 and on 7 October overwintered forage was removed by burning. Nitrogen was applied the following day.

Forage production was minimal during October and early November because of the ensuing dry spell. The late spring nitrogen was applied on 10 November after some rain had been recorded. The first heads were emerging at this time but the majority of reproductive tillers were still at the 'boot' stage.

Between 15 and 18 December 1972 five samples were cut with hand clippers to within 5-8 cm of the soil surface. Each sample removed all material (seedheads and forage) from an area 40 cm square from within the outer metre of each plot. In 1972 300 samples were thus removed for analysis.

After the samples had been collected, the outer metre of each plot was cut using an Allan motoscythe, leaving an area 7 m long and 1 m wide for seed harvest. The harvesting of seedheads began on 29 December 1972 and continued until 2 January 1973.

Two weeks after seed harvest the plots were cut to within about 8-10 cm off ground level with a tractor-mounted mower and the crop residue removed. At this time the second application of phosphorus and potassium was given. The same rates as in the previous year, viz. 80 kg/ha were again applied.

No further nitrogen was applied until 20 March 1973 after the experimental area had been cut for hay.

On 14 September 1973 the experimental area was burnt following good rains early in September. The early spring nitrogen was applied on the same day. Late spring nitrogen was applied on 25 October.

Sampling each plot was completed by 16 December and harvesting of seedheads began on 27 December 1973.

d) Observations and Recordings

i. Crop growth and development. Times of initial ear emergence and initial and peak anthesis were recorded. Any treatment differences in degree of ripeness of the crop were also noted. Ear emergence was defined as that time when the two most distal spikelets of the inflorescence had emerged from the flagleaf sheath in 10 per cent of fertile tillers sampled. Initial anthesis occurred when anthers had exerted from at least one spikelet in 10 per cent of seedheads studied. Peak anthesis was reached when anther exertion was evident in 40-50 per cent of spikelets in 50 per cent of sampled seedheads. At each time the sampling unit was 100 tillers.

ii. Seedhead sampling. Each year, the vegetative material in each of the 300 samples was separated from the reproductive tillers, dried in an oven at 90° C for 24 hours and weighed to determine the dry mass of forage produced up to the time of seed harvest. The culms comprising both stems and inflorescences were counted, air-dried and weighed to determine the size of individual culms.

In 1973 the size of the seedhead and hence its capacity to produce seed was determined for the control treatment and for those treatments supplied with 120 kg N/ha as a single dressing in autumn, early spring and late spring. In each of 10 seedheads randomly selected from each sample taken from those plots subjected to these treatments the number of primary branches and number of spikelets was recorded. A basal, an intermediate and an upper primary branch were then removed from the inflorescence ¼, ½ and ¾ along the central axis and on each the mean total and the number of fertile florets which

developed in each spikelet was determined.

iii. Seed yield. In each plot all seedheads were cut by hand from the 7 m x 1 m central strip and allowed to air-dry in the laboratory. After 10 weeks the seed was threshed from the heads and cleaned using a small laboratory thresher-cleaner. The threshed seed was weighed and yield determined. Three samples of 250 seeds were taken from the threshed seed and weighed to determine 1 000 seed mass at a constant moisture content. A further three samples of 100 seeds each were used to determine seed viability 15 weeks after seed harvest in 1973. The procedure adopted to test germination was the same as that described in Experiment 4 (Section 3, Chapter III).

Each year a record was made of the increase in seed yield in each treatment above that obtained in the control treatment in response to applied nitrogen. This is expressed as the 'production efficiency factor' which is therefore a measure of the quantity of seed produced in excess of the control yield for every kilogram of nitrogen applied.

iv. Response to residual nitrogen. In 1973 samples of forage were removed from each plot six weeks after seed harvest. The procedure adopted was the same as that used for pre-harvest sampling. Using hand clippers the forage was cut to within 5-8 cm of the soil surface from 5 sites per plot, each site measuring 40 cm square. The cut forage was oven-dried and weighed.

e) Statistical Analysis

In each analysis of variance the treatment sum of squares was subdivided to compare (a) the effect of rate of nitrogen application, (b) the effect of the timing of nitrogen application, and (c) the overall effect of applied versus no applied nitrogen (control). Standard errors (S.E.) were calculated (a) between treatment means, including control, (b) between rate of application means, and (c) between time of application means. Where F tests showed significance (Appendix B, Tables 1-7) least significant differences (L.S.D.) were

calculated at the 5 per cent and 1 per cent levels of probability.

3. RESULTS

a) Development of the Seed Crop

The application of nitrogen had no effect on either time of head emergence or anthesis. However the seed crop in the control plots matured earlier than in the remaining plots in both years. In 1973 seed from control plots at harvest contained an average 4-6 per cent less moisture than seed in the nitrogen supplied plots. There were no visible differences in the time of maturity of seedheads between plots supplied with nitrogen.

b) The Production of Seed

i. Yield of cleaned seed (Table 63). In both 1972 and 1973 the response to the high level of nitrogen was not significantly greater than the response to the low nitrogen level. However, there was a significant response to time of nitrogen application in both years.

In 1972 the optimum time of application appeared to be at ear formation in late spring. Applying all the nitrogen in late spring produced a mean seed yield that was higher than that produced when all nitrogen was applied at the resumption of growth in early spring and significantly higher than that produced when a single dressing was applied in autumn ($p = 0,01$). The marked response to late spring nitrogen was also obtained when applied as a split dressing.

In 1973, an analysis of time of application means showed that a single application of nitrogen at the resumption of growth in early spring was far superior to a single dressing in either autumn or late spring; these differences were highly significant ($p = 0,01$). Seed yields were maintained at a reasonable level when the annual nitrogen input was split into two equal dressings as long as one of the dressings was given in early spring. The split autumn and late spring mean was significantly lower than the early spring mean ($p = 0,01$).

TABLE 63 Effect of rate and time of nitrogen application on yield of cleaned seed (kg/ha) in weeping lovegrass (figures in brackets represent percentage increase in yield above control)

a) 1972

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	112 (3)	122 (12)	117
Early Spring	156 (43)	134 (23)	145
Late Spring	186 (71)	155 (42)	171
Autumn + Early Spring	129 (18)	130 (19)	130
Autumn + Late Spring	146 (34)	169 (55)	158
Early + Late Spring	169 (55)	155 (42)	162
Autumn + Early + Late Spring	136 (25)	163 (50)	150
Rate Mean	148	147	148
Control	109		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (inc.control)	± 2,01	40,6	54,4
Between rate application means	± 7,6		
Between time application means	±14,2	28,7	38,4

b) 1973

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	286 (21)	334 (41)	310
Early Spring	474 (100)	395 (67)	435
Late Spring	313 (32)	319 (33)	316
Autumn + Early Spring	384 (62)	446 (88)	415
Autumn + Late Spring	322 (36)	328 (38)	325
Early + Late Spring	423 (78)	348 (47)	386
Autumn + Early + Late Spring	316 (33)	367 (55)	342
Rate Mean	360	362	361
Control	237		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (including control)	± 48,1	97,2	130,1
Between rate of application means	± 18,2		
Between time of application means	± 34,0	68,7	91,9

The overall effect of applied nitrogen was to increase seed yield by an average 36 per cent in 1972 and 54 per cent in 1973 when compared with the no nitrogen treatment (control). The greatest response in 1972 was a 71 per cent increase when 120 kg N/ha was applied in late spring. A single application in late spring and split early spring and late spring dressings gave consistently high yields for both nitrogen rates and resulted in significant increases in yield when compared with the control mean to at least the 5 per cent level of probability.

In 1973, seed yield was doubled over the control yield when the lower nitrogen rate was applied in early spring. Both rates of nitrogen applied in early spring or split into autumn and early spring dressings were responsible for highly significant increases in yield ($p = 0,01$) compared with the control yield. Applying both rates as split early spring and late spring dressings also produced yields that were higher than when no nitrogen was applied. These differences were highly significant for the lower rate ($p = 0,01$) and significant for the higher rate ($p = 0,05$).

In both years autumn-applied nitrogen at either the high or low rate generally had little effect on seed yield. The application of 240 kg N/ha in autumn in 1973 did however increase yield by 41 per cent. This was almost a significant increase ($p = 0,05$). There was also little response to the application of 120 kg N/ha split into three equal dressings at each time of application in both years. However, the triple application of 80 kg N/ha significantly increased seed yield in 1972 and 1973 ($p = 0,01$).

ii. Production efficiency factor (Table 64). The production efficiency factor for the lower rate of nitrogen was double that of the higher rate in both years, the variation between the rate of application means being highly significant ($p = 0,01$). The high rate factor was consistently lower than that for the lower rate at each time of

TABLE 64 Effect of rate and time of nitrogen application on the 'production efficiency factor' (kg seed/kg N) in weeping lovegrass

a) 1972

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	0,02	0,05	0,04
Early Spring	0,39	0,10	0,25
Late Spring	0,64	0,19	0,41
Autumn + Early Spring	0,17	0,09	0,13
Autumn + Late Spring	0,31	0,25	0,28
Early + Late Spring	0,50	0,19	0,34
Autumn + Early + Late Spring	0,22	0,22	0,22
Rate Mean	0,32	0,16	0,24
Control	-		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (including control)	± 0,153	0,309	0,414
Between rate of application means	± 0,058	0,117	0,157
Between time of application means	± 0,108	0,218	0,292

b) 1973

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	0,40	0,40	0,40
Early Spring	1,98	0,66	1,32
Late Spring	0,63	0,34	0,49
Autumn + Early Spring	1,23	0,87	1,05
Autumn + Late Spring	0,71	0,38	0,54
Early + Late Spring	1,55	0,46	1,01
Autumn + Early + Late Spring	0,65	0,54	0,60
Rate Mean	1,02	0,52	0,77
Control	-		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (including control)	± 0,369	0,746	0,998
Between rate of application means	± 0,139	0,281	0,376
Between time of application means	± 0,261	0,527	0,706

application.

In 1972 the highest efficiency factor corresponded with the highest yield which was obtained when 120 kg N/ha was applied in late spring. Similarly, in 1973 the most efficient use of applied nitrogen for seed production was recorded when 120 kg N/ha was applied in early spring. There were few treatments in each year which did not differ significantly from the respective maximum recorded efficiency factors; the reduction in efficiencies was highly significant ($p = 0,01$) for all but one of the treatments supplying 240 kg N/ha in 1972 and again in 1973.

The average efficiency of applied nitrogen in 1973 was more than three times that in 1972. The variation between years can be attributed to the more suitable environmental conditions in 1973 compared with 1972.

c) Number of Seedheads Produced per m^2 (Table 65)

In 1972 the main effects of both rate and time of application of nitrogen were not significant. Also, the overall response to nitrogen was small and not significant.

In 1973, variation in mean seedhead numbers per m^2 due to the level of nitrogen was again small and not significant. However, there was a significant response to time of application.

Applying all the nitrogen in early spring in 1973 resulted in a significantly larger population mean than when all nitrogen was applied either in autumn or late in spring ($p = 0,05$). Applying nitrogen as a split dressing, particularly in autumn and late spring, produced smaller means than when all nitrogen was applied in early spring, but the differences were not significant. There was little response to the application of nitrogen as three equal dressings at each time of application. There can be little doubt that the optimum time of application for seedhead production in 1973 was in early spring.

TABLE 65 Effect of rate and time of nitrogen application on the number of seedheads produced per m^2 in weeping lovegrass

a) 1972

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	917	915	916
Early Spring	986	1085	1036
Late Spring	881	1055	968
Autumn + Early Spring	834	866	850
Autumn + Late Spring	856	983	920
Early + Late Spring	894	955	925
Autumn + Early + Late Spring	863	937	900
Rate Mean	890	971	931
Control	875		

	S.E.
Between treatment means (including control)	± 111,5
Between rate of application means	± 42,1
Between time of application means	± 78,8

b) 1973

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	829	982	906
Early Spring	1001	1108	1055
Late Spring	816	708	762
Autumn + Early Spring	1006	1063	1035
Autumn + Late Spring	1018	848	933
Early + Late Spring	1103	876	990
Autumn + Early + Late Spring	832	830	831
Rate Mean	944	916	930
Control	645		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (including control)	± 97,8	192,7	254,0
Between rate of application means	± 37,0		
Between time of application means	± 69,2	136,3	179,7

The analysis of variance showed that the overall effect of nitrogen in 1973 was to significantly increase head numbers ($p = 0,01$). All nitrogen treatments increased head numbers when compared with the control treatment. However, increases were not significant when the lower rate was applied in autumn or when both rates were applied either as single dressings in late spring or split into three equal dressings.

The mean number of seedheads per m^2 showed a highly significant positive correlation ($p = 0,01$) with yield of cleaned seed in 1972 (Figure 23) and 1973 (Figure 24). Seed yield is dependent to a large extent, therefore, on the size of the seedhead population. In both years about 50 per cent (r^2) of the variation in seed yield could be explained on the basis of the variation in number of heads produced.

d) Seed Quality

i. Mass of 1 000 seeds (Table 66). In 1972 the variation between the two rate means was not significant. However, in the following year there was a highly significant response to the higher rate ($p = 0,01$).

The mass of 1 000 seeds was markedly affected by time of fertilisation in 1972 and in 1973. Nitrogen applied as a single dressing in late spring in both years resulted in a heavier mean 1 000 seed mass than when all was applied in either early spring or autumn; differences were highly significant ($p = 0,01$).

In 1972 the influence of late spring-applied nitrogen on seed size can be seen also in the split application means. Split autumn and late spring applications resulted in seeds that were significantly heavier than when all the nitrogen was applied in autumn ($p = 0,01$). Similarly, split early spring and late spring applications were responsible for a heavier 1 000 seed mass mean than when a single application of nitrogen was applied in early spring. The difference between the two means was highly significant ($p = 0,01$). In 1973 no

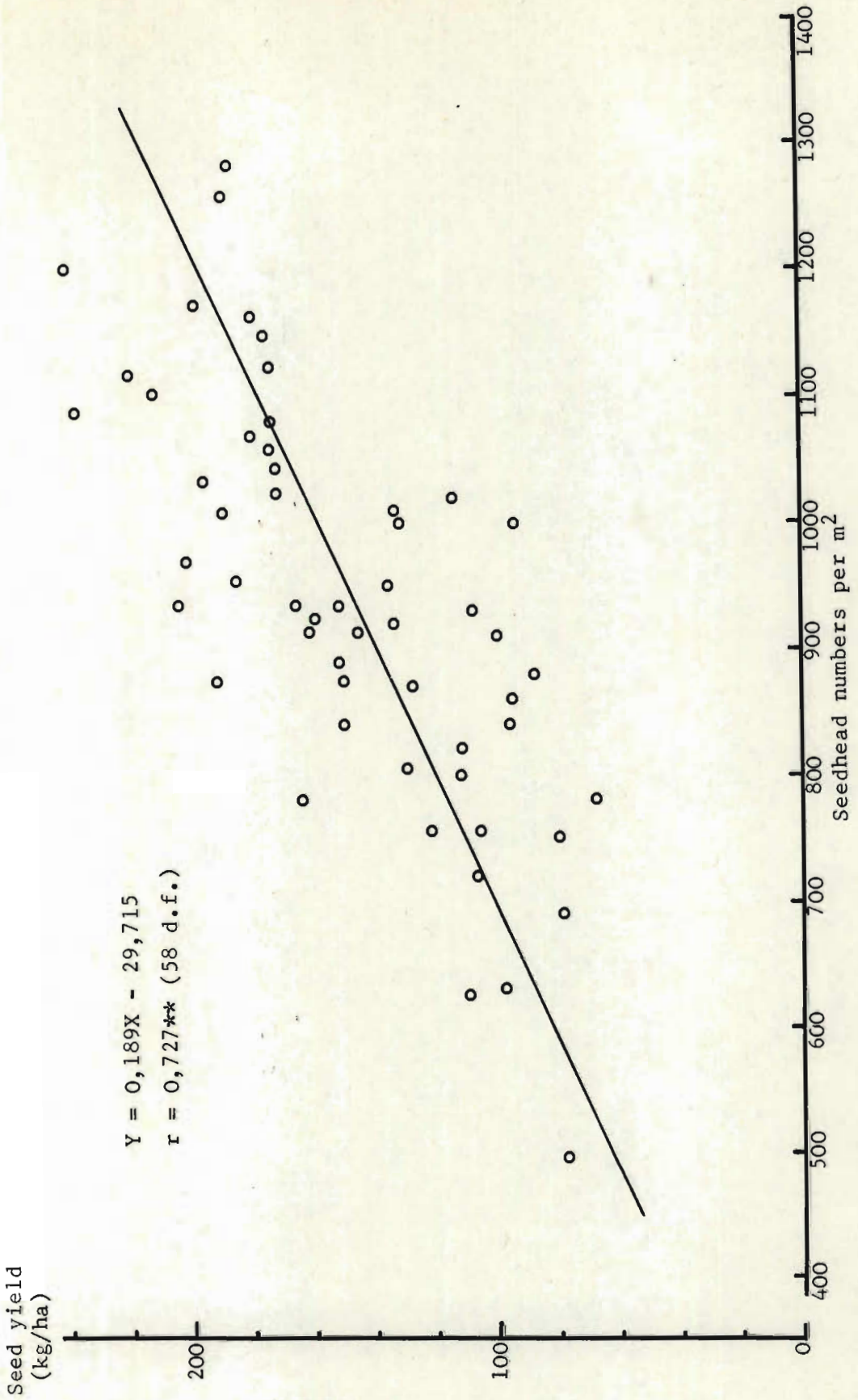

FIGURE 23 Relationship between yield of cleaned seed (kg/ha) and seedhead number per m^2 in weeping lovegrass in 1972

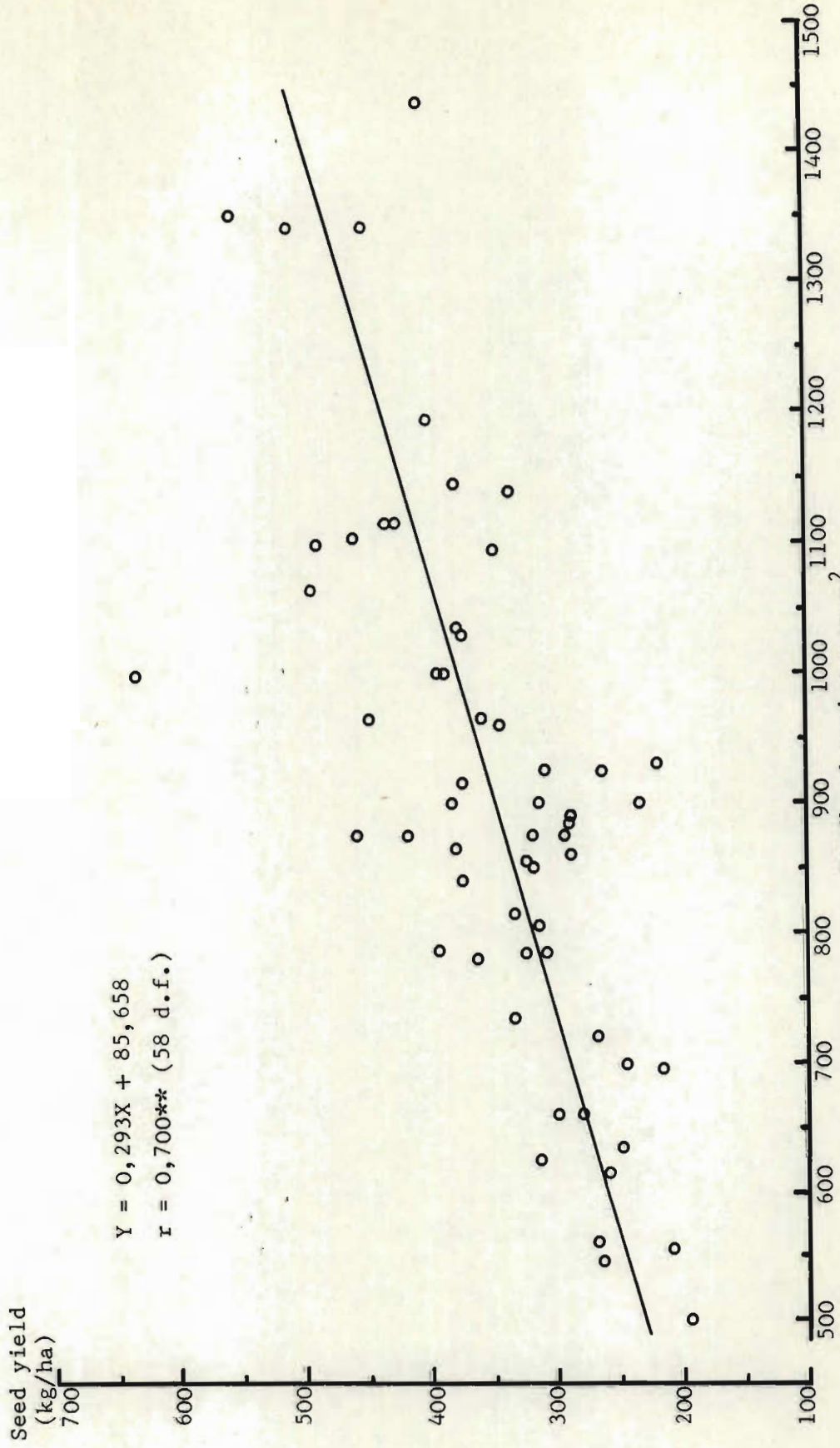

FIGURE 24 Relationship between yield of cleaned seed (kg/ha) and seedhead number per m^2 in weeping lovegrass in 1973

TABLE 66 Effect of rate and time of nitrogen application on the mass of 1 000 seeds (mg) in weeping lovegrass

a) 1972

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	242,5	250,8	246,7
Early Spring	256,3	250,1	253,2
Late Spring	274,8	262,6	268,5
Autumn + Early Spring	254,0	257,0	255,5
Autumn + Late Spring	260,3	260,7	260,5
Early + Late Spring	268,5	265,3	266,9
Autumn + Early + Late Spring	252,0	267,0	259,5
Rate Mean	258,3	259,0	258,7
Control	247,0		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (including control)	± 4,80	9,70	12,98
Between rate of application means	± 1,81		
Between time of application means	± 3,39	6,85	9,17

b) 1973

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	319,0	320,4	319,7
Early Spring	321,4	324,2	322,8
Late Spring	346,2	336,9	341,6
Autumn + Early Spring	319,1	308,4	313,8
Autumn + Late Spring	317,8	330,1	324,0
Early + Late Spring	321,8	323,3	322,6
Autumn + Early + Late Spring	306,5	335,0	320,8
Rate Mean	321,7	325,5	323,6
Control	299,8		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (including control)	± 3,73	7,35	9,69
Between rate of application means	± 1,41	2,78	3,66
Between time of application means	± 2,64	5,20	6,86

similar response to split-applied nitrogen was obtained.

In each year there was a highly significant interaction ($p = 0,01$) between rate and time of application (Appendix B, Tables 1 and 4). The high rate produced significantly lighter seed ($p = 0,05$) than the lower rate when applied late in spring in 1972 and in 1973. Conversely, applying the high rate in three equal dressings at each time of application resulted in a highly significant increase in 1 000 seed mass when compared with the lower rate ($p = 0,01$).

In both years the overall response to nitrogen was highly significant ($p = 0,01$). The response was greater in 1973 than in the previous year. Differences in the mass of 1 000 seeds between control (no nitrogen) and all nitrogen treatments in 1973 were highly significant ($p = 0,01$). In the previous year approximately half the treatments had no significant effect on 1 000 seed mass when compared with the control mean.

ii. Germination. No record was made of possible treatment effects on germination capacity of seed in 1972. In 1973 germination ranged from 90 per cent to 96 per cent as recorded in Table 67 and although there was no overall response to applied nitrogen when compared with the control treatment, analyses of variance of germination capacity gave significant variations for rate ($p = 0,05$) and time of application ($p = 0,01$).

The mean viability of seed for early spring-applied nitrogen was significantly lower as compared with the autumn ($p = 0,01$) and late spring means ($p = 0,05$). However, the reduction in viability following the application of early spring nitrogen depended ultimately on the quantity of nitrogen applied. Differences in viability between early spring nitrogen and either autumn or late spring nitrogen were not significant for the lower rate but were highly significant for the higher rate ($p = 0,01$). Applying nitrogen as split applications also significantly reduced germination capacity compared with single appli-

cations in either autumn or late spring (p = 0,01).

There was a highly significant interaction (p = 0,01) between rate and time of application (Appendix B, Table 4). Applying 240 kg N/ha as split autumn and early spring dressings produced seed of lower viability than when 120 kg N/ha was applied in the same manner; the variation between both treatment means was highly significant (p = 0,01). However, the higher rate when applied as a split dressing in autumn and late spring resulted in a highly significant increase in germination capacity compared with the low rate (p = 0,01). The variation between both rates applied as three equal dressings was also highly significant (p = 0,01).

TABLE 67 Effect of rate and time of nitrogen application on the percentage germinating capacity of weeping lovegrass seed, 12 weeks after seed harvest in 1973.

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	95,7	96,1	95,9
Early Spring	94,6	93,3	94,0
Late Spring	94,6	96,5	95,5
Autumn + Early Spring	95,1	90,9	93,0
Autumn + Late Spring	89,9	93,7	91,8
Early + Late Spring	91,4	92,9	92,2
Autumn + Early + Late Spring	90,7	95,8	93,2
Rate Mean	93,1	94,2	93,6
Control	93,8		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (including control)	± 1,02	2,01	2,65
Between rate of application means	± 0,39	0,77	1,01
Between time of application means	± 0,72	1,42	1,87

e) Inflorescence Size (Table 68)

The results show that the capacity of heads to produce seed in 1973 was greatest when 120 kg N/ha was applied at the resumption of growth in early spring. In this treatment the average inflorescence was longer and had a greater number of primary branches than when

TABLE 68 Effect of 120 kg N/ha applied at three times and the effect of no nitrogen (control) on some seedhead characteristics in weeping lovegrass in 1973

Seedhead Characteristic	Control (no N)	Time Application 120 kg N/ha			S.E.	L.S.D. (5%)	L.S.D. (1%)
		Autumn	Early Spring	Late Spring			
Inflorescence length (cm)	18,7	20,4	21,1	17,9	± 0,37	1,04	1,39
Primary branches/inflorescence	22,6	23,5	24,0	22,1	± 0,25	0,72	0,95
Spikelets per inflorescence	150	173	185	143	± 3,8	10,8	14,4
Florets per spikelet	5,4	5,8	6,3	7,1	± 0,14	0,40	0,53
Florets per inflorescence	796	978	1146	990	±26,8	75,9	100,9
Floret fertility (%)	46,5	48,4	52,3	48,9	± 0,80	2,26	3,01

nitrogen was applied in either autumn or late spring or when no nitrogen was applied; these differences were highly significant ($p = 0,01$).

Inflorescences produced after the application of early spring nitrogen also contained the most spikelets, significantly more than either the late spring or control treatments ($p = 0,01$) and the autumn-applied nitrogen treatment ($p = 0,05$). Late spring nitrogen had no effect on spikelet production compared with the control treatment, but produced spikelets containing significantly more florets than any other treatment ($p = 0,01$). Spikelet size declined the earlier nitrogen was applied so that the mean number of florets developed per spikelet after nitrogen had been applied in early spring was significantly greater than when nitrogen was applied in the previous autumn ($p = 0,05$).

Applying 120 kg N/ha in early spring produced more florets per inflorescence than when it was applied in autumn or late in spring; differences were highly significant ($p = 0,01$). The difference in floret numbers between autumn and late spring nitrogen treatments was not significant. All three treatments produced significantly more florets per inflorescence than the control treatment ($p = 0,01$).

The highest fertility of florets was recorded after 120 kg N/ha had been applied in early spring. Differences in floret fertility between this treatment and the other three were highly significant ($p = 0,01$).

f) Correlation Coefficients between Certain Characters (Table 69)

The relationship of various components of yield with each other and with final seed yield were analysed from data collected in 1973 from the control and from those treatments in which 120 kg N/ha was applied in a single dressing.

The number of seedheads per m^2 showed a highly significant positive correlation with seed yield ($p = 0,01$) and significant correlations with both the number of florets developed per inflor-

TABLE 69 Correlation coefficients between eight characters with each other and with seed yield (kg/ha) in weeping lovegrass (analysis from data from four treatments: (1) No N (control); and 120 kg N/ha in (2) autumn, (3) early spring and (4) late spring)

	2	3	4	5	6	7	8	9
1. Seedheads per m^2	+0,490	+0,311	+0,364	+0,366	+0,598*	+0,551*	+0,195	+0,802**
2. Inflorescence length (cm)		+0,670**	+0,806**	-0,034	+0,610*	+0,583*	-0,229	+0,539*
3. Primary branches/inflor.			+0,931**	-0,323	+0,465	+0,352	-0,268	+0,289
4. Spikelets/inflorescence				-0,233	+0,595*	+0,388	-0,221	+0,413
5. Florets per spikelet					+0,639**	+0,188	+0,777**	+0,378
6. Florets per inflorescence						+0,484	+0,441	+0,657**
7. Floret fertility (%)							+0,137	+0,668**
8. 1 000 seed mass (mg)								+0,166
9. Seed yield (kg/ha)								-

* Significant at 5% level

** Significant at 1% level

Multiple correlation coefficient

r = 0,897** (14 d.f.)

escence and the capacity of florets to set seed ($p = 0,05$). The two latter components were also significantly correlated with seed yield ($p = 0,01$).

Inflorescence length showed highly significant positive correlations with the number of primary branches and spikelets per inflorescence ($p = 0,01$) and significant correlations with floret number per inflorescence and floret fertility ($p = 0,05$). These latter relationships appeared to contribute to the high correlation between inflorescence length and seed yield ($p = 0,05$).

The number of florets per inflorescence showed a stronger relationship with floret number per spikelet ($p = 0,01$) than with the number of spikelets per inflorescence ($p = 0,05$). Consequently the variation in spikelet size was more important than the variation in spikelet number in the treatments analysed.

g) Reproductive and Vegetative Growth

i. Mass of 100 culms at seed harvest (Table 70). In 1972 the variation between the two rate means was negligible and not significant, but analysis of the main effects of time of application showed that significantly lighter culms were produced when nitrogen was applied as split autumn and either early spring or late spring dressings when compared with single applications of nitrogen in autumn ($p = 0,01$), early spring ($p = 0,01$) or late spring ($p = 0,05$). The only nitrogen treatments to produce significantly heavier culms than the control treatment were those in which 120 kg N/ha was applied in autumn ($p = 0,01$) or in early spring ($p = 0,05$).

In 1973, the difference between the two rate means was significant ($p = 0,05$). However, the only significant reduction ($p = 0,05$) in the mass of 100 culms following the application of the higher rate of nitrogen was recorded when all the nitrogen was applied in autumn.

The heaviest culms were produced when 120 kg N/ha was applied in autumn. Significantly lighter culms were produced when the same rate

TABLE 70 Effect of rate and time of nitrogen application on the mass of 100 culms (g) in weeping lovegrass

a) 1972

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	52,2	48,6	50,4
Early Spring	51,1	48,8	50,0
Late Spring	47,6	49,7	48,7
Autumn + Early Spring	43,0	46,6	44,8
Autumn + Late Spring	45,6	45,1	45,4
Early + Late Spring	46,9	48,2	47,6
Autumn + Early + Late Spring	48,5	45,5	47,0
Rate Mean	47,8	47,5	47,7
Control	46,5		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (including control)	± 2,19	4,31	5,69
Between rate of application means	± 0,83		
Between time of application means	± 1,53	3,05	4,03

b) 1973

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	54,9	49,9	52,4
Early Spring	51,8	49,3	50,5
Late Spring	50,3	49,5	49,9
Autumn + Early Spring	50,5	45,9	48,2
Autumn + Late Spring	52,4	50,7	51,5
Early + Late Spring	47,4	47,0	47,2
Autumn + Early + Late Spring	49,7	51,4	50,5
Rate Mean	51,0	49,1	50,0
Control	46,1		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (including control)	± 2,41	4,75	6,26
Between rate of application means	± 0,98	1,90	2,53
Between time of application means	± 1,70	3,35	4,41

of nitrogen was applied as split early spring and late spring dressings ($p = 0,01$) or as three equal dressings at each time of application ($p = 0,05$). Applications of 240 kg N/ha as split dressings in autumn and late spring or as three equal dressings in autumn, early and late spring were the only treatments supplying the higher nitrogen rate which did not produce significantly lighter culms than when 120 kg N/ha was applied in autumn.

ii. Forage yield at seed harvest (Table 71). In 1972 the higher rate of nitrogen generally increased the quantity of dry matter (DM) removed at seed harvest when compared with the lower rate, irrespective of time of application. However, the overall effect of the higher rate was not significant.

Variations between time of application means in 1972 were highly significant ($p = 0,01$). Applying all the nitrogen in early spring produced a mean DM yield that was significantly higher than when all the nitrogen was applied in autumn or in late spring ($p = 0,01$). Splitting the nitrogen application generally resulted in increased forage production when compared with the single application. There were significant differences between the autumn-applied nitrogen mean and either the split autumn and early spring mean ($p = 0,01$) or the split autumn and late spring mean ($p = 0,05$). Similarly, the difference between the late spring-applied nitrogen mean and the split early and late spring mean was highly significant ($p = 0,01$).

The overall effect of nitrogen was to significantly increase DM yields at seed harvest in 1972. Variation between the control treatment mean and all nitrogen treatment means was highly significant ($p = 0,01$) except when 120 kg N/ha was applied in autumn ($p = 0,05$).

In 1973 the difference between the two rate means was highly significant ($p = 0,01$) and the analysis of variance of DM yields at seed harvest gave a highly significant variation ($p = 0,01$) for time of application.

TABLE 71 Effect of rate and time of nitrogen application on the yield of forage (kg DM/ha) removed at seed harvest in weeping lovegrass

a) 1972

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	5684	6248	5966
Early Spring	7321	7308	7315
Late Spring	6256	6440	6348
Autumn + Early Spring	6844	7578	7211
Autumn + Late Spring	6845	7023	6934
Early + Late Spring	7162	7589	7376
Autumn + Early + Late Spring	6740	7117	6929
Rate Mean	6693	7043	6868
Control	4828		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (including control)	± 541,5	1066,8	1406,3
Between rate of application means	± 204,7		
Between time of application means	± 382,9	754,3	994,4

b) 1973

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	2334	2471	2402
Early Spring	2478	2861	2670
Late Spring	3373	3583	3478
Autumn + Early Spring	2282	2775	3089
Autumn + Late Spring	2772	3405	2983
Early + Late Spring	2860	3107	2564
Autumn + Early + Late Spring	2384	2744	2816
Rate Mean	2640	2992	2816
Control	1991		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (including control)	± 246,3	485,2	639,6
Between rate of application means	± 93,1	183,4	241,8
Between time of application means	± 174,1	343,0	452,1

Applying all the nitrogen in late spring produced DM yields significantly higher than when all nitrogen was applied in either autumn or early spring ($p = 0,01$). As in the previous year, applying nitrogen as split autumn and either an early spring or late spring application resulted in a highly significant increase in DM yield ($p = 0,01$) when compared with the effect of a single application in autumn.

Both nitrogen rates applied in autumn increased DM yields when compared with the control treatment but the effect was not significant. Other treatments which had no significant effect on forage production included the low rate either split into autumn and early spring dressings or applied as three equal dressings at each time of application.

iii. Ratio of reproductive to vegetative growth at seed harvest (Table 72). In 1972, the data show no significant response to either the level of nitrogen or time of application. However the analysis of variance shows that the overall effect of nitrogen was to significantly reduce the ratio as compared with the control treatment mean ($p = 0,01$).

In 1973 the average ratio was almost three times the size of the 1972 ratio and variations between rate and time of application means were highly significant ($p = 0,01$). However, the overall response to applied nitrogen was not significant when compared with the control treatment mean. This was due largely to a considerable reduction in the ratio when the higher rate of nitrogen was applied as compared with the lower rate.

Analysis of time of application means shows that the ratio declined as nitrogen was applied later. The late spring-applied nitrogen mean was significantly smaller than the autumn and early spring means ($p = 0,01$). In addition, the quantity of reproductive growth relative to vegetative growth was significantly reduced if the autumn application was split into autumn and late spring applications

TABLE 72 Effect of rate and time of nitrogen application on the ratio of reproductive to vegetative growth at seed harvest in weeping lovegrass

a) 1972

Time of N Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	0,88	0,61	0,75
Early Spring	0,70	0,70	0,70
Late Spring	0,68	0,82	0,75
Autumn + Early Spring	0,52	0,55	0,54
Autumn + Late Spring	0,55	0,63	0,59
Early + Late Spring	0,58	0,61	0,60
Autumn + Early + Late Spring	0,54	0,61	0,58
Rate Mean	0,64	0,65	0,65
Control	0,96		

	S.E.
Between treatment means (including control)	± 0,14
Between rate of application means	± 0,05
Between time of application means	± 0,10

b) 1973

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	1,99	2,03	2,01
Early Spring	2,08	1,90	1,99
Late Spring	1,24	1,05	1,15
Autumn + Early Spring	2,19	1,77	1,98
Autumn + Late Spring	1,93	1,31	1,62
Early + Late Spring	1,84	1,31	1,58
Autumn + Early + Late Spring	1,73	1,60	1,67
Rate Mean	1,86	1,57	1,71
Control	1,57		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (including control)	± 0,24	0,49	0,65
Between rate of application means	± 0,09	0,18	0,24
Between time of application means	± 0,17	0,34	0,46

(p = 0,05). Conversely the ratio was significantly increased when a late spring dressing of nitrogen was combined with either an autumn (p = 0,01) or early spring (p = 0,05) application.

The highest ratio recorded in 1973 was obtained when 120 kg N/ha was applied as split autumn and early spring dressings. This ratio, and also that recorded when 120 kg N/ha was applied as a single dressing in early spring, was significantly higher than the control treatment mean (p = 0,05). The higher rate of nitrogen had little effect on the size of the ratio when compared with the control treatment although an application of 240 kg N/ha in late spring resulted in a significant reduction in the ratio (p = 0,05).

iv. Forage yield 8 weeks after seed harvest (Table 73). In 1973, the residual effects of nitrogen on forage production were recorded. Variation between time of application means was not significant, but analysis of variance gave significant variations for nitrogen level (p = 0,05).

TABLE 73 Effect of rate and time of nitrogen application on the yield of forage (kg DM/ha) recorded 8 weeks after seed harvest in weeping lovegrass in 1973

Time of Nitrogen Application	Rate of N Application (kg/ha)		Time Mean
	120	240	
Autumn	1382	1668	1525
Early Spring	1665	1828	1747
Late Spring	1738	1893	1816
Autumn + Early Spring	1525	1687	1606
Autumn + Late Spring	1583	1720	1652
Early + Late Spring	1637	1813	1725
Autumn + Early + Late Spring	1458	1665	1562
Rate Mean	1570	1753	1662
Control	1207		

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatment means (including control)	± 209,8	424,0	567,3
Between rate of application means	± 79,3	160,3	214,4
Between time of application means	± 148,3		

The overall effect of nitrogen was to significantly increase the amount of post-harvest residue when compared with the control treatment ($p = 0,01$). All treatments supplying 240 kg N/ha produced DM yields that were significantly higher than the control mean yield, to at least the 5 per cent level of probability. The lower rate applied as single or split dressings in early or late spring produced significantly higher DM yields after seed harvest ($p = 0,05$) but when applied in autumn had no significant residual effect on DM production.

4. DISCUSSION

a) Overall Effects of Nitrogen

The most striking feature of this present experiment was the wide variation in productivity of the weeping lovegrass seed crop between the two years of study. This variability can be attributed to the seasonal variation in rainfall as recorded in Table 56. The dry conditions which prevailed during the spring in 1972 not only reduced seed production but also modified the effect of nitrogen on seed production in that year. The average seed yield in 1973 was approximately 2,5 times larger than that in 1972 and the overall effect of nitrogen in 1973 was to increase yields by about 54 per cent compared with the 36 per cent increase in the previous year (Table 63). Similar responses have been recorded for components of yield measured, notably for seedhead production.

The average size of the seedhead population in plots supplied with nitrogen was virtually identical in both years (Table 65). However, the overall effect of nitrogen on seedhead production in 1973 resulted in a 44 per cent increase in head numbers compared with a 6 per cent increase recorded in 1972. Although not as marked, the variation in the overall response of seed size to nitrogen between the two years showed the same trend (Table 66).

It would appear that the reduced response to nitrogen in 1972 was

due to the reduced ability of the weeping lovegrass plant to take up nutrients. The smaller seed size may have been caused by a restriction of the movement of nutrients to the seedhead brought about by lack of moisture. Evans (1953) suggested that dry weather at ear emergence reduced yield by limiting the transfer of nutrients to the seedhead. The dry period in 1972 was particularly acute in early November, immediately prior to emergence of the first heads.

The relatively low seed yield in 1972 gives some indication of the direct effect of moisture stress in the seed crop. Seedhead numbers were, on average, similar in both years when nitrogen was applied but yields were much higher in 1973. In addition, it is noted that the control treatment in 1973 contained fewer heads per m^2 than in 1972 but produced a yield double that of 1972. The reduced yields in 1972 appear to be due therefore to the development of smaller seedheads producing fewer and lighter seeds. Although no record was made of inflorescence size in 1972 the data in Table 66 show that the mass of 1 000 seeds was greater by an overall 25 per cent in 1973 in nitrogen-supplied plots and by 22 per cent in control plots. The improved moisture status of the soil during the spring in 1973 resulted therefore in a considerable increase in the size of seed produced.

It is apparent therefore that seed production in weeping lovegrass is dependent to a large extent on the availability of water during seed crop development. Boonman (1972a) found that seed production in Setaria sphacelata was extremely sensitive to climatic variations especially during the early stages of seed crop development, at early heading. In temperate grasses moisture tension during inflorescence initiation and the subsequent development of heads has been found to be critical in pot experiments (Lambert, 1963b) and Smika and Newell (1965; 1966) reported that the most critical period for water utilisation for maximum production of seed by perennial grasses is during ear emergence.

The ratio of reproductive to vegetative growth as an average for the 1973 seed crop was almost three times the size of the ratio for the 1972 crop (Table 72). From data presented in Tables 70 and 71 it would appear that the variation in the quantity of vegetative growth present in the stand at seed harvest between the two years was the greatest factor influencing the size of the ratio.

The number of culms per m^2 and the size of each culm varied little between the two years. As a consequence variation in the mass of culms per unit area was small. While this may have had a slight positive effect on the 1973 ratio its effect would appear to be negligible compared with the effect brought about by the variation in forage production.

The overall effect of nitrogen in 1972 was to produce approximately 4 000 kg DM/ha above that recorded at seed harvest in 1973. There can be little doubt that the quantity of forage present in the crop at seed harvest in 1972 was excessive. The seed crop was unable to utilise most of the nitrogen applied in 1972 because of the moisture stress which existed during spring. With good rains in early summer, soil and residual nitrogen became increasingly available to the plant and was utilised for forage production as the seed crop matured.

The severe lodging in the seed crop in 1972 can be directly attributed to the quantity of forage present and also to the high rainfall conditions in December. Under field conditions lodging in the seed crop increases harvesting difficulties and lowers yields (Lewis, 1959; Garrison, 1960; Griffiths et al., 1966). Seed losses were accentuated in 1972 by wet conditions which existed immediately prior to seed harvest. The damp, humid atmosphere in the already lodged crop caused premature germination of seed in the seedheads. Despite the damper conditions prevailing in December in 1973, the lodging that occurred was not as severe because of reduced quantities of forage produced in the seed crop.

In this present experiment, the vulnerability of seed production in weeping lovegrass to unpredictable climatic conditions was exposed. The dry conditions in early spring in 1972 reduced the productivity of the seed crop through the direct influence of moisture stress and also indirectly by reducing the plant's ability to utilise available nitrogen.

b) Effects of Rate of Nitrogen

The use of nitrogen fertiliser, providing other nutrients are not limiting, is the most direct method available for increasing seed production in grasses. In most grass seed crops it appears that above a certain optimum the grass is unable to utilise nitrogen for seed production and excessive vegetative growth results. This optimum will vary according to the species or cultivar, climate, management practices and inherent fertility of the soil. Results obtained in the present experiment indicate clearly that the optimum level of nitrogen for seed production in weeping lovegrass in the high rainfall regions of Natal is closer to the lower level of 120 kg N/ha than to the higher, double rate. There was certainly no evidence that the double rate led to increased seed yields compared with the lower rate (Table 63). In fact the only yield component measured which was significantly increased by the application of 240 kg N/ha was seed size (Table 66). This effect was however only recorded in 1973 when moisture was not limiting during development of the seed crop.

The optimum rate does however appear to be higher than that generally recommended in the seed producing areas of the United States (Ahring, 1970; Ahring et al., 1971) although Dalrymple (1969) recommended levels of nitrogen for maximum seed production in the range 55 to 110 kg N/ha. The lower rates are recommended for crops grown under dryland conditions or in areas of low rainfall, while the higher rates are necessary if the crop is irrigated or grown in higher rainfall conditions.

The present experiment was conducted in an area characterised by high rainfall and therefore an optimum rate approximating to 120 kg N/ha is not unrealistic.

At no time during crop development did the higher rate appear to be detrimental for seed production. Even in 1972 when dry conditions predominated in spring, the application of 240 kg N/ha did not noticeably affect the stand. However, the higher rate was responsible for the production of large quantities of forage. In practice this may reduce seed yield because of an increased risk of lodging resulting in harvesting difficulties and seed losses due to shedding. Plots in the present trial were harvested by hand so that most lodged heads were harvested with a minimum of disturbance.

In 1972 DM yields were decidedly excessive for seed production. The large quantity of forage cut at seed harvest in 1972 seems to indicate that even the lower nitrogen rate was too high for seed production in that dry year. Most of the nitrogen applied appeared to be eventually utilised by the plant to produce forage as the seed crop matured. The effect of excessive amounts of forage in the crop at seed harvest has been discussed when the overall effects of nitrogen on seed production were considered. In the more normal growing conditions in 1973 the higher rate resulted in a significant ($p = 0,01$) increase in forage production during seed crop development (Table 71). As a result, therefore, there was a significant reduction in the amount of reproductive growth relative to vegetative growth at seed harvest (Table 72).

While this present experiment provides a good indication of the optimum level of nitrogen required for seed production in weeping lovegrass in the Natal Region, the actual amount in a particular circumstance will depend ultimately on climatic conditions, as there is little doubt that even the lower rate of nitrogen was excessive in 1972. This tendency for the optimum level of nitrogen to vary with the

climate needs to be confirmed over a much longer period.

c) Effects of Time of Nitrogen Application

The data in Table 63 indicate that the optimum time of application of nitrogen for maximum seed production varied from late spring in 1972 to early spring in 1973. Autumn-applied nitrogen had little effect on seed production, except when given in excessive amounts, and there was no benefit by splitting the annual nitrogen dressing.

The reversal in yield response to early versus late spring nitrogen between the two years is apparently the result of the variation in growing conditions. Because of the dry conditions in 1972 there was little effect of time of application on the size of the seed-head population. However, early spring-applied nitrogen had a slightly greater effect on head numbers than nitrogen applied in late spring (Table 65). The increased yield following the late spring application was due therefore to either an increase in seed production from larger seedheads or to the production of larger, heavier seeds. No record was made of inflorescence size in 1972 but the mass of 1 000 seeds was significantly increased ($p = 0,01$) when 120 kg N/ha was applied in late spring compared with applications in either autumn or early spring (Table 66).

In 1973 seed yield was increased following the application of nitrogen in early spring largely through a considerable increase in head numbers (Table 63) and size of seedheads (Table 68). It is clear that an early application of nitrogen in spring is essential for maximum seed production in weeping lovegrass when soil moisture status is high. Nitrogen applied in early spring is considered best for maximum seed yield in weeping lovegrass in the United States (Dalrymple, 1969; Ahring, 1970), for other warm season grasses (Harlan and Kneebone, 1953; Ahring et al., 1973) and also for many temperate grasses (Anslow, 1962; Griffiths et al., 1967).

According to the results of Experiments 1 and 4 (Chapter III) it

appears necessary to produce as great a percentage of early heads as possible to maximise the productivity of the weeping lovegrass seed crop. Early heads have the greatest capacity to produce seed. There is however little information on the optimum times to apply nitrogen for maximum tiller production by perennial grasses in South African environments. Autumn-applied nitrogen could be expected to stimulate tillering at this time, thus increasing the proportion of early-formed tillers in the stand. In this present experiment autumn nitrogen appeared to have been applied too late in the season to increase tillering and so benefit the seed crop through an increased number of larger inflorescences. It is suggested that nitrogen should be applied earlier than in the present experiment, perhaps as soon after the previous seed harvest as possible. While early spring is suggested as the optimum time of application, further research in the post harvest period is necessary to determine the best time nitrogen should be applied at this time.

Apart from producing heavier seed, late spring-applied nitrogen had little effect on other yield components measured. In Paspalum plicatulum Chadhokar and Humphreys (1970) observed that seed production was independent of nitrogen nutrition after head emergence. Boonman (1972c) also found no evidence that nitrogen applied one week after initial head emergence increased seed size in Setaria sphacelata. As Griffiths et al. (1967) advise for temperate grasses, spring nitrogen for seed production should be applied at an earlier date in relation to inflorescence development rather than at a later one.

That late spring nitrogen was not utilised entirely for seed production is evident in the data recorded in Table 71. Nitrogen, and particularly the lower rate, applied late in spring in 1973, produced as much as 900 kg DM/ha more than early spring-applied nitrogen during seed crop development. Applying nitrogen at this late stage was not only of little benefit to seed production in weeping lovegrass in this

year but also induced lodging because of an increase in forage production. Early spring nitrogen resulted in only a slight increase in forage production compared with nitrogen applied in autumn. Therefore nitrogen applied in early spring was optimum for seed production in the weeping lovegrass seed crop in 1973 and also produced an acceptable level of forage while the crop matured.

Splitting the annual nitrogen input into two equal dressings in this present experiment showed no increased response compared with single applications. In general, the use of small dressings of nitrogen at each split application of the lower level was inefficient. At the higher rate, each split application was as large as a single application of the lower rate and therefore generally sufficient to bring about a response, particularly when applied in late spring in 1972, or in early spring in 1973.

However, it is interesting to note that perhaps the most consistent treatment in both years was the application of nitrogen as split dressings in early spring and again in late spring. The highly variable and unpredictable seasonal weather conditions experienced in Natal may mean that the seed producer in Natal should apply nitrogen as split dressings in early and late spring to ensure a reasonable and consistent response each year. However, more data from several years research is required before any such recommendation can be made.

The seed producing capacity of inflorescences was considerably affected by time of application of nitrogen in 1973 (Table 68). Early spring-applied nitrogen had the greatest effect on inflorescence size due largely to a marked increase in spikelet numbers. Even the application of nitrogen in autumn and in late spring resulted in highly significant ($p = 0,01$) increases in floret numbers per inflorescence when compared with the size of inflorescence produced when no nitrogen was applied. Compensatory effects were evident when nitrogen applied in the vegetative stage in autumn increased spikelet numbers but

but resulted in a reduced number of florets per spikelet compared with the effect of late spring applied nitrogen.

The ability of florets to set seed was also influenced by time of application (Table 68). The highly significant correlation ($p = 0,01$) between this yield component and seed yield (Table 67) shows clearly the importance of seed set in determining the productivity of the crop. Again, seed set was significantly increased when nitrogen was applied in early spring. While it is suspected that the increased supply of nitrogen to the seedhead when nitrogen was applied at this time increased floret fertility by reducing the incidence of competition for assimilates, there is no conclusive evidence that this is the main explanation. Rawson and Evans (1970), working with wheat, have suggested that some interaction between florets, probably hormonal in nature, is involved.

EXPERIMENT 6 THE EFFECT OF CUTTING AND EARLY-SPRING CONTROLLED BURNING ON THE SEED-PRODUCING CAPACITY OF WEEPING LOVEGRASS

1. INTRODUCTION

While grass seed production can be introduced into most farming systems and seed can provide a valuable cash crop the over-riding consideration must be acceptance of the disciplines essential for the maintenance of genetic purity and the production of weed-free crops. Maximum yields of high quality seed are generally associated with grass crops established in widely spaced rows and managed exclusively for the production of seed. In weeping lovegrass wide row spacings of not less than 60 cm are recommended (Ahring et al., 1971) but most crops managed especially for seed production are grown in rows spaced about 90 cm apart. One management problem often associated with specialised seed production of any grass species is that of removing excess autumn and/or spring vegetative growth.

This problem can be readily solved when seed producing stands are grazed, thus providing at the same time valuable forage for grazing. Excess forage can also be cut for hay. There is little doubt that management for seed production and for forage utilisation can be successfully combined (Hayward, 1959; Garrison, 1960; Anslow, 1962; Griffiths et al., 1967). Experiments with the more important temperate perennial grasses (Green and Evans, 1957; Hayward, 1959; Roberts, 1965; 1966) have clearly shown that judicious autumn grazing can actually increase seed yields. Nevertheless, for consistently high yields it is essential that seed production must never be regarded or allowed to become a 'by-product' of any stock enterprise. The pastures should not be directly related to stock-feed requirements when, of necessity, injudicious grazings may be inevitable and may be detrimental to the seed crop.

In South Africa (Field-Dodgson, 1973) and the United States of

America (Ahring, 1970) few weeping lovegrass stands are established solely for seed production. Most are grown as a multipurpose crop for intensive forage utilisation by grazing or for hay production in combination with seed production. These stands are established at narrow row spacings which compromise between good forage production and good seed production.

The time of grazing or mowing in autumn depends mainly on the amount of growth present and the suitability of climatic conditions for defoliation. Generally, however, the timing of this autumn treatment is not critical. The most important aspect of forage removal is the actual time of defoliation in spring. Experiments with most of the important temperate grass species have been reviewed by Anslow (1962) and Griffiths et al. (1967) and have shown that defoliation after the critical period of ear formation in late spring is decidedly detrimental to seed production. In most crops spring defoliations tend to suppress seed yields unless the crop is supplied with adequate quantities of nitrogen fertiliser, although a defoliation at or immediately after ear formation may significantly reduce yields even in the presence of adequate nutrition (Griffiths et al., 1967). Results obtained by Roberts (1965) and by Lewis (1969) have confirmed that grazing late in spring reduces seedhead numbers in the crop and restricts head size. Cutting during stem elongation removes the early-formed ears which normally have the highest seed-producing potential (Langer, 1956; Lewis, 1963; Ryle, 1964) and although these are replaced by later-formed tillers, there is little compensation in terms of seed production because of the naturally lower fertility of these late-formed tillers and their reduced capacity for seed production (Wilson, 1959; Lewis, 1962; 1963; Ryle, 1964). With later defoliations the damage becomes increasingly severe as more tillers which become fertile and develop a seedhead are removed.

Few weeping lovegrass stands managed for seed in the United States

are defoliated once growth has commenced in early spring following the dormant winter period (Dalrymple, 1969). However, during late autumn and winter forage and litter accumulate which, if excessive, can inhibit vigorous growth in spring and subsequently depress seed yields. Overwintered aftermath must be removed in order to facilitate optimum seed producing conditions from early spring on, and therefore the stand must be defoliated at some stage prior to the onset of spring growth. From about mid-winter the frosted aftermath can be successfully grazed (Shoop and McIlvain, 1970b). Dalrymple (1969) has reported the grazing or mowing old residue prior to early spring can increase seed production by about 50 per cent.

Although seed crops are generally not cut until seed harvest, a few crops in the United States are grazed lightly during the first 20-30 days of spring growth; grazing is then deferred to allow for seedhead formation (Dalrymple, 1969). Random observations in Natal have indicated that forage production during the spring may be excessive and therefore detrimental to seed production (Field-Dodgson, 1973). The normally high rainfall experienced at this time was considered the main cause of prolific growth. It is possible that the removal of forage during the spring may be of benefit to seed production in Natal.

Early spring controlled burning, immediately following the first reliable spring rains, is a very effective method of removing old growth and has been responsible for considerable increases in seed production. Results obtained in Oklahoma, United States of America, have shown that burning can double seed yield as compared with mowing (Dalrymple, 1969). McIlvain and Shoop (1970a) have shown that yields can be increased by about 60 per cent when the crop is burnt in early spring as compared with a mowing treatment. Spring controlled burning of the weeping lovegrass sward also has many other beneficial effects (McIlvain and Shoop, 1970a) which include reducing excessive

accumulations of forage and litter, promoting early growth, controlling weeds and controlling the incidence of disease and pests (Ahring et al., 1971).

No published data on the effect of cutting and burning in spring on seed productivity in weeping lovegrass are available in South Africa. However, recent research has shown that removal of the previous season's growth by mowing or burning at the resumption of growth in spring stimulates seed production in another indigenous warm-season grass, Anthephora pubescens Nees (Nursey and Kruger, 1973).

In view of the widespread use of weeping lovegrass as a multi-purpose pasture in South Africa the influence of forage utilisation on seed production must be critically assessed and recommendations made available as soon as possible on the management of the stand for efficient integration of forage and seed production. Therefore, to determine the effect of spring defoliation on subsequent seed production an experiment, in which the treatments included mowing at different stages of growth in the spring, was conducted on a six-year old stand of weeping lovegrass. In addition methods of removing over-wintered material and their effects on seed production were also investigated.

2. EXPERIMENTAL METHODS

The experiment was laid out as a 4 x 4 Latin square with four randomised subplots in each main plot. Each subplot measured 9 m long and 3 m wide. Pathways, 2 m wide, separated each main plot.

a) Trial Site

The experiment was carried out in close proximity to the previous trial (Experiment 5) and in the same stand of weeping lovegrass. A description of the stand and the climatic conditions at the trial site therefore have been given in Experiment 5.

Soil samples were randomly collected from the trial site prior to

the imposition of any treatments and a summary of the chemical analysis is presented in Table 74. There was little difference between the analysis of this present experiment and the preceding one (Table 61).

TABLE 74 Summary of chemical analyses on ten soil samples taken from the upper 15 cm of soil at the experimental site in February 1972

KCl pH	Element (kg/ha)				
	P	K	Al	Ca	Mg
4,3	29	104	238	756	166

b) Treatments

The main plot and subplot treatments which were applied are presented in Table 75. The main plot treatments removed overwintered material which was produced in the previous autumn. The late autumn mowing did not directly remove overwintered forage but reduced the quantity of forage present in the plot at the resumption of growth in the spring.

The first spring cut subplot treatment was imposed at a time when sufficient growth was available for grazing. The second spring cut, when reproductive growth was observed in tillers for the first time, was equivalent to an early hay cut. In practice, the double cutting treatment (Subplot treatment 4) represents a double grazing of the plot.

TABLE 75 Main plot treatments and subplot treatments to show the influence of defoliation at various times on seed production in weeping lovegrass

Main Plot Treatments

A. No cut (Control)
B. Late autumn cut
C. Early spring cut, after the first reliable spring rain
D. Early spring burn, after the first reliable spring rain

Subplot Treatments

1. No cut (Control)
2. First spring cut, when about 20 cm growth present
3. Second spring cut, at inflorescence initiation
4. First spring cut and second spring cut

c) Procedure

The experiment was laid out on 20 March 1972 after the whole stand had been cut for hay for the second time in the late summer and autumn period. On 10 April 1972 the late autumn cut was imposed on the respective main plots. The plots were mown with an Allen motoscythe leaving a 5-10 cm stubble height. The cut forage was raked up by hand and removed. All subsequent mowings were carried out in the same manner.

The first rainfall was recorded during the first week of October (Table 56). On 7 October 1972 the early spring mowing and controlled burning treatments were imposed. Prior to burning, the 2 m wide pathways, surrounding each of the main plots which were to be burnt, were closely mown and the remaining stubble and soil surface liberally sprayed with water to prevent uncontrolled fires. The plots were burnt in mid-morning in warm, sunny and calm conditions which ensured a good, even and complete burn.

Despite the good rainfall in early October, the remainder of October was particularly dry and hot. Growth during this month was negligible and it was considered that there would be insufficient growth to support all three mowing treatments. Therefore subplot treatments 2 and 4 were withdrawn from the experiment for 1972. Subplot size was doubled as a consequence. So as to avoid confusion with the treatments imposed in 1973, the remaining subplot treatment will still be referred to as the 'second spring' cut even though it was the only one carried out in 1972. The subplots subjected to this defoliation were mown on 4 November 1972.

On 11 and 13 December 1972 all forage and reproductive culms within an area 40 cm square were cut with hand clippers and removed for sampling. Five sampling areas were randomly selected and harvested from within the outside (border) metre of each subplot. In 1972, 160 samples were thus cut and removed to the laboratory.

When all samples had been removed, the outer metre of each subplot was mown with the Allen motoscythe and the material removed, leaving an area 7 m long and 1 m wide in the centre of each subplot for seed harvest. The control subplots were eventually harvested on 23 December and the remainder on 27 and 28 December 1972.

After seed harvest the experimental area was cut with a tractor-mounted mower to an even stubble height of about 7-10 cm. On 19 February 1973 a hay crop was harvested. Treatments resumed on 22 March 1973 when the late autumn cut was applied.

Following good rains in early September, the remaining main plots, except for the control plots, were either mown or burnt on 13 and 14 September 1973. The first of the subplot treatments, the first spring cut, was carried out on 5 October and 18 days later, on 24 October, the second spring cut was given for subplot treatments 3 and 4.

The sampling of seedheads began on 16 December 1973 and continued for three days during which time 320 samples were removed. Seed harvest began on 30 December when the control subplots were harvested.

d) Fertiliser Applications

Each subplot was topdressed with a 0:1:1 (N:P:K) fertiliser supplying 80 kg/ha each of phosphorus and potassium on 22 March 1972 and again on 25 March 1973. The low values recorded in the soil analysis (Table 74) together with the high rate of nitrogen applied prompted the application of such high levels.

In 1972 each subplot received 180 kg/ha of nitrogen (N); 60 kg N/ha was applied in late autumn on 22 March and the remainder was split equally into two dressings applied on 7 October with the resumption of growth in spring and on 4 November 1972 after the only subplot cutting treatment had been applied.

In 1973 the same dressings at the same stages of growth were applied in late autumn on 25 March and in spring on 14 September and 24 October 1973. All subplots received an additional 60 kg N/ha on

6 October 1973 following the first spring cut. Therefore in the second year of the experiment all subplots were topdressed with 240 kg N/ha.

The additional nitrogen dressing applied in 1973 was withheld in 1972 because of the dry conditions and the withdrawal of two subplot treatments.

e) Observations and Recordings

i. Crop growth and development. Inflorescence initiation and thus the onset of reproductive growth in the first tillers was determined by the regular dissections of tillers to examine the condition of the apical meristem.

In 1972 ear emergence in those main plots subjected to an early spring controlled burn was first observed 2-3 days after initial ear emergence in the main plots cut in early spring. This was investigated further when, in 1973, emerged heads were counted every four days in the control subplots of two main plots burnt in early spring and two main plots mown in early spring. Counting began as soon as the first heads were observed. In each subplot heads were counted in five randomly chosen areas each 40 cm square. A seedhead was defined as having emerged when at least the upper third of the head was free of the flagleaf sheath.

Seedhead development was observed in subplots to gauge any possible treatment effects on seed crop development and maturity. The colour of the seedhead and of the seed and the consistency of the seed were used as measurements of maturity. Seed moisture content was determined immediately after harvesting.

ii. Forage production. The quantity of forage DM removed with each subplot or main plot mowing was determined when five cut samples were removed immediately prior to mowing. Each sample was cut with hand clippers from an area 40 cm square leaving a 5 cm long stubble. The samples were oven-dried at 90^{o} C for 24 hours and weighed.

iii. Pre-harvest sampling. From each sample collected before seed harvest the vegetative material was separated from the reproductive culms, oven-dried and weighed to determine dry matter yield at seed harvest. The culms were then counted and air-dried in the laboratory before being weighed.

In 1973 the influence of main plot treatments on inflorescence size was investigated. From each sample removed from the control subplots of each main plot ten culms were selected at random and stem and inflorescence lengths measured. In each inflorescence the number of primary branches and number of spikelets per inflorescence were recorded. The number of florets and the number of these which were fertile were recorded in spikelets on the basal, an intermediate and the penultimate primary branches of each seedhead. In each subplot 50 seedheads were thus analysed in this manner.

iv. Seed yield. All seedheads in the central strip of each subplot were harvested by hand, bulked and tied in bundles, and hung in the laboratory to dry prior to threshing.

The heads were threshed and the seed cleaned in a small laboratory thresher-cleaner. The cleaned seed was weighed and seed yield per hectare determined.

Small samples of cleaned seed were used to determine 1 000 seed mass and seed viability, ten weeks after seed harvest. The mass of 1 000 seeds was determined when five samples of 250 seeds each were weighed from each subplot. The germination procedure was the same as that used in Experiment 4 (Chapter III, Section 3).

f) Statistical Analysis

Standard errors (S.E.) were calculated (a) between main plot and (b) subplot treatment means, (c) between subplot treatments in the same main plot and (d) between the same subplot treatment in different main plots.

Analyses of variance were carried out on the data. Where F tests

showed significance (Appendix C, Tables 1-9) least significant differences (L.S.D.) were calculated to the 5 per cent and 1 per cent levels of probability.

3. RESULTS

a) Forage Production

i. DM yield from main plot cutting treatments (Table 76). The variation in forage DM yields between both years can be attributed to varying climatic conditions and the time of mowing in the autumn. Yields were greater in 1973 than in 1972 because the period of active growth following the late autumn cut was longer in that year than in 1972. In 1973 the plots were cut about 20 days earlier than in the previous year and active growth had generally ceased at about the same time in both years, viz. during the first week of May when the first frosts were recorded.

Although some growth may have occurred prior to mowing in early spring, the quantity of material harvested at this time in 1973 suggests that a second hay crop could have been harvested in late autumn and still allowed for adequate regrowth before the first frosts.

TABLE 76 The quantity of forage (kg DM/ha) removed in late autumn and early spring in 1972 and 1973

	Time of Cut	
	Late Autumn	Early Spring
1972	1060 ± 147,1	1398 ± 179,2
1973	2346 ± 460,7	4773 ± 720,3

ii. DM yield from subplot treatments (Table 77). In both years the greatest quantity of forage was removed from control main plots because of the retention of overwintered material. A comparison of forage yields obtained from the first and second spring cuts in 1973 in control main plots shows that overwintered forage inhibited spring

TABLE 77 Forage yield (kg DM/ha) at each time of cutting in spring, prior to the onset of reproductive growth in weeping lovegrass (subplot treatments)

a) 1972

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	-	-	-	-	-
Second Spring Cut	3111	2244	1793	1888	2259
Main Plot Treatment Mean	-	-	-	-	-

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between treatments	± 38,0	76,0	101,1

b) 1973

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	-	-	-	-	-
First Spring Cut	5812	3360	1249	1402	2956
Second Spring Cut	5640	3517	2220	2572	3487
Both Spring Cuts	7851	5282	3084	3268	4871
Main Plot Treatment Mean	6434	4053	2185	2414	3771

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between main plot treatment means	± 203,0	496,8	752,7
Between subplot treatment means	± 96,8	190,7	251,3
Between subplots in same main plot	± 193,6	381,3	502,7
Between subplots in different main plots	± 280,5	622,7	891,6

growth; the first (early spring) cut in fact producing a higher yield (5612 kg DM/ha) than the second (late spring) cut (5640 kg DM/ha). Spring growth was also low in those subplots cut in late autumn in 1973 and cut again in late spring at inflorescence initiation. They also carried overwintered material into the spring growing period. Plots burnt in early spring produced consistently more forage in each subplot cutting treatment than those plots cut in early spring. However, the variation at each mowing was not significant.

Subplots cut twice during spring in 1973 produced the highest DM yields, significantly higher than either the first cut or second cut yields ($p = 0,01$) in all main plots.

A comparison of DM yields obtained in each main plot following the second spring cut in 1972 and 1973 shows evidence of the detrimental effect of the dry period in early spring in 1972 on forage production. In fact, the quantity of forage DM removed with this defoliation in 1972 was not much greater than the DM yield obtained when plots were subjected to the first spring cut the following year.

iii. DM yield at seed harvest (Table 78). Despite the dry early spring in 1972 the average quantity of forage DM removed at seed harvest was 5 700 kg/ha. This was almost 1 000 kg DM/ha more than the crop average in 1973.

In both years over 7 000 kg DM/ha was removed at seed harvest from the uncut (control) subplots in the control main plots. In 1973 this was more than double the DM yield of the subplot burnt in early spring and then cut twice prior to inflorescence differentiation. Defoliation in spring generally reduced the quantity of forage present at seed harvest and the effect became greater the later the defoliation. In all main plots, the subplots cut twice in spring produced the least amount of forage at seed harvest.

Forage production during seed crop development was greater in those plots mown in early spring than in those burnt at the same time.

TABLE 78 Effect of defoliation at different times on the quantity of forage (kg DM/ha) removed from a weeping lovegrass stand at seed harvest

a) 1972

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	7089	7139	6311	6150	6672
Second Spring Cut	4415	4729	5390	4624	4790
Main Plot Treatment Mean	5752	5934	5852	5387	5731

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between main plot treatment means	± 315,4		
Between subplot treatment means	± 220,5	436,6	577,0
Between subplots in same main plot	± 441,0	868,7	1145,2
Between subplots in different main plots	± 625,4		

b) 1973

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	7233	6856	4827	4378	5823
First Spring Cut	5501	5284	4772	3795	4838
Second Spring Cut	5544	5128	4195	3417	4571
Both Spring Cuts	4639	4878	3889	3401	4201
Main Plot Treatment Mean	5729	5536	4420	3748	4858

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between main plot treatment means	± 297,1	766,9	1101,2
Between subplot treatment means	± 179,1	352,9	465,2
Between subplots in same main plot	± 358,3	705,8	930,5
Between subplots in different main plots	± 429,6	944,2	1343,6

The variation in forage production between these main plot treatments only reached significance (p = 0,05) in subplots subjected to the first spring cut when about 20 cm growth was present.

iv. Total forage production. A combination of yield data in Tables 77 and 78 show that approximately 6 800 kg DM/ha was harvested during the period from early spring to seed harvest in 1972. Production was higher in those plots cut in spring, compared to the uncut subplots. The highest production, 7 500 kg DM/ha, was recorded in those subplots in the uncut main plots which were cut at the onset of inflorescence development as well as at seed maturity.

In 1973 the crop average was 7 687 kg DM/ha. The figures recorded in Table 79 show that the greatest amount of forage DM was removed from the uncut (control) main plot because of the overwintered material retained in these plots during spring. When the overwintered material was removed in early spring by either burning or mowing, up to 7 000 kg DM/ha was produced between early spring and seed harvest. Forage production was higher following the early spring cut compared with production after burning but the variation between these two main plot treatment means and between the subplot treatments was not significant.

In each main plot forage production in subplots cut twice in spring was consistently higher than in those plots cut only once; viz. either the first or second spring cut. The difference in production between the single and the double cutting treatments reached significance in the uncut main plots (p = 0,01) and in those plots cut in late autumn (p = 0,01).

The difference in production in subplots subjected to either the first or second spring cut varied between main plot treatments. There was no difference between both subplot treatments in main plots cut in late autumn. In main plots cut in early spring production was higher in those subplots cut at inflorescence initiation (second spring

cut) but the difference was not significant. The second spring cut also resulted in higher forage production than the first spring cut in the main plots burnt in early spring. The difference of approximately 750 kg/ha between the two subplot treatments was significant ($p = 0,05$).

Defoliation obviously stimulated forage production as all subplot cutting treatments resulted in significantly higher total dry matter yields than the control (subplot) treatment in all main plots ($p = 0,01$).

TABLE 79 Effect of defoliation at different times on the amount of forage (kg DM/ha) produced in a weeping lovegrass stand from early spring to seed harvest in 1973

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	7233	6856	4827	4378	5823
First Spring Cut	11312	8644	6021	5196	7806
Second Spring Cut	1118	8645	6416	5939	8046
Both Spring Cuts	12490	10160	6972	6669	9072
Main Plot Treatment Mean	10554	8576	6071	5545	7687

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between main plot treatment means	± 357,8	875,4	1326,2
Between subplot treatment means	± 188,1	370,6	488,5
Between subplots in same main plot	± 376,2	741,1	977,0
Between subplots in different main plots	± 483,9	1079,4	1550,3

b) Production of Seedheads

i. Seed crop development. The influence of the various cutting treatments on date of initial ear emergence in 1973 is shown in Table 80. The slightly later emergence of seedheads in the uncut subplots of the control main plots indicated that excess (overwintered) forage delayed seedhead development. The dissection of tillers showed that inflorescence initiation was also delayed in these subplots.

The greatest delay in ear emergence was recorded in those main

plots which were burnt in early spring. The first ears to emerge in these plots were recorded four days after those emerging in plots cut in early spring.

TABLE 80 Effect of defoliation at different times on the date of initial ear emergence in weeping lovegrass in 1973

Subplot Treatment	Main Plot Treatment			
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn
No Cut (Control)	7 November	4 November	5 November	9 November
First Spring Cut	4 November	5 November	5 November	9 November
Second Spring Cut	5 November	5 November	6 November	10 November
First + Second Cut	6 November	7 November	7 November	10 November

Spring (subplot) defoliation had little effect on time of initial ear emergence, although there was a slight delay in ear emergence when subplots were cut at the onset of reproductive growth (second spring cut).

Ear emergence following an early spring burn occurred over a much shorter period of time than after an early spring cut. This is illustrated in Figure 25. The delayed onset of ear emergence and the earlier date on which the seedhead population reached maximum numbers in the burnt plots meant that the seed crop was more uniform than that in plots cut in early spring. Following a spring burn the crop reached maximum ear numbers at least four days before those in the early spring cut plots, despite the 4-day delay in initial ear emergence.

No noticeable differences in seed crop maturity were observed between the various treatments. Unfortunately a critical assessment of seed development was not possible. However, seed sampled immediately after harvesting the crop showed that the moisture content of the seed was reasonably similar among the treatments, ranging from between 24 and 27 per cent. Seedheads harvested in the control

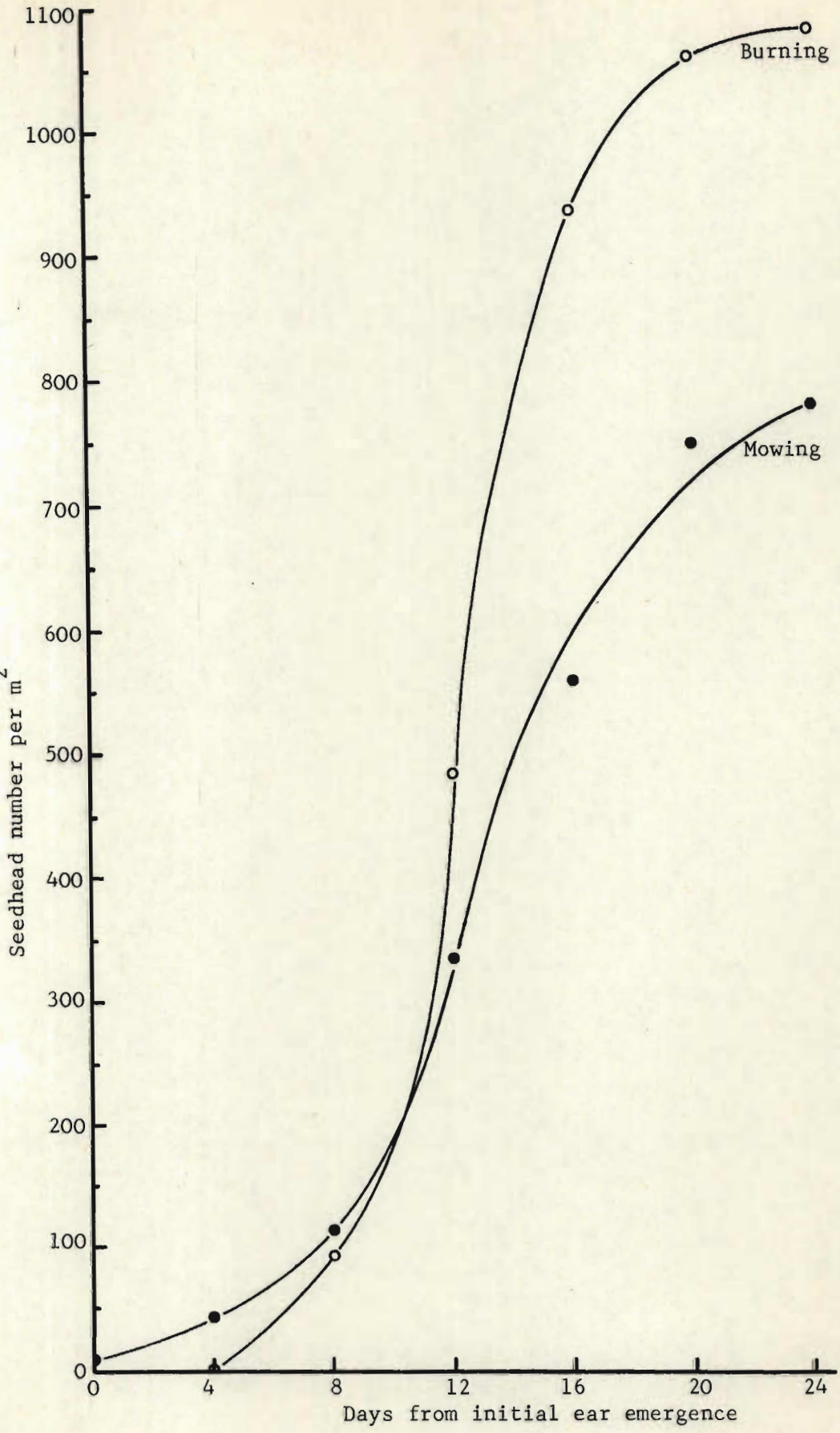

FIGURE 25 The influence of early spring mowing and burning on the rate of seedhead appearance in weeping lovegrass in 1973

subplots of each control main plot were more mature and had an approximate 20-22 per cent moisture content at harvest. This was attributed to the reduced population of seedheads in these subplots and the absence of lodging.

ii. Number of seedheads per m^2 (Table 81). In 1973 the crop average of 876 seedheads per m^2 was more than double the 1972 crop average. Nevertheless the main effects of the main plot treatments were similar in both years.

Main plots cut in late autumn contained more seedheads than the uncut (control) main plots at seed harvest in both years. However, variation between these two treatment means was not significant. The early spring cut also increased the size of the seedhead population. The effect was not significant in 1972 but in 1973, when almost 1 000 seedheads were produced per m^2, the variation between this treatment mean and either the control mean or the late-autumn cut mean was highly significant ($p = 0,01$).

Seedhead production was affected most by the early spring burn. The mean number of heads in burnt plots was more than double the number in the uncut plots, the difference between treatment means in both years being highly significant ($p = 0,01$). In both years the burnt plots also contained an average 200 heads per m^2 more than plots cut in early spring, but the effect was significantly greater in 1972 ($p = 0,01$) than in 1973 ($p = 0,05$).

In 1972 the defoliation of subplots at the onset of reproductive growth (second spring cut) had no effect on the size of the seedhead population but in 1973 the effect of each subplot treatment varied according to the main plot treatment. In main plots either mown or burnt in spring the spring defoliations had no significant effect on the size of the seedhead population when compared with seedhead numbers in the uncut subplots. In main plots cut in late autumn, all subplot cutting treatments increased seedhead numbers when compared

TABLE 81 Effect of defoliation at different times on the number of seedheads produced per m^2 in weeping lovegrass at seed harvest

a) 1972

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	246	359	372	582	390
Second Spring Cut	278	347	389	571	396
Main Plot Treatment Mean	262	353	381	577	393

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between main plot treatment means	± 51,9	127,1	192,5
Between subplot treatment means	± 27,1		
Between subplots in same main plot	± 54,1		
Between subplots in different main plots	± 84,2	181,7	255,2

b) 1973

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	370	548	937	1203	765
First Spring Cut	775	923	922	1306	981
Second Spring Cut	415	629	1001	1225	817
Both Spring Cuts	827	748	1096	1092	941
Main Plot Treatment Mean	597	712	989	1206	876

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between main plot treatment means	± 67,5	165,3	250,4
Between subplot treatment means	± 51,5	101,4	133,7
Between subplots in same main plot	± 102,9	202,8	267,2
Between subplots in different main plots	± 111,8	239,8	335,7

with the control (subplot) treatment. However the only significant increase followed the first spring cut when subplots were defoliated when 15-20 cm of growth was present (p = 0,01).

The greatest response to spring (subplot) defoliation was recorded in the uncut main plots. The size of the seedhead population was more than doubled following the first spring cut and increased even further in those subplots cut twice in spring. These increases were highly significant (p = 0,01). The second spring cut had no effect on seedhead population in the uncut main plots.

iii. Relationship between forage production and seedhead production. From the data recorded in Table 78 and Table 81 it would appear that excess forage production during seed crop development was detrimental to seedhead production. There was in fact a highly significant negative correlation (p = 0,01) between the number of seedheads produced and the quantity of forage present at seed harvest as illustrated in Figure 26.

iv. Culm size (Table 82). In 1972, the lightest culms were produced in the uncut subplots of main plots burnt in early spring. The heaviest culms were recorded in the uncut subplots of control main plots. However, the variations in mass of 100 culms between subplots in the same main plot or in different main plots were not significant.

In 1973, analysis of main plot treatment means showed that removal of forage in early spring by either mowing or burning significantly reduced individual culm size (p = 0,01). This was noted particularly in the uncut subplots where the mass of 100 culms was about 15 g lighter than in uncut subplots of the control main plots.

The subplot cutting treatments had a much greater effect on culm size than the main plot treatments. The mean mass of 100 culms following either the first or second spring cuts was reduced by more than 10,0 g when compared with the 100 culm mass of the uncut subplots. The mean was reduced by a further 10,0 g when the plots were cut twice

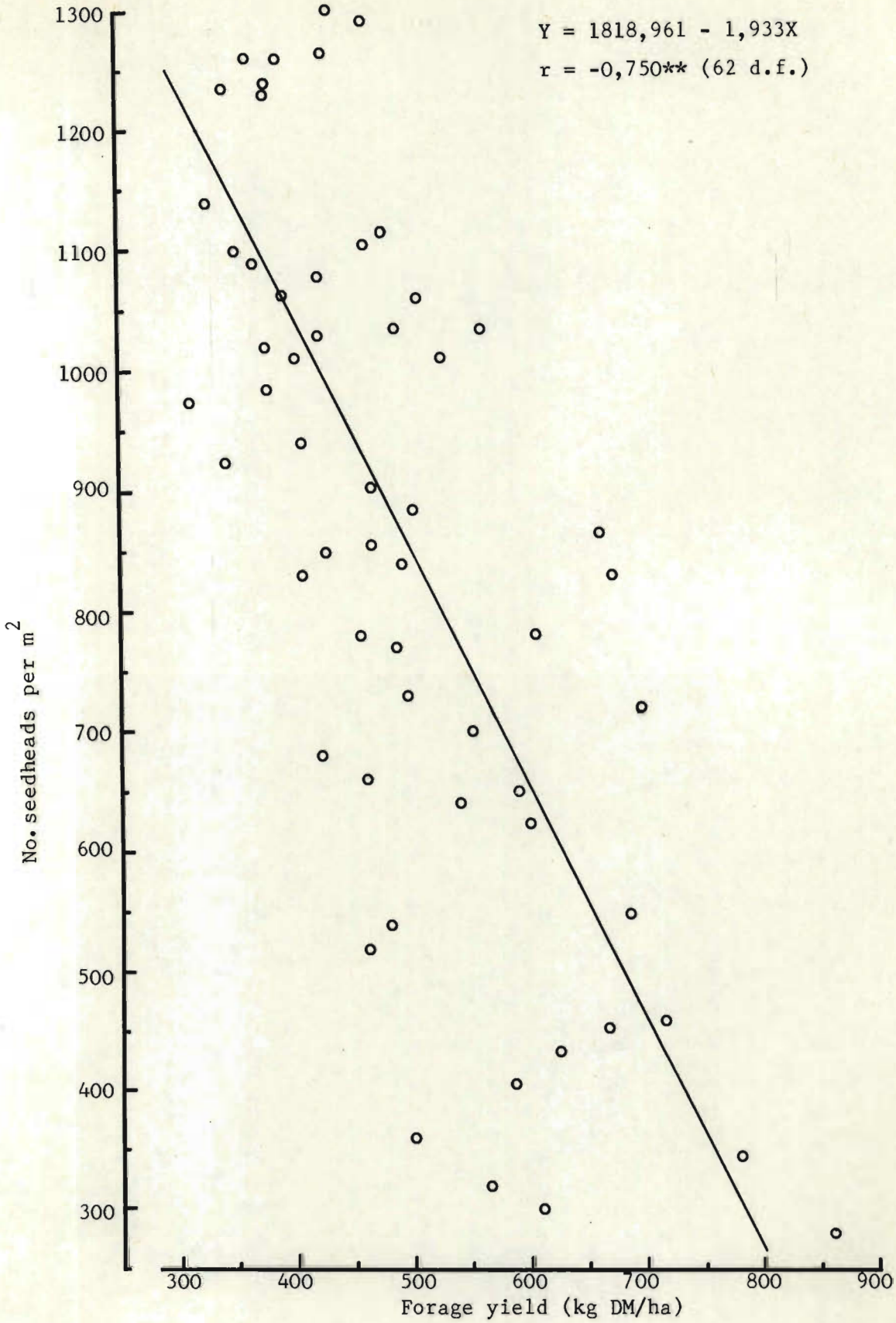

FIGURE 26 Relationship between number of seedheads produced per m^2 and forage yield (kg DM/ha) at seed harvest in weeping lovegrass in 1973

TABLE 82 Effect of defoliation at different times on the mass of 100 culms (g) at seed harvest

a) 1972

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	63,9	63,6	61,2	55,9	61,1
Second Spring Cut	61,3	63,3	61,1	56,3	60,5
Main Plot Treatment Mean	63,6	63,5	61,1	56,1	60,8

	S.E.
Between main plot treatment means	± 3,59
Between subplot treatment means	± 1,71
Between subplots in same main plot	± 3,42
Between subplots in different main plots	± 5,52

b) 1973

Subplot Treatment	Main Plot Treatments				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	77,4	75,5	61,0	62,3	69,8
First Spring Cut	61,0	61,5	53,3	58,1	58,4
Second Spring Cut	63,3	61,2	53,8	51,8	57,5
Both Spring Cuts	53,2	52,2	43,3	43,3	48,0
Main Plot Treatment Mean	63,7	62,6	52,8	54,6	58,4

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between main plot treatment means			
Between subplot treatment means	± 1,62	3,20	4,22
Between subplots in same main plot			
Between subplots in different main plots	± 3,25	6,40	8,44

in spring. The variations in 100 culm mass between the control mean, the single cut treatment means and the double cutting treatment mean were highly significant ($p = 0,01$).

v. Ratio of reproductive to vegetative growth (Table 83. The mass per m^2 of culms relative to that of forage at seed harvest was recorded for each subplot and expressed as a ratio of reproductive to vegetative growth.

In 1972 all subplots contained a greater mass of forage than reproductive growth at seed harvest. Analysis of main plot treatment means shows that both the late autumn and early spring cuts resulted in a higher ratio than the control but the effect was not significant. Plots burnt in early spring had a significantly higher mean ratio when compared with the control mean ($p = 0,01$), with the late autumn cutting mean ($p = 0,01$) and also with the early spring cutting mean ($p = 0,01$).

Of the subplot treatments the positive effect of the second spring cut was only significant in plots which were burnt in early spring ($p = 0,01$).

As in 1972 the removal of forage at various stages of growth in 1973 resulted in a higher ratio at seed harvest and the greatest effect was obtained following the early spring burn. The mean ratio following the early spring burn was significantly higher than that following the early spring cut ($p = 0,01$) which, in turn, was significantly higher than the mean ratio recorded for the late autumn cutting treatment ($p = 0,05$); the variation between the latter treatment mean and the control treatment mean was not significant.

There was little variation in the size of the ratio between subplot treatment means in 1973. The highest ratio was obtained following the first spring cut. This subplot treatment mean was significantly higher than the control subplot treatment mean ($p = 0,01$).

TABLE 83 Effect of defoliation at different times on the ratio of reproductive DM to vegetative DM in weeping lovegrass at seed harvest

a) 1972

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	0,24	0,33	0,37	0,56	0,38
Second Spring Cut	0,39	0,49	0,53	0,75	0,54
Main Plot Treatment Mean	0,31	0,41	0,45	0,66	0,46

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between main plot treatment means	± 0,064	0,158	0,239
Between subplot treatment means	± 0,041	0,081	0,107
Between subplots in same main plot	± 0,082	0,162	0,213
Between subplots in different main plots	± 0,119	0,252	0,349

b) 1973

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	0,41	0,63	1,24	1,93	1,05
First Spring Cut	0,89	1,14	1,07	2,10	1,30
Second Spring Cut	0,43	0,76	1,40	1,97	1,14
Both Spring Cuts	0,94	0,82	1,26	1,52	1,14
Main Plot Treatment Mean	0,67	0,84	1,25	1,88	1,16

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between main plot treatment means	± 0,133	0,375	0,492
Between subplot treatment mean	± 0,082	0,162	0,213
Between subplots in same main plot	± 0,164	0,323	0,426
Between subplots in different main plots	± 0,195	0,426	0,606

Analysis of variance showed a highly significant interaction ($p = 0,01$) between the main plot and subplot treatment effects in 1973 (Appendix C, Table 7). In the uncut (control) main plots the double spring cut resulted in a significantly ($p = 0,01$) higher ratio (0,94) compared with the ratio obtained in the uncut subplot (0,41). On the other hand, the ratio obtained with the same subplot treatment in main plots burnt in early spring (1,52) was significantly smaller than the uncut subplot ratio (1,93) ($p = 0,05$).

The highest ratio was recorded following an early spring burn and a cut when 15-20 cm growth was present (first spring cut). This ratio was significantly higher than those of the same subplot treatment in each of the remaining main plot treatments ($p = 0,01$).

c) Production of Seed

i. Yield of cleaned seed (Table 84). The mean yield of seed harvested from plots burnt in early spring, 1972, was more than double that obtained in the uncut (control) main plots and significantly higher than the means recorded for the late autumn and early spring mowing treatments ($p = 0,05$). Mowing in late autumn or early spring increased mean seed yields by approximately 20 per cent compared with the control mean, but this increase was not significant.

Mowing at inflorescence initiation (second spring cut) had no effect on yield in 1972.

In 1973 the highest mean yield was again recorded in those main plots burnt in early spring. The early spring burn increased seed yield by approximately 55 per cent compared with the control treatment mean and this increase was highly significant ($p = 0,01$). Mowing in early spring increased mean yield by approximately 25 per cent compared with the control treatment mean but this increase was not significant. Cutting in late autumn had no effect on seed yield.

An analysis of subplot treatment means has shown that all subplot mowings in the spring in 1973 increased seed yield when compared with

TABLE 84 Effect of defoliation at different times on the yield of cleaned seed (kg/ha) in weeping lovegrass

a) 1972

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	110	131	137	225	150
Second Spring Cut	118	132	141	204	149
Main Plot Treatment Mean	114	131	139	215	150

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between main plot treatment means	± 26,5	65,0	98,4
Between subplot treatment means	± 9,8		
Between subplots in same main plot	± 19,5		
Between subplots in different main plots	± 29,9	71,5	106,8

b) 1973

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	187	319	399	532	359
First Spring Cut	372	415	390	547	431
Second Spring Cut	330	313	448	473	391
Both Spring Cuts	452	316	441	529	434
Main Plot Treatment Mean	335	341	419	520	404

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between main plot treatment means	± 37,2	91,1	138,1
Between subplot treatment means	± 25,7	52,3	70,1
Between subplots in same main plot	± 51,5	104,5	140,2
Between subplots in different main plots	± 58,1	127,6	181,7

the control subplot mean. Increases in yield were highly significant following the first spring cut and the double spring mowing treatment ($p = 0,01$).

When compared with the yield obtained in the uncut subplots the second spring cut had no effect on seed yield in the main plots cut in late autumn and reduced yield in those plots burnt in early spring, although the effect was not significant. In the control main plots and in those cut in early spring, the second spring cut increased seed yield compared with the control subplot treatment. The effect was significant in the control main plots ($p = 0,01$).

Similarly, while the double cut (subplot) treatment had no effect on seed yield in those plots burnt in early spring it significantly increased yield ($p = 0,01$) in the control main plots (when compared with the uncut subplot treatment). The greatest response to the subplot defoliation treatments was recorded in the uncut main plots; each of the three treatments significantly increased seed yield when compared with the control subplot treatment ($p = 0,01$).

There appeared to be a very close relationship between seed yield and the size of the seedhead population in both years. The actual relationship is shown in Figures 27 and 28 for 1972 and 1973 respectively. In both years there was a highly significant positive correlation between seed yield and seedhead numbers ($p = 0,01$).

ii. 1 000 seed mass. Defoliation either prior to or after the onset of forage production in spring had no effect on seed size in 1972. The mass of 1 000 seeds ranged from $239,2 \pm 14,78$ mg to $243,5 \pm 15,29$ mg.

In 1973 there was also little variation in seed size as shown in Table 85. There was a slight positive response to defoliation prior to the onset of spring growth but this was not significant.

Mowing during active spring growth in 1973 had a detrimental effect on seed size. An analysis of the subplot treatment means

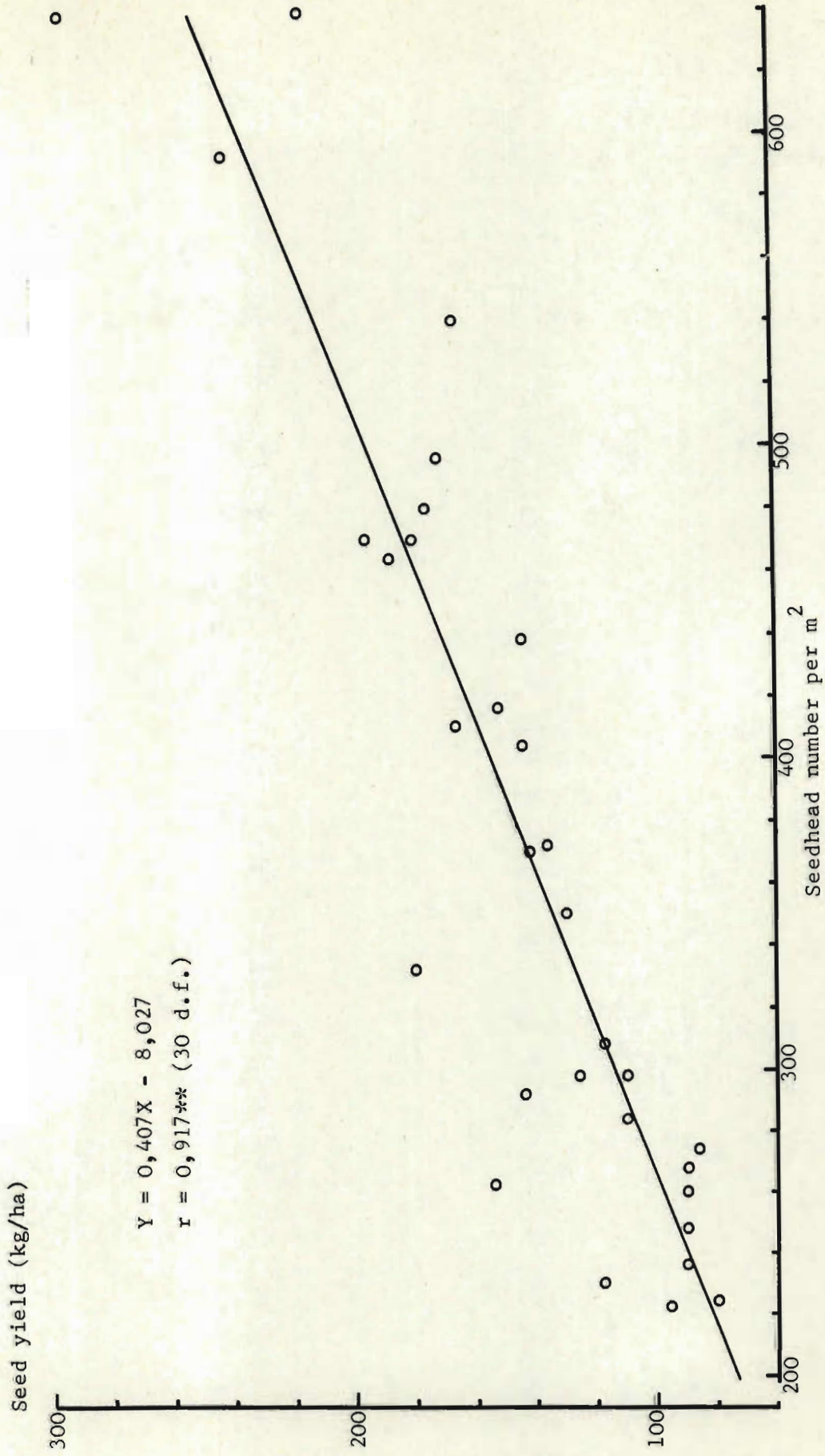

FIGURE 27 Relationship between seed yield (kg/ha) and seedhead number per m^2 in weeping lovegrass in 1972

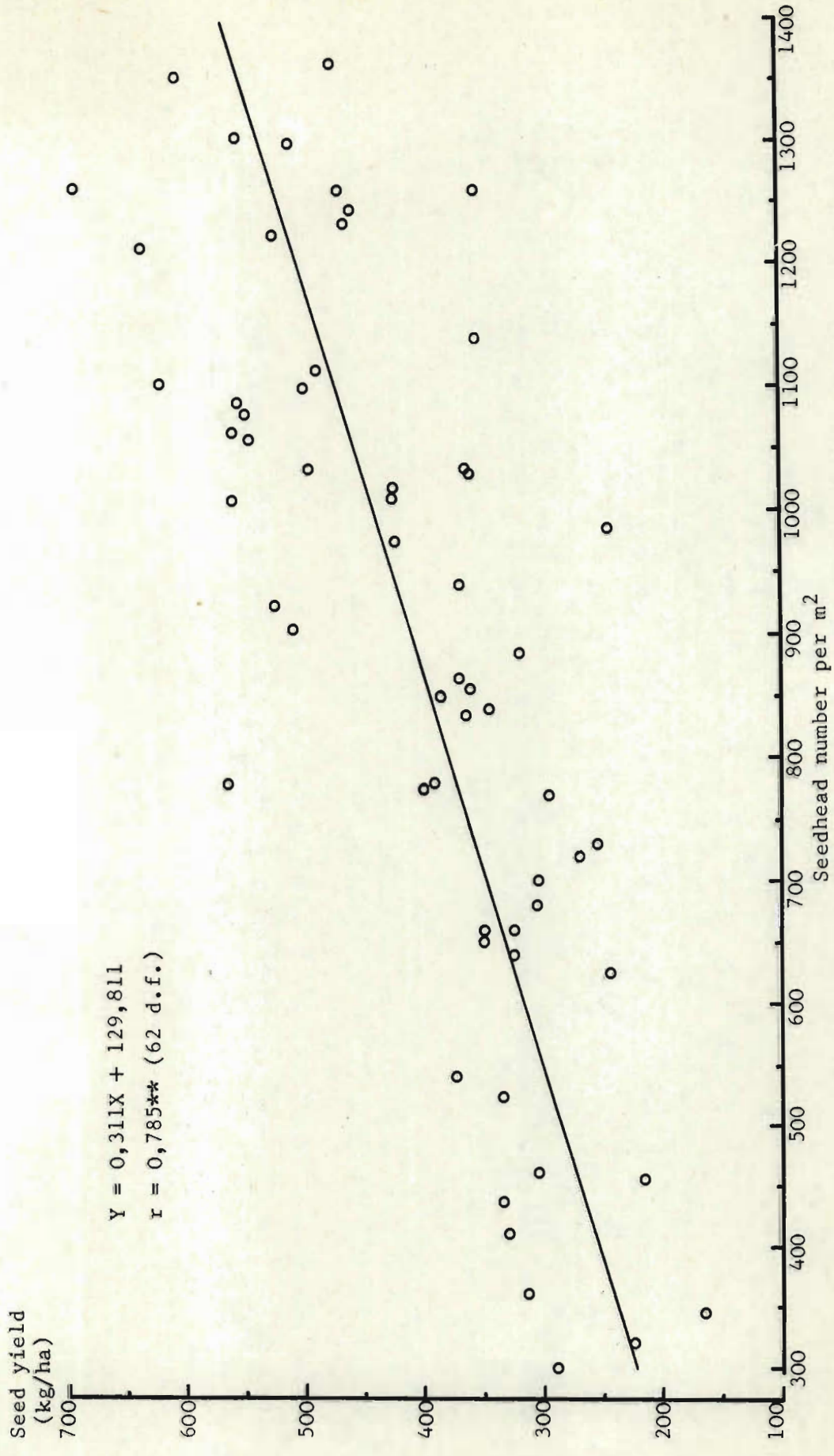

FIGURE 28 Relationship between seed yield (kg/ha) and seedhead number per m^2 in weeping lovegrass in 1973

reveals a significant decline in the mass of 1000 seeds in each subplot defoliation treatment compared with the control (subplot) mean ($p = 0,01$). The effects of each subplot cutting treatment were reasonably consistent for each main plot treatment. Spring cutting significantly reduced the 1 000 seed mass to at least the 5 per cent level of probability when compared with the control (subplot) treatment.

TABLE 85 Effect of defoliation at different times on 1 000 seed mass (mg) in weeping lovegrass in 1973 (recorded at uniform 12,0% moisture content)

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	293,5	315,6	313,7	311,5	308,6
First Spring Cut	289,0	299,7	296,6	300,3	296,4
Second Spring Cut	287,2	306,8	305,9	296,2	296,0
Both Spring Cuts	289,2	296,3	297,7	302,5	296,4
Main Plot Treatment Mean	289,7	304,6	303,4	302,6	300,1

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between main plot treatment means	± 8,68		
Between subplot treatment means	± 1,60	3,57	4,15
Between subplots in same main plot	± 3,18	6,30	8,26
Between subplots in different main plots	± 9,12	21,62	32,83

iii. Germination capacity. The crop mean in 1972 was 82 per cent. The treatments imposed in that year had no effect on seed viability.

The viability of seed harvested from each subplot in 1973 is recorded in Table 86. In 1973 the crop mean was 91 per cent. As in the previous year the main plot treatments had no significant effect on germination capacity.

In general the first and the second (subplot) cutting treatments reduced viability to the extent that the means of these two subplot

treatments were significantly lower than the control (subplot) mean ($p = 0,01$). The double spring cut had no overall effect on germination when compared with the control subplot mean but resulted in the production of seed with significantly greater viability when compared with the mean of the first and the second cutting treatments ($p = 0,05$).

Defoliation of the uncut (control) main plots in spring had the greatest detrimental effect on seed viability. Both the first and second spring cuts significantly reduced viability by almost 5 per cent ($p = 0,01$) and mowing twice in spring by 3 per cent ($p = 0,05$) when compared with the germination capacity of seed in the uncut subplot of the control main plot.

TABLE 86 Effect of defoliation at different times on the percentage germination of weeping lovegrass seed three months after seed harvest in 1973

Subplot Treatment	Main Plot Treatment				Subplot Treatment Mean
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn	
No Cut (Control)	92,0	92,3	90,8	92,1	91,8
First Spring Cut	87,6	90,7	90,5	91,8	90,1
Second Spring Cut	87,5	92,0	90,6	90,4	90,1
Both Spring Cuts	89,1	93,5	90,6	92,8	91,5
Main Plot Treatment Mean	89,0	92,1	90,6	91,8	90,9

	S.E.	L.S.D.(5%)	L.S.D.(1%)
Between main plot treatment means	± 1,54		
Between subplot treatment means	± 0,58	1,15	1,51
Between subplots in same main plot	± 1,16	2,29	3,01
Between subplots in different main plot	± 1,84	4,25	6,22

iv. Inflorescence size (Table 87). While the main plot cutting treatments had no significant effect on culm length, inflorescence length was significantly reduced when plots were either cut or burnt in early spring ($p = 0,01$). However, both the number of primary

TABLE 87 The influence of method of removal of overwintered forage (main plot treatments) on inflorescence size and other associated characters in weeping lovegrass in 1973

Seedhead Characteristic	Main Plot Treatment				S.E.	L.S.D. (5%)	L.S.D. (1%)
	No Cut (Control)	Late Autumn Cut	Early Spring Cut	Early Spring Burn			
Culm length (cm)	110,7	111,4	108,7	110,1	± 2,98		
Inflorescence length (cm)	24,1	24,9	22,8	22,4	± 0,34	0,96	1,28
Prim. branches/inflorescence	24,9	24,0	25,3	27,0	± 0,29	0,82	1,09
Spikelets per inflorescence	215	201	227	260	± 8,13	23,00	30,50
Florets per spikelet	6,7	6,8	5,6	5,3	± 0,14	0,40	0,52
Florets per inflorescence	1439	1345	1249	1365	±43,35	122,60	163,00
Floret fertility (%)	47,3	47,0	49,1	48,1	± 0,91		

branches and number of spikelets per inflorescence were significantly increased following the early spring burn when compared with control treatment ($p = 0,01$). Cutting in early spring increased both these components but the increase was not significant. Inflorescences produced in those plots cut in late autumn had significantly fewer primary branches ($p = 0,05$) and fewer spikelets than inflorescences in the uncut main plots.

The largest inflorescence in terms of number of florets was produced in the uncut plots. Mowing or burning in early spring produced an inflorescence with significantly fewer florets per spikelet than inflorescences in the uncut (control) plots ($p = 0,01$). The late autumn cut had no effect on spikelet size.

Defoliation by mowing or burning prior to the onset of vegetative growth in spring reduced floret numbers per inflorescence; the effect was only significant in those plots cut in early spring ($p = 0,01$).

None of the main plot treatments had any effect on the capacity of florets to set seed. In 1973, the mean fertility of florets was approximately 48 per cent.

v. Correlation coefficients between certain components of yield (Table 88). The number of seedheads per m^2 was the only character analysed that showed a highly significant positive correlation with seed yield ($p = 0,01$). The number of spikelets per inflorescence was significantly correlated with seed yield ($p = 0,05$).

There was a highly significant positive correlation between seedhead numbers and the number of spikelets per seedhead ($p = 0,01$). Both these yield components showed a significant negative correlation with the number of florets per spikelet ($p = 0,01$) which, in turn, was negatively correlated (significantly) with seed yield ($p = 0,01$). This negative relationship was undoubtedly due to reduced spikelet size in those plots mown or burnt in early spring (Table 87).

Floret fertility and seed size had very little relationship with

other yield components and with seed yield.

TABLE 88 Correlation coefficients between five characters with each other and with seed yield (kg/ha) in weeping lovegrass (analysis of data from control subplots of the four main plot treatments in 1973)

	2	3	4	5	6
1. Seedheads/m^2	+0,675**	-0,912**	+0,183	+0,202	+0,842**
2. Spikelets per seedhead		-0,691**	+0,153	-0,081	+0,532*
3. Florets per spikelet			-0,083	-0,188	-0,755**
4. Floret fertility				+0,001	+0,110
5. 1000 seed mass (mg)					+0,430
6. Seed yield (kg/ha)					-

* Significant at 5%
** Significant at 1%

Multiple correlation coefficient:
r = 0,885** (14 d.f.)

4. DISCUSSION

a) Main Plot Treatment Effects

Of the different methods of removing overwintered forage investigated in this experiment, the late autumn cutting treatment, while not removing overwintered material as such, was still responsible for a reduction in the quantity of forage present in the stand at the resumption of growth in early spring.

There is evidence that cutting in late autumn can be deleterious to weeping lovegrass swards. McIlvain and Shoop (1970b) have reported that grazing or mowing weeping lovegrass to 5 cm stubble height in late autumn or early winter can result in the death of between 30 per cent and 70 per cent of plants in the stand. Weeping lovegrass is most susceptible to winter kill. The implications of this on the seed crop are obvious, particularly when the majority of seedheads in the crop are developed in tillers arising prior to the dormant winter period as found in Experiment 1 (Chapter III, Section 1). However, in this present investigation the crop was mown sufficiently early to

allow some regrowth before the colder, drier weather began. Consequently the bases of plants in the stand were well insulated and protected by a good forage cover. In fact the quantity of material removed in early spring in 1973 (Table 76) suggests that a further hay crop would have been possible in autumn and still allowed for adequate regrowth.

The removal of overwintered forage at or prior to the resumption of growth in spring had a considerable effect on the development and size of the seedhead population. The autumn and early spring mowing treatments were both responsible for initial head emergence occurring 2 to 3 days before the same stage of development was reached in control main plots in 1973 (Table 89). Rather than any direct stimulatory effect by mowing, it is suspected that excess forage in the uncut plots caused a marked reduction in the amount of light penetrating the sward which delayed or retarded reproductive development and therefore initial ear emergence.

The apparent delay in ear emergence in the burnt plots is attributed to the death of those tillers which would normally have initiated the first inflorescences. From the results obtained in Experiment 1 (Chapter III, Section 1) it is considered likely that these same tillers emerged in the late summer or autumn of the previous season remained dormant throughout the winter, were the first to resume active growth in the spring and were consequently killed by the burn, which occurred following the resumption of active growth in spring. As shown in Experiment 4 (Chapter III, Section 3) early-emerged seedheads are also the largest and produce the most seed, but are of little consequence to total crop seed yield because of their small numbers. Therefore their loss by burning in early spring should have had little effect on the seed productivity of the crop.

Seedheads in the burnt plots were more uniform in age than those in the cut plots (Figure 25). The implications of this are profound.

A study of seed crop development (Experiment 4, Chapter III, Section 3) revealed the great variability in the time of seed maturity between inflorescences which emerged at different times. It was concluded that if a more uniform seed crop could be obtained seed development and ripening would be more uniform, seed loss due to under- or over-ripeness would be reduced and yields accordingly increased. In this present investigation burning had induced a more uniform seed crop and this may have contributed in part to the higher yields obtained after burning (Table 84).

The actual causes of the greater uniformity in ear emergence after burning were not investigated. However, it seems likely that the burn stimulated tillering and broke dormancy to a much greater extent than mowing. This resulted in greater uniformity in the growth of tillers from early spring.

Forage removal by mowing or burning in late autumn and early spring in 1972 and 1973 also increased the size of the seedhead population (Table 81). In both years the early spring cut had a greater effect on ear production than the late autumn cut. However, the greatest response to defoliation was obtained following the early spring burn. McIlvain and Shoop (1970b) have also reported an increase in seedhead numbers when weeping lovegrass was burnt in early spring.

The reduced number of seedheads per m^2 in the uncut (control) main plots and the associated increase following the removal of forage suggests that excess forage is detrimental to reproductive growth in weeping lovegrass. The highly significant negative correlation between seedhead numbers and forage dry matter yields at seed harvest (Figure 26) is evidence of this detrimental effect.

Excess forage in the crop at the onset of reproductive growth causes intense shading within the sward. This restriction of light by shading is considered sufficient to inhibit seedhead formation in the majority of tillers. Studies on light penetration in perennial grass

stands of temperate species have shown the reduced ability of grasses to produce seedheads when light intensity is reduced (Ryle, 1966). Therefore the removal of old accumulated growth in early spring increased light penetration in the sward and normal tiller development was presumably able to proceed.

Defoliation by mowing or burning removes any excess forage which may inhibit light penetration and therefore both methods of defoliation should have had similar effects on seedhead production. However, the response to burning was consistently greater than the mowing response and consequently some further factor must be involved. Little is known of the actual causes of the burning effect (McIlvain and Shoop, 1970a). There have been reports that weeping lovegrass forage has a higher protein content after burning than in unburnt stands (Dalrymple, 1969; McIlvain and Shoop, 1970a). It is possible therefore that burning may be responsible for an increase in nitrogen uptake by the plant and so increasing the efficiency of nitrogen utilisation by the seed crop. This may induce greater tiller production in early spring and the production of more seedheads as a consequence.

The effects of the main plot defoliation treatments on seed yield in weeping lovegrass (Table 84) were very similar to their effects on seedhead production. The high positive correlations between seedhead numbers and seed yield in 1972 (Figure 27) and 1973 (Figure 28) substantiated this observation. Previous research has shown the importance of fertile tiller numbers as a major determinant of seed yield in several grass species (Canode and van Keuren, 1963).

The influence of the size of the seedhead population on seed yield was further substantiated when correlation coefficients between five components of yield with each other and with seed yield were calculated (Table 88). Of the components studied, the number of heads per m^2 showed the strongest positive relationship with seed yield.

The only other component to show a high positive correlation was the number of spikelets developed in each seedhead. It is interesting to note the highly significant negative correlation between spikelet numbers per inflorescence and the number of florets per spikelet. As a consequence spikelet size showed a high negative correlation with seed yield.

This negative relationship between these two yield components is also shown in the data recorded in Table 87. The mean number of spikelets per inflorescence was increased when the crop was burnt in early spring but this had little effect on the total number of florets per inflorescence because of the smaller size of each spikelet. The reduction in floret numbers per spikelet following the early spring mowing or burning treatments appeared to be the result of competition for assimilates within each inflorescence rather than the direct effect of defoliation. An increase in spikelet numbers per inflorescence may have increased competition between spikelets, thus reducing the potential number of florets each spikelet could produce and resulting in this negative relationship.

These findings are in agreement with those obtained in the glasshouse experiments (Experiments 2 and 3, Chapter III, Section 2). In these experiments there was a high negative correlation between floret number per spikelet and spikelet number per inflorescence which suggested that some compensatory mechanism was active in the weeping lovegrass inflorescence to maintain floret numbers per inflorescence within a definite range. This mechanism was considered to be competition between spikelets for assimilates.

The significant increase in number of spikelets per inflorescence following the early spring burn (Table 87) must be attributed to some burning effect. Spikelet numbers increased with head numbers whereas in normal circumstances the greater density of heads, directly related to increased tiller production, would be expected to have a detri-

mental effect on inflorescence size and therefore on the number of spikelets produced per inflorescence. Increased tiller density intensifies competition between tillers, bringing about a reduction in the size of the apical meristem and ultimately in the number of spikelet initials on the primordia. The early spring burn in this present investigation presumably increased the size of tillers produced and therefore, by implication, increased the size of the apical meristem by reducing the intensity of competition, possibly through an increase in nitrogen uptake by the plant.

There is little doubt that controlled burning can be a useful and profitable management tool for seed production in weeping lovegrass in South Africa. Research into the use of fire in the management of weeping lovegrass has received much attention in the United States of America (McIlvain and Shoop, 1970a) and there is definitely a need for further research in South African conditions. The results obtained from this present investigation give some knowledge of the benefit of burning weeping lovegrass seed crops but in no way do they furnish all necessary information, showing in particular the long term effects of burning.

b) Subplot Treatment Effects

The subplot treatments in the present experiment represented different methods of spring utilisation of forage and were correlated with definite stages in the growth and development of the plant rather than with different calendar dates. Experimental results can be more effectively translated into practice if the treatments imposed are correlated with a definite stage in the life of the plant.

The first cut was related to a stage when about 15-20 cm of growth was present. This represented a possible grazing stage in weeping lovegrass. The second cut was related to the onset of reproductive growth in the crop when the first tillers became fertile. Cutting at this stage was equivalent to harvesting a hay crop although

the results recorded in Table 77 show that forage yields in those plots originally defoliated in early spring were not sufficient in practice to harvest for hay. Forage removed at the onset of reproductive growth in those plots uncut or cut in late autumn was mostly over-wintered material and of very low quality.

The double cutting subplot treatment, when both the first and second cuts were imposed, could be considered as a double grazing of the stand. Results show that this treatment was responsible for the highest production of forage during the period from the resumption of growth in early spring to the onset of reproductive growth in early summer.

The initial stages of seedhead formation was considered the latest stage at which weeping lovegrass could be defoliated with no adverse effect on seed production. Many studies have shown the adverse effect of either mowing or grazing beyond the stage of initial head formation in perennial grasses (Roberts, 1958; 1959; 1965; 1966; Lewis, 1969). Delaying the defoliation until stems are elongating can be extremely detrimental. The rapidly changing shoot apices at this stage are raised above ground level and their removal by cutting will result ultimately in a reduced population of seedheads. Even if the developing inflorescence is not removed, the removal of newly-formed upper leaves is likely to have a deleterious effect on subsequent tiller growth. Lambert (1966b) associated reduced seed yield potential in cocksfoot after cutting in spring with a shortage of metabolites which brought about a restriction in the growth of floral parts or had a detrimental effect on seed development.

According to the results obtained in Experiment 4 of this present research programme (Chapter III, Section 3) the first tillers to become fertile did so at least 10 days before the bulk of tillers initiated inflorescences. Therefore, in the present experiment, the chances of destroying a large number of developing seedheads at the

onset of reproductive growth in the crop were remote. In fact, the weeping lovegrass stand was given several days in which to recover before the main crop of seedheads was initiated. Initial ear emergence in plots cut at this stage was however, slightly delayed (Table 80) indicating that the second cut did have some effect on tiller growth and development.

The response to spring defoliation apparently varies between different grass species or varieties. This present investigation showed that any defoliation in the spring had little detrimental effect on either the production of seedheads (Table 81) or subsequent seed yield in weeping lovegrass (Table 84). In fact seed productivity was increased in several cases. However, the favourable effects of the subplot treatments must be dependent at least in part on the high levels of nitrogen applied in spring. Research has shown that seed yields can be significantly depressed if nitrogen is not applied after grazing in spring (Roberts, 1958; 1966).

The response to spring defoliations varied according to the main plot treatment imposed initially, and was therefore closely associated with the quantity of forage in each main plot in early spring. The greatest response was recorded in the uncut (control) main plots and the least response in those plots either cut or burnt in early spring. Obviously all discussion refers to the results obtained in 1973. Only the second cut was imposed in 1972 because of unfavourable weather conditions and in general this cut had little or no effect on the seed productivity of weeping lovegrass in that year.

The first spring cut was imposed at a sufficiently early stage, relative to the onset of reproductive growth, to significantly increase the size of the seedhead population in the uncut main plots and in those plots cut in late autumn. As previously discussed, in relation to main plot treatment effects, removal of forage increased light penetration to the base of the sward, allowing normal tiller

development to take place. It would appear that the second spring cut occurred too late to have much effect on seedhead production. The increased seedhead numbers in subplots cut twice in spring was therefore presumably brought about by the first of the two defoliations.

Although the subplot cutting treatments had little or no detrimental effect on seedhead production they generally reduced the size of culms (Table 82). The decline in the mass of 100 culms was generally associated with an increase in the number of seedheads per m^2. For example, the removal of forage in spring increased seedhead numbers in the uncut and late autumn cut main plots and this may have intensified competition between developing culms for assimilates, resulting in the development of lighter culms. However, this argument cannot be used to explain the variation in culm mass in the main plots either cut or burnt in early spring. There was little variation in seedhead numbers in these plots following the implementation of the subplot treatments (Table 81).

However culm size was considerably reduced in subplots cut twice in spring (Table 82). Culm size was also reduced in subplots subjected to the second spring cut in plots burnt in early spring. After studying seed productivity in cocksfoot, subjected to various cutting treatments, Lambert (1966b) concluded that a critical factor in defoliation was the rate of development of fertile tillers in relation to the size of the photosynthetic system, and therefore to the amount of substrate available for growth during this period. It is suggested that the double cutting treatment in particular in this present experiment removed photosynthetically active tissue which was not replaced to the same extent as in those subplots cut only once in spring. The movement of assimilates to developing culms was presumably reduced as a consequence, and at a time when demand for assimilates was steadily increasing. Competition for assimilates between developing culms intensified accordingly and this ultimately resulted

in the production of lighter culms.

The subplot cutting treatments not only reduced culm size but also reduced seed size (Table 85) and the viability of seed (Table 86). Seed size and seed viability are important factors of seed quality. The actual causes of the decline in seed quality following the subplot cutting treatments are not clear. The first spring cut, and not the second, was consistent in bringing about the greatest decline in seed quality. However, seed yields were generally highest in subplots subjected to the first spring cut (Table 84). The size of the seedhead population was also larger in this subplot treatment than in any other, which infers that competition between seedheads, or intra-plant competition (Donald, 1954), was most intense in these plots and the developing seeds presumably did not have the capacity to reach their potential size.

Despite causing a decline in culm size, seed size and seed viability, a spring cut prior to inflorescence initiation was generally of some benefit to the production of seed in weeping lovegrass (Table 84). One important factor which has definite practical implications was the removal of excess forage in spring to promote seed crop development and to facilitate seed harvest. High rainfall conditions and high rates of nitrogen fertiliser can be responsible for the production of excessive forage during seed crop development. The large mass of forage and the wet conditions can cause severe lodging which not only has a deleterious effect on seed production and development (Lewis, 1959; Garrison, 1960) but also causes difficulties at harvesting (Griffiths et al., 1967). In the present experiment the quantity of forage produced during seed crop development and present at seed harvest in 1973 was considered excessive and detrimental to good seed production in most plots (Table 78). The situation was even more extreme in 1972 despite the cut in late spring. In 1972, seed in badly lodged areas germinated while still in the seedhead following a

warm, wet period immediately prior to seed harvest. The excess forage compounded this effect for humid conditions were maintained within the canopy of the crop following the rains. The wet conditions also introduced other problems associated with seed harvest.

The climatic conditions prevailing in Natal during seed crop development and maturity in weeping lovegrass are therefore, not conducive to good seed production and to high seed yields. Every effort must be made to reduce the susceptibility of the seed crop to the wet, humid conditions. It is apparent that the removal of forage in spring, and so a reduction in the quantity of forage in the crop at seed harvest to a manageable level, is one method available to the seed producer. Therefore, the results of these trials show that if adequate nitrogen is available, forage can be successfully utilised in the spring with no detrimental effect to to the potential seed productivity of the crop. In fact it is suggested that the removal of forage in the spring, even after an early spring burn or cut, is essential in Natal as a method of reducing seed losses due to lodging and to reduce harvesting difficulties, thus increasing the seed productivity of the crop.

c) Climatic Effects

As in the previous experiment in this research programme (Experiment 5) the results of each year have been presented separately because of considerable variation brought about by the extreme variability in the rainfall for the two years. Rainfall figures taken in close proximity to the experimental site are presented in Table 56 and show the extremely dry conditions in the spring, almost to the time of ear emergence in 1972.

Even though the dry spell in 1972 had little effect on the size of the seedhead population in the previous experiment (Table 65) it appears to be responsible for a marked reduction in seedhead production in this present experiment. The crop mean in 1972 was less than 45 per

cent that of the 1973 mean (Table 81). Other components of yield measured and which were similarly affected included individual seed size and seed viability. The crop mean for the mass of 1 000 seeds harvested in 1972 was approximately 241 mg, 60 mg lighter than the crop mean obtained the following year. The germination capacity of seeds in 1972 was 82 per cent compared with 91 per cent in 1973.

Relatively little forage was produced in the spring of 1972 so that two subplot treatments were withdrawn. However, as moisture conditions improved during the development of the seed crop, forage production was so rapid that the dry matter yield at seed harvest in the subplots was greater than that obtained in equivalent subplots at the same time in 1973 (Table 78). Consequently the ratio of reproductive growth to vegetative growth at seed harvest in 1972 was considerably lower than in 1973, except perhaps in those plots which were burnt in early spring (Table 83). These plots contained a significantly larger population of seedheads than the remaining plots in 1972 so that the quantity of reproductive growth at seed harvest was sufficient to record a higher ratio. Even so the mean ratio in the burnt plots was only about one-third of the ratio obtained following the same main plot treatment in 1973.

Even though applied nitrogen was reduced from the planned 180 kg/ha to 120 kg/ha in spring of 1972, it would appear that this was still excessive for the dry conditions. A certain percentage of the nitrogen was therefore utilised by the plant for forage production, presumably as the seed crop matured.

The rainfall pattern in the spring of 1972 is a clear example of the complexities which can arise in the management of seed crops. After a reasonable 'first' spring in September no further rain of any consequence was recorded until early November (Table 56). The forage yields obtained at seed harvest in 1972 show that a defoliation prior to the onset of the reproductive stage of development was of little

consequence as a method to reduce the quantity of forage at seed harvest. It would appear that some control of forage production in similar situations could be obtained if nitrogen was applied according to the prevailing conditions. In this instance, the application of nitrogen to the seed crop should have been split into smaller amounts and applied according to soil moisture conditions.

CHAPTER V

GENERAL CONCLUSION

This research programme can be regarded as a preliminary investigation of seed production in weeping lovegrass in Natal and in South Africa as a whole. Consequently it covers a reasonably wide field of study. The experimental work has been grouped arbitrarily into physiological (Chapter III) and agronomic studies (Chapter IV). The physiological studies have generally shown the ability of individual tillers of weeping lovegrass to become fertile and produce seed while the agronomic research has revealed some knowledge of the seed-producing capacity of the weeping lovegrass crop in Natal.

In Natal, and South Africa in general, most marketed seed is harvested from multi-purpose stands which are utilised predominantly for hay. All research therefore, apart from the first three experiments, was conducted in established multi-purpose stands as it was considered that results obtained would be of greater interest to the majority of seed producers in South Africa than if carried out in wide-row spaced specialist seed-producing stands.

In the dense, narrow-row spaced stands growing in Natal, the field research has shown that yields of over 500 kg/ha can be obtained as long as climatic conditions, and particularly rainfall, are suitable. The harvested seed was generally of good quality with a germination capacity of over 90 per cent. These yields compare well with those obtained in the United States of America.

The main conclusion from the available data is that seed yield can be increased substantially in weeping lovegrass stands in Natal, as long as climatic conditions permit.

In the short term this can be brought about by adopting the right husbandry techniques of (a) adequate and timely topdressing with

nitrogen fertiliser; (b) controlled burning in early spring; (c) utilisation of forage in spring, prior to the onset of reproductive growth, and (d) correct choice of harvesting time.

Nitrogen is generally regarded as the most crucial agronomic factor in grass seed production. High yields can only be achieved when the right combination of rate and time of application is obtained. In normal growing conditions in Natal it would appear that high yields can be achieved with a rate of about 120 kg N/ha is applied early in spring (Experiment 5). The efficiency of nitrogen utilisation by the plant for reproductive growth appears to reach a peak when nitrogen is applied at this time.

The principal effect of nitrogen in the present investigation was to increase the number of seedheads in the crop (Experiment 5), although the seed-producing capacity of individual tillers was also increased (Experiments 2, 3 and 5). The number of florets per inflorescence was generally increased and in the field the capacity of florets to set seed was also increased when nitrogen was applied early in spring (Experiment 5).

The optimum time of nitrogen application for maximum seed yield appears to be prior to the onset of reproductive growth in single plants (Experiments 2 and 3) and in the crop (Experiment 5). Nevertheless, it has been shown that the majority of heads present in the crop at harvest develop from tillers which emerged prior to the winter dormant period (Experiment 1). Therefore, although the optimum time of application may be early spring, autumn applications of nitrogen should not be reduced because of the importance of tillers emerging at this time to seed production in the following summer.

Although nitrogen had a significant effect on seed production in weeping lovegrass the response to an early-spring controlled burn was perhaps the more impressive (Experiment 6). Controlled burning early in spring, after the first spring rains, is an effective management

tool used to remove overwintered forage which, if left undisturbed, impedes the subsequent growth and development of the stand. Overwintered material can be removed by mowing and presumably by grazing but the ultimate effect on seed production does not appear to be as great as that obtained by burning.

In the present investigation the main effect of the spring burn was to increase head numbers. It was also observed in 1973 that greater uniformity existed between tillers at time of ear emergence. Although not investigated this presumably indicates greater uniformity in seedhead development and this may have important consequences at seed harvest.

Further research into the effects of burning for increased seed production in weeping lovegrass in Natal is required. Information is required particularly of the long-term effects of annual spring burning on the stand.

Burning in early spring stimulates forage production at this time if soil moisture conditions permit (Experiment 6). However, excess forage in the seed crop has been found to be detrimental to seed production (Experiments 5 and 6) for it induces lodging which, in turn, restricts seed production, impedes seed development and gives rise to harvesting difficulties. Under normal growing conditions the amount of excess forage carried by the crop can be reduced if the stand is grazed or cut in spring.

Time of defoliation in spring is important. The present investigation (Experiment 6) showed that cutting as late as inflorescence initiation had little effect on seed yield when adequate quantities of nitrogen were applied during spring. It is suggested that the later the stand is cut in spring the greater is the necessity to apply adequate nitrogen to allow for vigorous regrowth particularly of reproductive shoots. Although not studied in this experiment it has been established in previous research with other grass species that

any defoliation after the onset of reproductive growth is entirely detrimental to seed production, even if the supply of nitrogen is considered adequate.

The available data show that the quantity of forage actually present during development of the seed crop and at seed harvest will depend on the time and intensity of cutting, the time and rate of nitrogen application and ultimately on prevailing climatic conditions.

While lodging and excessive forage production in late spring may cause difficulties at harvest and consequently result in seed losses and reduced yields, the greatest loss of seed in South Africa may occur because of poor harvesting technique. It appears that only 50 per cent or less of seed produced by the weeping lovegrass crop is ultimately threshed. The economic consequences of this need no explanation.

One important factor influencing final seed yield is the actual time of harvesting weeping lovegrass. Results obtained in the present investigation (Experiment 4) show that optimum time of harvest must be a compromise between seed loss due to either under- or over-ripeness because of the variability in degree of ripeness between heads and within individual heads. This compromise is best reached by measuring the moisture content of seeds. Optimum harvest time appears to be correlated with a seed moisture content of approximately 25 per cent in the crop. However, further research on time of harvest for maximum seed yields is required before any definite recommendations can be made.

Improved agronomic techniques are instrumental in raising the seed yield of any given species in the short term. However, the difference between actual and potential yields in weeping lovegrass still remains large and this can only be overcome to any appreciable extent by either breeding or selecting.

With the present data it is tempting to suggest that selection for a more uniform heading date and good seed-setting may increase yields in the long term. Heading in weeping lovegrass appears to be more uniform than in most tropical species but not as uniform in temperate grasses. It is possible that more uniform heading in weeping lovegrass, resulting in uniform seed development, may reduce seed losses at harvest and consequently increase yields. On the other hand, it is possible that the variability in development between and within heads in the seed crop is a characteristic of the growing conditions in Natal and that little can be done from the genetical point of view.

Greater uniformity in the seed crop may lead to increased seed yields but the principal gains in seed yield would appear to come from the selecting for better seed-setting. There is evidence that seed set in weeping lovegrass in Natal is never greater than 50 per cent and consequently the potential yield is theoretically reduced by one half. Seed set in many temperate species can be as high as 75 per cent. Selection in weeping lovegrass for a similar figure would undoubtedly increase yields. Again, it is possible that low seed set in Natal may be due to prevailing climatic conditions and not to any internal factor.

The influence of climate on reproductive growth in grasses is profound. In Natal the highly variable growing conditions which exist from year to year appear to have a marked effect on seed production in weeping lovegrass.

Although the present studies give some clues as to the productivity of weeping lovegrass seed crops in Natal and the influence of cultural and management techniques on seed production, they also allowed for an (unintentional) investigation of the effects of climate, and particularly rainfall, on seed production in weeping lovegrass. Lack of moisture in the spring of 1972 had a detrimental

effect on most components of yield that were studied. Seed size and seed viability were particularly affected and, on one occasion (Experiment 6) seedhead production was considerably reduced. In addition the ability of the plant to utilise applied nitrogen appeared to be reduced and forage production in spring was virtually negligible. Surprisingly, seed set was little affected by the dry conditions (Experiment 4).

It was noted that the most consistent nitrogen treatment over the two-year period of study was the application of split dressings of nitrogen in early spring and in late spring, at or close to the onset of reproductive growth in the crop. Although further research is obviously necessary, it would appear that applying nitrogen in this manner may result in consistently high yields each year in a region where seasonal climatic variation is expected by cannot be anticipated.

Irrigation would certainly overcome any variability in rainfall particularly in early spring. However, the economics of irrigating weeping lovegrass seed crops in Natal would need to be studied at some length before any decision was made.

SUMMARY

In 1972 a programme of research was initiated at the University of Natal, in association with the Department of Agricultural Technical Services to study seed production in weeping lovegrass.

A series of experiments were carried out initially to investigate the growth and development of tillers to seed maturity. The age of the tillers was found to have a marked effect on its ability to become fertile and its capacity to produce seed. Approximately 90 per cent of seedheads at seed harvest were produced by tillers which emerged prior to the onset of the winter dormant period. The importance of correct management during the late summer and autumn period is therefore stressed.

In any one year it was also found that the highest orders of tillers that were present in sufficient numbers provided the majority of inflorescences at seed harvest. A decline in inflorescence size was recorded with each successive lower order of tillers of the same age.

The influence of the order of tillers, or the position of the tiller in the plant on the capacity of the inflorescence to produce seed, was investigated further in single plants growing in a glasshouse. Generally, seed production per inflorescence declined with increasing order of succession of tillers in the plant. The primary inflorescences, and the secondary tillers to an even greater extent, generally contained fewer florets and fewer and lighter seeds than the main shoot inflorescence. The capacity of florets to set seed was higher in the main shoot inflorescence than in the lower order tillers and there was a progressive decline in fertility between the lower orders.

Nitrogen had a marked effect on seed yield per inflorescence. Floret number per inflorescence was generally increased when nitrogen was supplied to the plant. Seed size was also considerably increased,

but nitrogen had no effect on the capacity of florets to set seed. The response to nitrogen increased with increasing order of succession of tillers. Nitrogen had little effect on 100 seed mass in the main shoot inflorescence but had a highly significant effect in the secondary inflorescence.

It was found that the nitrogen status of the shoot at inflorescence initiation determined the manner in which the number of florets was increased in the inflorescence. Nitrogen applied during inflorescence development significantly increased the number of florets per spikelet but had no significant effect on spikelet production. On the other hand, the number of spikelets per inflorescence was considerably increased when nitrogen was applied prior to inflorescence initiation but spikelet size was little effected.

It is concluded that the optimum time of nitrogen supply for seed production in individual inflorescences is at, or immediately prior to, the onset of reproductive growth in the tillers.

The study of weeping lovegrass seedhead characteristics was continued in the field in conjunction with a study of the development of the seed crop to maturity. It was found that time of head emergence not only influenced the capacity of seedheads to produce seed but was also responsible for considerable variation in seed maturity within the crop.

Seed development was studied by measuring changes in the fresh mass and dry mass of seed, seed moisture content and the viability of seed. Maximum seed dry mass was generally reached when the moisture content of seeds was between 20 and 25 per cent. Maximum viability was attained prior to the attainment of maximum dry mass.

It is suggested that the pattern of maturation in the crop is reflected to a considerable extent in the moisture content of seed. The range in moisture content, and also seed viability, has given some indication of the variation in seed maturity in the crop not only

between inflorescences but also within individual inflorescences.

Another measure of crop ripeness is the degree of shedding. In the present study seed was retained in the spikelet and not shed until the spikelet was reasonably mature. Shedding increased markedly when seed was close to maximum dry mass and its moisture content had declined to below 30 per cent.

Optimum harvest time is defined as that time when the maximum yield of viable seed has been reached in the crop and is discussed in relation to the contribution made by early-, intermediate- and late-emerged heads. In 1973 the maximum yield of viable seed was obtained 44 days after initial anthesis. At this time the average moisture contents of seed in early-, intermediate- and late-emerged heads were 19 per cent, 22 per cent and 31 per cent respectively. Mean losses due to shedding at this time were 33, 11 and 3 per cent in early-, intermediate- and late-emerged heads respectively. All seed in the crop had achieved maximum viability.

From the data available it is concluded that the relationship between seed mass and seed moisture content is the most reliable and the most consistent index to optimum harvest time.

The influence of the prevailing climate on seed crop development was shown to be an important factor determining the rate of maturity of the crop and therefore the time of harvest.

The prevailing climate, and particularly rainfall, also had a considerable effect on the productivity of the seed crop as shown in a study of the effects of the rate and timing of nitrogen applications on seed production in weeping lovegrass. In 1972, when the spring was considerably dry, the maximum yield recorded was 186 kg/ha. In 1973 growing conditions were more conducive to high productivity and the maximum yield recorded was 474 kg/ha. Although not investigated it is concluded that the reduced yields in 1972 were due to the development of smaller heads which produced fewer and lighter seeds.

Results obtained in this study clearly show that the optimum level of nitrogen for seed production in dense stands of weeping lovegrass growing in an area characterised by high rainfall is about 120 kg N/ha. There was no evidence that the higher rate of 240 kg N/ha led to increased seed yield when compared to the lower rate, and at no time was the higher rate detrimental to plant growth and seed production.

The higher rate did, however, result in the excessive production of forage during seed crop development and in practice this may increase the intensity of lodging resulting in harvesting difficulties and reduced seed yields. In the present study plots were harvested by hand so that lodged heads were harvested with a minimum of disturbance.

The optimum time of application of nitrogen varied depending on the climate. However, under normal growing conditions obtained in 1973, it is concluded that an application following the resumption of growth in spring and prior to the onset of reproductive growth was best for seed production. Autumn-applied nitrogen had little effect on seed production except when given in excessive amounts, and there was no benefit by splitting the annual nitrogen dressing. However, it is noted that the most consistent treatment in both years was the application of nitrogen as split dressings in early spring and late spring. Response to this treatment is discussed in relation to the highly variable and unpredictable seasonal climate experienced in Natal.

Nitrogen applied in late spring in 1973, during initial development of the seedhead had little effect on seed yield but increased the quantity of forage present in the crop at seed harvest.

The influence of forage production on reproductive growth and development in weeping lovegrass was studied in a field experiment designed primarily to determine if both forage and seed production can be successfully integrated in a multi-purpose stand.

The removal of overwintered forage was necessary for good seed production and removal by controlled burning at the resumption of growth in spring in both years had the greatest effect on seed yield. In 1973 a mean yield of 520 kg/ha was obtained following an early spring burn compared with a yield of 419 kg/ha recorded when overwintered forage was removed by mowing.

Early spring controlled burning considerably increased the size of the seedhead population and also increased the seed-producing capacity of individual seedheads. Heading was more uniform after an early spring burn and the implications of this are discussed with reference to the study on seed crop development.

Any defoliation in spring and as late as the onset of reproductive growth in the plot had no detrimental effect on either the production of seedheads or subsequent seed yield. In several instances seed productivity was actually increased, particularly when overwintered forage was not removed early in spring. It is noted that the favourable effects of cutting in spring may be dependent at least in part, on the high level of nitrogen applied (180 kg N/ha) in spring. The results of this study show that if adequate nitrogen is available, forage can be utilised successfully in the spring with no detrimental effect to the potential productivity of the seed crop. In fact, the present data suggests that forage removal in spring in Natal is essential to reduce the quantity of forage in the crop at seed harvest and so reduce the intensity of lodging and remove any harvesting difficulties which may arise as a consequence of excess forage in the crop.

As in the previous study there was considerable variation in the data brought about by the difference in the rainfall for the two years. The results are discussed therefore in terms of climatic variability between both years.

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APPENDIX A

APPENDIX A TABLE 1 Source of variation for the effects of applied nitrogen and position of the tiller in the plant on various components measured

	d.f.	Stem length (cm)		Stem mass (mg)		Inflor. lgth (cm)	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
Reps	4	41		17126		22,5	
Nitrogen (N)	7	268	N.S.	79022	N.S.	29,8	**
Error (a)	28	114		41942		7,9	
Tiller Position (P)	4	7258	**	414652	**	227,8	**
N x P	28	57	N.S.	13965	N.S.	9,0	**
Error (b)	128	76		10997		4,4	
		c.v. = 8,5%		c.v. = 11,9%		c.v. = 5,3%	

Prim. br./inflor.		Spikelets/inflor.		Florets/inflor.		Seed mass/inflor. (mg)	
Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
2,4		7560		169697		2537	
12,1	N.S.	4234	N.S.	956724	**	29379	*
10,4		4410		123305		9897	
307,9	**	62156	**	2418866	**	224044	**
1,9	N.S.	1525	N.S.	100461	N.S.	3135	N.S.
4.6		1351		62837		3003	
c.v. = 6,2%		c.v. = 9,4%		c.v. = 11,4%		c.v. = 14,7%	

N.S. = not significant * = significant at 5% level ** = significant at 1% level

TABLE 2 Source of variation for the effects of applied nitrogen, position of the tiller in the plant and primary branch position on the inflorescence on (a) number of florets per spikelet, (b) floret fertility (%) and (c) 100 seed mass (mg)

Source	d.f.	Florets/spikelet		Floret fertility		100 seed mass (mg)	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
Reps	4	2,08		107		35,4	
Nitrogen (N)	7	9,77	**	326	N.S.	148,3	**
Error (a)	28	2,00		265		32,1	
Tiller Position (P)	4	147,72	**	1157	**	139,2	**
N x P	28	0,98	N.S.	81	N.S.	29,1	*
Error (b)	128	1,00		86		15,6	
Prim. Branch Position (B)	2	0,15	N.S.	128	*	170,8	**
B x N	14	0,20	N.S.	40	N.S.	2,8	N.S.
B x P	28	3,56	**	20	N.S.	8,1	**
B x N x P	56	0,25	N.S.	26	N.S.	1,8	N.S.
Error (c)	320	0,24		35		2,4	
		c.v. = 8,6%		c.v. = 14,1%		c.v. = 3,8%	

N.S. Not significant * Significant at 5% ** Significant at 1%

TABLE 3 Source of variation for the effects of applied nitrogen on the number of fertile and vegetative tillers per plant, the total number of tillers per plant and the DM yield (g) per plant

Source	d.f.	No. Inflors		No. veg. tillers		Total No. tillers		DM yield (g)	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
N Treatments	7	25,3	**	954	**	1175	**	159,0	**
Error	32	3,6		98		102		8,3	
		c.v. = 15,0%		c.v. = 12,1%		c.v. = 10,7%		c.v. = 10,8%	

** Significant at 1%

TABLE 4 Source of variation for the effects of applied nitrogen and position of the tiller in the plants on the components measured.

Source	d.f.	Time ear emerg.		Stem length (cm)		Stem mass (mg)		Inflor. length(cm)	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
Reps	4	22,6		165		150601		13,3	
Nitrogen (N)	7	72,3	*	244	N.S.	70991	N.S.	290,4	**
Error (a)	28	28,1		116		92669		27,1	
Tiller position (P)	4	766,1	**	1325	**	1000668	**	190,1	**
N x P	28	19,2	**	40	N.S.	47608	N.S.	28,3	**
Error (b)	128	8,5		59		30099		5,6	
		c.v. = 6,7%		c.v. = 6,0%		c.v. = 13,3%		c.v. = 6,4%	

Prim. bran./inflor.		Spikelets/Inflor.		Florets/Inflor.		Seed mass/Inflor.(g)	
Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
16,4		28981		1846283		2537	
16,2	N.S.	37069	**	4378618	**	29379	*
8,8		8173		921596		9897	
319,3	**	223978	**	3518889	**	224044	**
3,1	N.S.	8040	**	436337	**	3135	N.S.
2,6		3157		171102		3003	
c.v. = 4,8%		c.v. = 12,4%		c.v. = 13,7%		c.v. = 14,7%	

N.S. Not significant * Significant at 5% ** Significant at 1%

TABLE 5 Source of variation for the effects of applied nitrogen, tiller position in the plant and primary branch position in the inflorescence on (a) florets per spikelet, (b) floret fertility (%) and (c) 100 seed mass (mg)

Source	d.f.	Florets/spikelet		Floret fertility		100 seed mass	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
Reps	4	7,8		170		121	
N Treatments (N)	7	22,7	N.S.	344	N.S.	229	*
Error (a)	28	12,7		359		68	
Tiller position (P)	4	190,5	**	3355	**	1925	**
N x P	28	5,9	N.S.	95	N.S.	34	N.S.
Error (b)	128	5,5		114		24	
Primary Branch position (B)	2	29,2	**	628	**	466	**
B x N	14	4,0	N.S.	25	N.S.	5	N.S.
B x P	8	3,4	N.S.	144	**	14	*
B x N x P	56	4,1	N.S.	25	N.S.	4	N.S.
Error (c)	320	4,9		33		5	
		c.v. = 32,3%		c.v. = 17,2%		c.v. = 6,1%	

N.S. Not significant * Significant at 5% ** Significant at 1%

TABLE 6 Source of variation for the effects of applied nitrogen, tiller position in the plant and spikelet position on the basal primary branch on (a) floret numbers per spikelet, and (b) floret fertility (%)

Source	d.f.	Florets/spikelet		Floret fertility	
		Mean Square	Signif. F value	Mean Square	Signif. F value
Reps	4	11,2		1355	
N Treatments (N)	7	36,8	**	1074	N.S.
Error (a)	28	7,0		1104	
Tiller position (P)	4	210,5	**	11664	**
N x P	28	3,3	N.S.	201	N.S.
Error (b)	128	2,1		368	
Spikelet position (S)	2	63,1	**	1675	**
S x N	14	1,0	**	70	N.S.
S x P	8	0,7	N.S.	155	N.S.
S x N x P	56	0,4	N.S.	84	N.S.
Error (c)	320	0,4		95	
		c.v. = 9,1%		c.v. = 33,3%	

N.S. Not significant

* Significant at 5%

** Significant at 1%

TABLE 7 Source of variation for the effects of applied nitrogen on the number of fertile and vegetative tillers per plant, the total number of tillers per plant and herbage DM yield per plant (g)

Source	d.f.	Fertile tillers		No. Veg. tillers		Total No. tillers		Herbage DM (g)	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
N Treatments	7	61,3	**	4138	**	3667	**	321	**
Error	32	5,9		197		968		9	
		c.v. = 14,3%		c.v. = 16,0%		c.v. = 21,6%		c.v. = 14,5%	

** Significant at 1%

APPENDIX B

TABLE 1 Source of variation for (a) seed yield (kg/ha), (b) 1000 seed mass, and (c) ratio of reproductive to vegetative growth at seed harvest (1972)

Source	d.f.	Seed Yield		1000 seed mass		Rep:Veg Growth	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
Replicates	3	14549		12		0,047	
Rate N	1	8	N.S.	5	N.S.	0,005	N.S.
Time N	6	2791	**	475	**	0,062	N.S.
Rate x Time	6	1006	N.S.	166	**	0,033	N.S.
Remainder	1	5365	**	506	**	0,383	**
Treatments	14	2011	*	311	**	0,069	N.S.
Error	42	810		46		0,040	
		c.v. = 19,7%		c.v. = 2,6%		c.v. = 30,0%	

TABLE 2 Source of variation for (a) number of seedheads per m^2, (b) mass of 100 culms (g), and (c) DM yield (kg/ha) at seed harvest (1972).

Source	d.f.	Seedheads/m^2		100 culm mass		DM yield	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
Reps	3	32576		1435		120779	
Rate N	1	453211	N.S.	2	N.S.	85750	N.S.
Time N	6	135005	N.S.	185	**	111073	**
Rate x Time	6	34330	N.S.	78	N.S.	6480	N.S.
Remainder	1	58098	N.S.	26	N.S.	777212	**
Treatments	14	109094	N.S.	115	**	112020	**
Error	282	124305		48		29325	
		c.v. = 38,0%		c.v. = 14,6%		c.v. = 25,4%	

N.S. Not significant

* Significant at 5%

** Significant at 1%

TABLE 3 Source of variation for (a) seed yield (kg/ha), (b) ratio of reproductive to vegetative growth at seed harvest, and (c) DM yield (kg/ha) 8 weeks after seed harvest (1973).

Source	d.f.	Seed Yield		Rep:Veg Growth		DM yield (8 wks)	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
Reps	3	12917		0,05		34272	
Rate N	1	88	N.S.	1,59	**	47084	*
Time N	6	20344	**	0,78	**	8878	N.S.
Rate x Time	6	6840	N.S.	0,04	N.S.	508	N.S.
Remainder	1	57106	**	0,08	N.S.	76926	**
Treatments	14	15735	**	0,47	**	12880	N.S.
Error	42	4636		0,12		8799	
		c.v. = 19,3%		c.v. = 20,0%		c.v. = 18,2%	

TABLE 4 Source of variation for (a) number of seedheads per m^2, (b) 1000 seed mass (mg), and (c) germination of seed (%) (1973).

Source	d.f.	Seedheads/m^2		1000 seed mass		Seed germ. (%)	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
Reps	3	738416		523		13,0	
Rate N	1	51030	N.S.	909	*	47,9	*
Time N	6	457976	**	2944	**	97,4	**
Rate x Time	6	253668	*	1813	**	102,8	**
Remainder	1	1517112	**	10538	**	0,2	N.S.
Treatments	14	397929	**	2857	**	89,2	**
Error	282	95630		139		10,4	
		c.v. = 33,9%		c.v. = 3,7%		c.v. = 3,4%	

N.S. Not significant

* Significant at 5%

** Significant at 1%

TABLE 5 Source of variation for (a) 100 culm mass (g) and (b) DM yield (kg/ha) at seed harvest (1973)

Source	d.f.	100 culm mass (g)		DM yield seed harvest	
		Mean Square	Signif. F value	Mean Square	Signif. F value
Reps	3	238		681540	
Rate N	1	250	*	866700	**
Time N	6	133	*	586369	**
Rate x Time	6	56	N.S.	29538	N.S.
Remainder	1	295	*	1271160	**
Treatments	14	120	*	416664	*
Error	282	58		60643	
		c.v. = 15,3%		c.v. = 28,2%	

TABLE 6 Source of variation for the 'Production Efficiency Factor' in (a) 1972 and (b) 1973

Source	d.f.	1972		1973	
		Mean Square	Signif. F value	Mean Square	Signif. F value
Reps	3	0,03		0,44	
Rate N	1	0,37	**	3,31	**
Time N	6	0,13	*	0,97	**
Rate x Time	6	0,07	N.S.	0,50	N.S.
Error	39	0,05		0,27	
		c.v. = 90,5%		c.v. = 67,6%	

N.S. Not significant

* Significant at 5%

** Significant at 1%

TABLE 7 Source of variation for components of inflorescence size and the seed productivity of the inflorescence (1973)

Source	d.f.	Inflor. length (cm)		Prim. bran./inflor.		Spikelets/inflor.	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
Reps	3	10,6		1,78		258	
Treatments	3	41,8	**	14,22	**	7792	**
Error	73	2,7		1,28		292	
		c.v. = 8,5%		c.v. = 4,9%		c.v. = 10,5%	

		Florets per spikelet		Florets per inflor.		Floret fert. (%)	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
Reps	3	0,19		7721		68	
Treatments	3	10,38	**	419595	**	117	**
Error	73	0,39		14400		13	
		c.v. = 10,2%		c.v. = 12,3%		c.v. = 7,3%	

** Significant at 1%

APPENDIX C

TABLE 1 Source of variation for yield of cleaned seed (kg/ha) (1972)

Source	d.f.	Mean Square	Signif. F value
Columns	3	2183	
Rows	3	2578	
Main Plot Treatments (M)	3	15832	*
Error (a)	6	2818	
Subplot Treatments (S)	1	20	N.S.
M x S	3	334	N.S.
Error (b)	12	763	
		c.v. = 18,45%	

TABLE 2 Source of variation for number of seedheads per m^2 and 100 culm mass (g) (1972)

Source	d.f.	No. heads per m^2		100 culm mass(g)	
		Mean Square	Signif. F value	Mean Square	Signif. F value
Columns	3	9929		230,4	
Rows	3	113412		195,0	
Main Plot Treatments (M)	3	703531	**	431,4	N.S.
Error (a)	6	53934		257,9	
Subplot Treatments (S)	1	1742	N.S.	17,6	N.S.
M x S	3	4694	N.S.	18,4	N.S.
Error (b)	140	29273		117,0	
		c.v. = 43,5%		c.v. = 17,8%	

N.S. Not significant

* Significant at 5%

** Significant at 1%

TABLE 3 Source of variation for (a) forage yield at seed harvest (kg DM/ha), (b) ratio of reproductive to vegetative growth at seed harvest (1972

Source	d.f.	(a) DM yield		(b) R:V Growth	
		Mean Square	Signif. F value	Mean Square	Signif. F value
Columns	3	4385		0,036	
Rows	3	42466		0,264	
Main Plot Treatments (M)	3	23283	N.S.	0,829	**
Error (a)	6	19901		0,083	
Subplot Treatments (S)	1	416769	**	1,096	**
M x S	3	65490	*	0,003	N.S.
Error (b)	140	19440		0,067	
		c.v. = 24,3%		c.v. = 56,5%	

TABLE 4 Source of variation for the forage DM yield at the second spring cut (subplot) treatment (1972)

Source	d.f.	Mean Square	Signif. F value
Columns	3	2268	
Rows	3	2971	
Treatments	3	72029	**
Error	70	2881	
		c.v. = 23,7%	

TABLE 5 Source of variation for yield of cleaned seed (kg/ha)(1973)

Source	d.f.	Mean Square	Signif. F value
Columns	3	17311	
Rows	3	41498	
Main Plot Treatments (M)	3	119955	**
Error (a)	6	11099	
Subplot Treatments (S)	3	20525	*
M x S	9	15504	*
Error (b)	36	5300	
		c.v. = 18,0%	

N.S. Not significant

* Significant at 5%

** Significant at 1%

TABLE 6 Source of variation for (a) number of seedheads per m^2, (b) 1000 seed mass (mg) and (c) germination capacity (%) of seed (1973)

Source	d.f.	No. heads per m^2		1000 seed mass		Germ. capacity	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
Columns	3	110770		355		93,5	
Rows	3	463533		6797		144,8	
Main Plot Treatments (M)	3	6048037	**	3877	N.S.	153,9	N.S.
Error (a)	6	182449		3014		95,3	
Subplot Treatments (S)	3	828798	**	2675	**	63,8	**
M x S	9	369499	**	347	**	24,7	N.S.
Error (b)	292	105947		102		13,5	
		c.v. = 37,2%		c.v. = 3,4%		c.v. = 4,0%	

N.S. Not significant * Significant at 5% ** Significant at 1%

TABLE 7 Source of variation for (a) mass of 100 culms (g), (b) DM yield at seed harvest (kg/ha) and (c) ratio of reproductive to vegetative growth at seed harvest (1973).

Source	d.f.	(a) 100 culm mass		(b) DM yield		(c) R:V Growth	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
Columns	3	322		75892		0,473	
Rows	3	1131		112526		0,669	
Main Plot Treatments (M)	3	2427	**	704903	**	23,269	**
Error (a)	6	81		35299		0,706	
Subplot Treatments (S)	3	6355	**	385525	**	0,855	*
M x S	9	108	N.S.	31339	N.S.	1,106	**
Error (b)	292	106		12836		0,269	
		c.v. = 17,6%		c.v. = 23,3%		c.v. = 44,7%	

N.S. Not significant * Significant at 5% ** Significant at 1%

TABLE 8 Source of variation for (a) total DM yield (kg/ha) and (b) DM yield (kg/ha) at each subplot mowing (1973)

Source	Total DM yield			Subplot DM yield		
	d.f.	Mean Square	Signif. F value	d.f.	Mean Square	Signif. F value
Columns	3	125309		3	9715	
Rows	3	92200		3	27913	
Main Plot Treatments (M)	3	4322581	**	3	2305889	**
Error (a)	6	51196		6	12367	
Subplot Treatments(S)	3	1476112	**	2	782250	**
M x S	9	99174	**	6	31506	*
Error (b)	292	14153		216	3746	

c.v. = 15,5% c.c. = 16,2%

* Significant at 5% ** Significant at 1%

TABLE 9 Source of variation for components of inflorescence size and seed producing capacity of the inflorescence (1973)

	d.f.	Culm length (cm)		Inflor. lgth (cm)		Prim. Br./Inflor.	
		Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
Columns	3	144		10,7		5,6	
Rows	3	195		1,8		4,5	
Treatments	3	157	N.S.	26,7	**	32,7	**
Error	70	178		2,3		1,7	
		c.v. = 12,2%		c.v. = 6,9%		c.v. = 5,4%	

Spikelets/inflor.		Florets/spikelet		Florets/inflor.		Floret fert. (%)	
Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value	Mean Square	Signif. F value
2092		0,98		183917		133	
1484		1,02		38107		28	
12505	**	11,57	**	123108	*	17	N.S.
1318		0,38		37558		16	
c.v. = 16,3%		c.v. = 10,4%		c.v. = 15,2%		c.v. = 9,7%	

N.S. Not significant * Significant at 5% ** Significant at 1%