

Growth of the grass plant in relation to seed production

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ABSTRACT. The specialized management techniques required for successful seed production in grasses must be based on a sound understanding of the physiology of the plant.

Seed yields depend strongly on the number of ears per unit area, and early-formed tillers are largely responsible for producing these ears. Numbers of fertile tillers are generally increased by early spring applications of nitrogen fertilizer and autumn grazings, but can be seriously reduced by defoliation after floral initiation and ear development have started.

Seed yields from later formed tillers can be improved by using nitrogen fertilizer to increase the numbers of seeds per ear and the mean seed weight.

Key words: Seed production, grasses, fertile tillers, nitrogen, grazing.

INTRODUCTION

In a recent paper (Ong *et al.*, 1978) the opinion was expressed that "it is surprising that the scientific literature on seed production in grasses is so limited". By comparison with wheat and other cereals this statement is undoubtedly true, but at the same time it is hardly surprising that research on grasses has predominantly been concerned with the production of forage rather than of seed. Although selection for improved seed yields is possible (Bean, 1972), it is not at all easy to achieve high levels of leaf and seed production in the same cultivar, and in fact there is often a negative relationship between these two components. Successful seed production in grasses therefore requires specialized management techniques, and these need to be based on a thorough understanding of the physiological principles involved. Any consideration of herbage seed production must begin with a study of the development of the plant and the effects of the environment upon it.

STAGES OF DEVELOPMENT

Before flower induction has occurred and as long as the day length is not adequate to cause inflorescence initiation, perennial grasses remain in the vegetative condition. The shoot apex continues to cut off new leaf primordia which unfold as foliage leaves at a rate depending on temperature and other environmental conditions. There is no stem elongation, and new tillers tend to appear, especially during early autumn.

In perennial ryegrass (*Lolium perenne* L.) and cocksfoot (*Dactylis glomerata* L.), but also in other perennial species, a profound physiological change occurs during the winter when, under the influence of low temperatures and short days, floral induction occurs. No morphological or biochemical change can be detected at the time, but tillers thus induced (or vernalized) are now capable, when temperature becomes favourable for growth, to respond to increasing photoperiod by initiating reproductive structures. When this occurs the shoot apex increases rapidly in length and forms primordia which are no longer destined to become foliage leaves. Instead, the primordia develop into spikelets in those grasses whose inflorescence is a spike, or, in panicle-producing species, they develop into branches which subdivide and bear spikelets. Each spikelet primordium differentiates further to produce individual florets, complete with lemma, palea, lodicules, anthers, stigmas and ovary. Meanwhile the internodes below the shoot apex elongate successively, pushing the developing inflorescence upwards within the encircling leaf sheaths. The onset of floral initiation depends on the photoperiodic requirement of each cultivar, but it may be modified to a certain extent by temperature levels in the spring. Similarly, the interval between initiation and the start of inflorescence emergence depends on the same variables but is usually

of the order of 25 to 40 days. Anthesis or exertion of the anthers occurs some 25 to 35 days later, and seed development takes approximately another 30 to 40 days.

YIELD COMPONENTS

Although external factors are capable of affecting the physiological events leading up to seed formation, the more important question from the point of view of management is whether and to what extent the components of yield can be modified by appropriate treatment. Before reviewing the present state of knowledge in this respect it is desirable and necessary to discuss the relationship of these components to seed yield as a whole so as to isolate those of most importance. In wheat and other cereals there is good evidence to show that yield depends primarily on the number of

grains produced per unit area, and that weight per grain varies only within relatively narrow limits (Langer and Dougherty, 1976). In practice it is the number of ears which has the most important influence on yield, as shown by the very high positive correlations which we have obtained consistently. Even though the effect of other yield components should not be underestimated, the evidence suggests that in perennial grasses the situation may well be similar. This is certainly borne out by the data of Field-Dodgson (1971), who showed that in Ruanui perennial ryegrass, fertilized at the rate of 45, 90 or 180 kg/ha given at the beginning of September or November or at both dates, total seed yield was highly significantly correlated with the number of ears per unit drill row (Fig. 1). Similar results have been obtained by Spiertz and Ellen (1972). In other species,

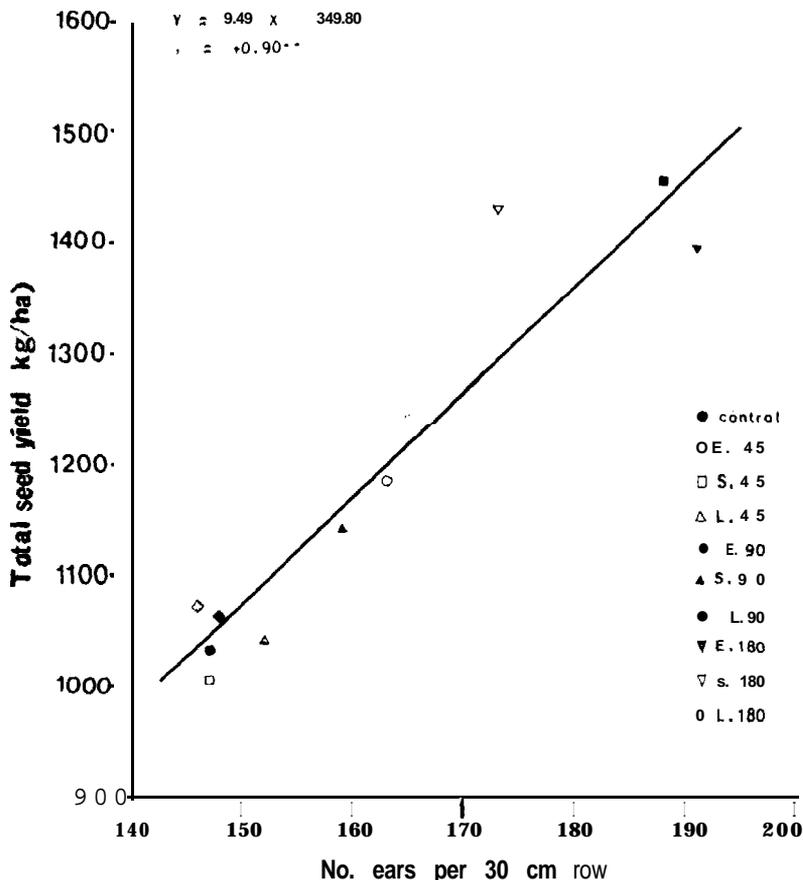


FIG. 1: The relationship between total seed yield and the number of ears per 30 cm length of row in Ruanui tyegrass (from Field-Dodgson 1971).

especially those bearing panicles, and in other conditions, this relationship may not be as clearly developed, but it is nevertheless strong enough to place considerable emphasis on the importance of fertile tiller production.

FERTILE TILLERS

Tillering is a continuous process, and thus at any one time the grass plant comprises a collection of tillers, differing in age, position on the plant and size. This will be true at the critical periods previously referred to when floral induction and initiation take place, and it follows that only a proportion of all tillers is likely to become fertile, while the rest will be subjected to increasing competitive stress, as stem elongation and seed development raise the demand for assimilates in the fertile ones. Tillers which by virtue of position and size are able to become reproductive do not generally support small, vegetative tillers which are attached to them, and these are often badly placed for active photosynthesis in the bottom of the canopy and eventually die (Ong *et al.*, 1978). In cocksfoot, timothy (*Phleum pratense* L.) and meadow fescue (*Festuca pratensis* Huds.) it is the tillers present in early autumn which make up the bulk of the seed crop the following year (Table 1), and this is of course highly important when it comes to the timing of fertilizer applications designed to raise seed yields.

TABLE 1: PERCENTAGE COMPOSITION OF COCKSFOOT EARS AT TIME OF HARVEST (after Lambert, 1963)

<i>Mm/11 of Tiller Origin</i> (<i>Northern Hemisphere</i>)	<i>% Ears at Harvest</i>
< August	73.3
September	3.4
October	1.8
November/December	12.0
January	3.0
Not labelled	2.9

These are British experimental results, but they are closely matched by data obtained in New Zealand. For example, Hill and Watkin (1975a) found that in a second-year crop of Ruanui perennial ryegrass only 3% of the ears present at harvest could be attributed to

tillers which appeared in September or later, and thus the bulk of the seed was produced by tillers formed in late summer or autumn. In Kahu timothy, 9% of the fertile tillers were produced in the spring, but in prairie grass (*Bromus catharticus* auct.) none of the spring tillers contributed to yield. However, in ryegrass it seems to be possible for a reasonably large proportion of spring-formed tillers to become fertile, as shown by Field-Dodgson (1971) in a first-year crop of Ruanui in which 85% of tillers present before 20 August became ear-bearing, as expected, but where in addition 64% of tillers appearing between then and the end of September also produced ears at harvest. Later spring tillers almost invariably remained vegetative or died. In annual grasses still greater flowering of spring tillers is possible. For instance, in Tama Westerwolds ryegrass (*Lolium multiflorum* Lam.) some 25% of the ear crop may be derived from spring tillers, and spring cutting at a time when shoot apices are removed can be followed by almost complete replacement of the older tillers (Davies, 1969).

If we are justified in concluding that seed yields depend strongly on the number of ears and if early-formed tillers are largely responsible for producing these ears, the next question to raise is how to influence tiller number and performance. This can be achieved most readily through the use of fertilizer nitrogen, and it is fortunate that at least in ryegrass the effects of time and rate of N are well documented. The general conclusion to emerge appears to be that nitrogen applied in the spring raises seed yield, largely through stimulating tiller formation and possibly survival, but apparently not by influencing the proportion of tillers becoming fertile. The range of values which may be obtained are well shown by the data obtained by Field-Dodgson (1971) in a first-year crop of Ruanui perennial ryegrass fertilized before floral initiation, after ear emergence or by split application (Table 2).

Early nitrogen applied at 90 kg/ha or more increased the number significantly and consequently raised seed yields. The percentage of ear-bearing tillers was not affected. Broadly similar results have been published elsewhere showing response to nitrogen mainly through

TABLE 2: EFFECT OF NITROGEN ON THE MEAN NUMBER OF EARS PER 30 CM OF DRILL ROW IN RUANUI RYEGRASS (after Field-Dodgson, 1971)

Rate of N (kg/ha)	Time of N application			Rate mean
	Early	Split	Late	
45	163	147	152	154
90	188	159	148	165
180	191	173	146	170
Time mean	181	160	149	

S.E. = ± 7.2 .

increased fertile tiller numbers, even though variability in the field is such that significant differences are not always easily established. Earliness of application may not always be very critical, as shown by Hebblethwaite and Ivins (1978), who found no difference in seed yields of S24 and S23 perennial ryegrass in response to nitrogen applied at different times between apical initiation and first ear emergence. Later-applied N had less effect. The optimum quantity of applied nitrogen will depend on the amount of N available in the soil. Under British conditions it was found to be 80 kg/ha where soil N was high (75 kg/ha), but 120 kg/ha where it was low (30 kg/ha) (Hebblethwaite and Ivins, 1977). However, raising the amount of fertilizer nitrogen still further may reduce yields through lodging of the crop. Under these conditions the number of fertile tillers is not increased, possibly because of unfavourable partition of assimilates between leaf growth and seed production, greater competition for assimilates in a lodged crop, and perhaps through inadequate pollination. As regards other environmental conditions, Spiertz and Ellen (1972) have shown that light intensity has a large effect on tillering, and Ryle (1967) has demonstrated that reduced light energy retards or inhibits ear initiation and decreases the number of fertile tillers.

There is little critical information on the effect of water supply on fertile tiller numbers. Although irrigation could be beneficial on very shallow soils, the time at which potentially fertile tillers arise does not generally coincide with periods of water stress.

One of the factors affecting seed yields which can be manipulated in the field is the time of cutting or grazing. For example, Roberts

(1966), working in Wales, has shown that more seed was obtained from stands of four different perennial ryegrass cultivars if they were grazed in the autumn, and in fact similar results were obtained after defoliation at any time up to early winter. However, in the spring, grass seed stands should not be grazed after a critical date which depends on the time of floral initiation and ear development. One possible exception to this rule which applies to ryegrass is the beneficial effect of early spring grazing to reduce the incidence of lodging. Both the increase in yield after autumn grazing and the much more serious drop if grazed after the critical date in the spring are attributable mainly to the number of fertile tillers at harvest. Some of these responses can be quite dramatic, as for example in S23 perennial ryegrass maintained at a medium level of fertilizer N in which the number of inflorescences rose by about 20% when grazed at the end of April. Experience in New Zealand is in broad agreement with these results, especially in relation to the date of closing paddocks for seed production. If seed stands are grazed early in the spring, then it becomes necessary to stimulate recovery growth by applications of nitrogen.

NUMBER OF SEEDS PER EAR

Although numbers of ears per unit area are the primary determinant of yield, the number of seeds produced by each ear is not entirely unimportant. Considerable differences can occur depending on the age and position of the tiller, particularly in plants grown from seed, as shown by results obtained in Manawa ryegrass (*Lolium X hybridum* Hausskn.) grown in controlled growth cabinets (Table 3). The effect of nitrogen is also well shown.

TABLE 3: NUMBER OF FERTILE FLORETS PRODUCED BY MANAWA RYEGRASS TILLERS IN GROWTH CABINETS AT 20°/14°C (after Field-Dodgson, 1971)

	Main	Stern	Tiller 1	Tiller 2
Control		101	96	86
Nitrogen (80 kg/ha equivalent)		131	127	118

These relationships play a part also under field conditions and they apply not only in the first harvest year. This has been shown by Hill

and Watkin (1975a), who measured the number of florets in groups of ears emerging on successively later days in the same crop. In perennial ryegrass and prairie grass the number of seeds per ear was just over 150 in the first emergence group but declined to about 80 in the fourth group emerging 8 weeks later. Timothy ears showed much less extreme differences. Spring grazing generally depressed seed number per ear, but nitrogen application increased it. The nitrogen effect was largely in terms of more florets per ear rather than an increase in the number of spikelets. Field-Dodgson (1971) also found large differences attributable to tiller age: 99 seeds per ear in early tillers and only 63 in those appearing in the spring. In cocksfoot, nitrogen has similarly been shown to increase the number of seeds per inflorescence (Lambert, 1963). Seasonal variation in floret fertility may be attributable to differences in temperature during fertilization of the ovule, as shown in controlled conditions by Akpan and Bean (1977).

In addition to these positive effects, there is also a negative aspect of seed number, and this relates to losses of seed through shedding. Depending on time of harvesting considerable quantities of seed can be lost in this way, amounting to 30 to 40 % in severe cases. Losses of this magnitude can be reduced by earlier cutting (Hill and Watkin, 1975b) and greater uniformity of ripening among tillers, although in the long run it remains a plant breeding problem to achieve greater seed retention, as has occurred in wheat for example.

MEAN SEED WEIGHT

In controlled environments the mean weight per seed in ryegrass and meadow fescue has been shown to be greatest at relatively low temperatures (15/10°C), and this resulted in slightly heavier seedlings being produced (Akpan and Bean, 1977). Those and other responses to temperature may possibly explain part of the year-to-year variations which are very common. Mean seed weight is also improved by late applications of nitrogen, as shown in S24 perennial ryegrass topdressed during ear emergence (Hebblethwaite and Ivins, 1978). The increases achieved were only

of the order of 8 to 9%, and similarly the differences among the first few tillers are also not very large. For example, mean 100-seed weights were 217 mg in the main stem, 214 mg in tiller 1 and 207 mg in tiller 2 of Manawa ryegrass plants grown in growth cabinets (Field-Dodgson, 1971). However, in field crops of ryegrass greater variation appears to exist, in that ears emerging late may have smaller seeds. This was found by Anslow (1964), who measured significantly lower seed weights in tillers producing ears 2 weeks or more later than the main crop. Late ears thus contribute not only smaller but also fewer seeds, and to wait for them to mature may not be the best policy, if in the meantime seed shedding begins in the earlier and more productive tillers.

CONCLUSION

Compared with wheat and other cereals, seed production in pasture grasses is governed by more complex factors. Consequently the production of good seed yields requires a high level of technical skill based on a sound knowledge of the scientific principle involved. The main characteristic of grass seed production is brought about by prolonged periods of tillering and by a considerable range in the size and position of the tillers. Fertile tiller numbers are the most important component of yield, and hence any management system that is designed to stimulate early tillering and tiller survival should be attended by improved yields. These early tillers do not only contribute the major proportion of the crop of ears, but individually they are also larger and thus more valuable. However, in spring tillers and after grazing there are differences in seed number and in size which play a significant part. All these aspects require close study, and it is to be hoped that the proceedings of this conference will provide useful information for New Zealand growers so that they can increase their seed production through a better understanding of the growth of the grass plant.

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