Developmental and Physiological Aspects of Seed Production in Herbage Grasses

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ABSTRACT

The developmental and physiological factors determining the potential seed yield of the grass inflorescence are discussed, especially in relation to the productivity of florets. Analysis of the difference between potential and actual seed yield of the inflorescence reveals that a large proportion of florets are unproductive; many set seed but then abort developing seeds. The physiological factors influencing seed abortion are not well understood but nutritional factors, particularly carbohydrate supply, may be important. The inflorescence is the major source of assimilate for seed growth and development, but some evidence suggests that vegetative tillers may compete with developing seeds for assimilate produced by the inflorescence. Such competition may be important in initiating, at least in part, the abortion of some developing seeds. The productivity of florets is increased by the application of certain plant growth regulators and fungicides, and this may be related to an improvement in the supply of assimilate to developing seeds.

Additional index words: **florets, seed set, seed abortion, seed growth, source-sink relations, ^{14}C-assimilate, growth regulators, fungicides.**

INTRODUCTION

The reproductive potential of the grass inflorescence is set by the number of spikelets and the number of fertile florets per spikelet. The degree to which this potential is realized in terms of yield depends on the proportion of florets that produce seed and the size of individual seed. Both herbage grasses and cereals show a characteristic pattern of under utilization of reproductive potential in that the number of seed produced per inflorescence is substantially less than the number of fertile florets, and this is especially the case in grasses where there may be a sevenfold difference between floret and seed numbers (Hebblethwaite et al., 1980). This emphasises the importance of the developmental processes occurring from anthesis onwards, namely pollination, fertilization, seed set and seed growth, and there is good evidence that deficiencies in each of these sequential steps restricts potential seed yield of the inflorescence (Hill, 1980). Agronomic studies suggest that there is a close relationship between the number of seeds produced per unit area and the yield of seed, and that this is primarily related to the number of seeds per spikelet rather than to the number of fertile tillers produced by the crop (Hebblethwaite et al., 1982; Hampton and Hebblethwaite, 1983). However, in the field it is evident that seed production falls far short of its potential due to the lodging of the crop canopy, as large increases in seed yield result if lodging is prevented or reduced (Hebblethwaite and Ivins, 1978; Hampton and Hebblethwaite, 1985a).

This paper will consider some of the phsysiological and developmental factors underlying the establishment of the yield potential of the grass inflorescence, and the subsequent utilization of this potential especially with respect to the fate of fertile florets.

The Components of Yield

In perennial grasses the population of flowering shoots is composed of tillers of varying age and origin, and these display a considerable range of yield potential. Studies on the yield components of the inflorescence of *Lolium perenne* have revealed relatively small differences in spikelet number between inflorescences of tillers appearing during the summer and winter months, but large differences in the number of florets formed per spikelet (Ryle, 1964; Hill and Watkin, 1975; Colvill and Marshall, 1984). In this species up to 14 florets may be produced per spikelet, but not all of these become fertile and produce a seed. The grass inflorescence thus produces far more florets than seeds and this is evident from the results shown in Fig. 1 where the inflorescences of successively appearing primary tillers display a progressive decline in the numbers of florets and seeds, with just under three-quarters of all florets bearing a seed. The difference between floret and seed numbers is less in later than earlier produced tillers, e.g. 65% of florets yield seeds in the first two primary tillers (T1 and T2) compared with almost 80% for the T7-T11 group, thus spikelets with relatively few florets tend to be more productive than those with a higher number of florets.

Despite these differences the seed yield of the inflorescence of the main shoot and early primary tillers is significantly greater than that of later appearing primary tillers as they produce many more seeds. This developmental pattern reflects the relationship between the time of tiller appearance and its reproductive potential, and also emphasizes the hierarchical structure of the reproductive capacity of the tillers of an individual plant, as shown by Darwinkel (1978) for winter wheat.

Observations on the pattern of floret production within an inflorescence of ryegrass have shown that the number of florets per spikelet varies relatively little with position, but that in certain cultivars the mid-region of the ear tends to be more productive than basal and tip regions (Burbidge et al.,

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1978). The percentage of florets setting seed is more or less independent of spikelet position, but where lodging occurs there is a marked profile of decreasing seed production per spikelet from the base to the tip of the ear (Burbidge et al., 1978). The latter observation matches the normal pattern of floret production in branching inflorescences foot and meadow fescue where the branches at the base of the inflorescence develop many more florets than those in the mid and apical regions (Ryle, 1964). This difference in floret distribution in these species is particularly evident in inflorescences borne by summer produced tillers compared with those of tillers appearing in early spring.

An analysis of reproductive development at the level of the tiller apex allows some explanation for the differences in spikelet and floret production in inflorescences of tillers of different age. As temperate grasses such as *L. perenne* initiate inflorescences in long days following vernalization (Langer, 1979), tillers appearing in the summer initiate spikelet primordia at more or less the same time as later appearing tillers and so have only a slightly earlier date of inflorescence emergence (Anslow, 1963; Ryle, 1964). Thus differences in spikelet number between tillers arising at different times primarily reflect differences in the size of the tiller apex, i.e. the availability of axillary sites for spikelet primordia to be laid down. As leaf primordia tend to accumulate with time in vegetative tillers (Langer, 1979) and as spikelet primordia arise in the axils of leaf primordia, then at the onset of spikelet initiation tillers appearing in summer and autumn will have additional sites for spikelets to develop compared with later appearing tillers (Ryle, 1964). The degree to which the apex continues to elongate to produce further sites for spikelet primordia is also important in determining final spikelet number, but it is not clear if this differs in tillers appearing at different times of the year.

In field experiments the application of nitrogen fertilizer in the spring has relatively little effect on spikelet production but greatly influences floret production, the greater the supply the higher the number of florets per spikelet (Hill and Watkin, 1975; Hebblethwaite and Ivins, 1977, 1978.) It therefore seems likely that the greater floret number of spikelets from summer appearing tillers, compared with later appearing tillers, reflects the greater availability of nitrogen within the older and correspondingly larger tillers during the critical period of floret differentiation. On the other hand, as shading at this time has been found to reduce the number of florets produced per spikelet (Ryle, 1966, 1967) differences in floret production may also reflect the availability of assimilate for floret development, with older tillers able to contribute assimilate more readily than smaller, younger tillers. This would particularly be the case if the latter become shaded within the crop canopy; alternatively some assimilate utilized by the differentiating apex may be derived from the seasonal decline in fructan level that occurs prior to the commencement of spring growth (Pollock and Jones, 1979; Pollock, 1981), in which case younger tillers might be expected to have a smaller pool of accumulated fructan reserve than older tillers.

Seed Set and Seed Development

As previously described many florets are unproductive. The reasons for this are not readily resolved as there is little information on the proportion of florets that are innately sterile, or those that are fertile but are not successfully pollinated or fertilized, or those that become fertilized but abort embryos or developing seeds. The situation is further complicated by the fact that some mature seeds may be lost by shedding prior to harvest. These uncertainties can only be resolved by detailed observations on the development and

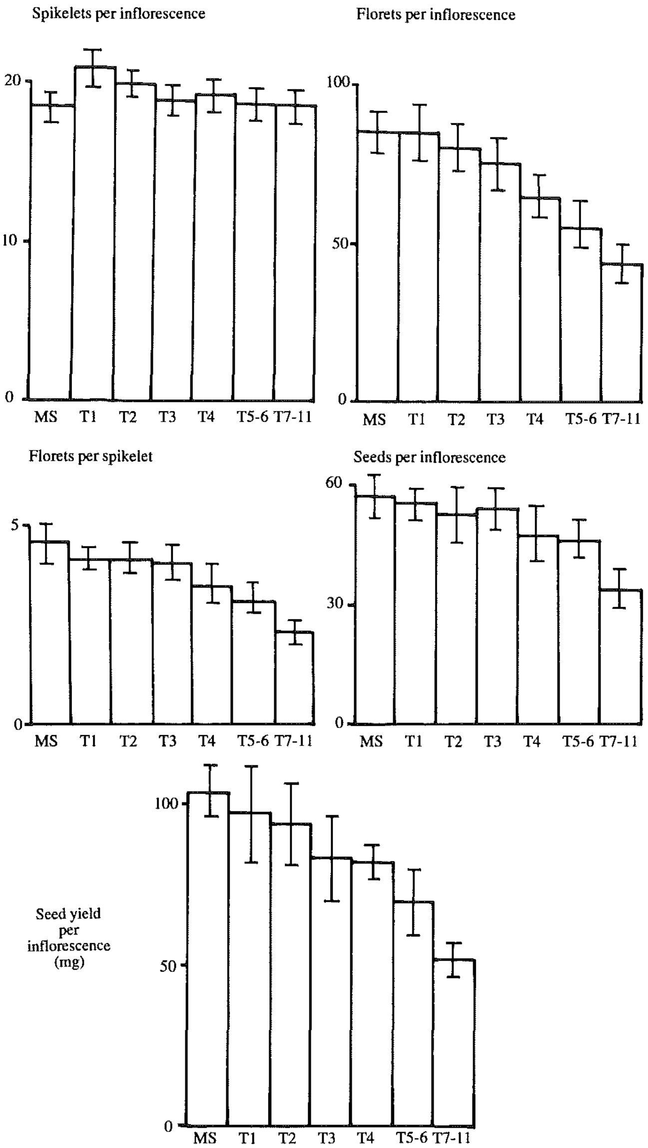

Figure 1. The components of seed yield and seed yield per inflorescence in relation to the identity of primary tillers in *L. perenne* (+ S.E.). MS = main shoot; T1 - T11 = primary tillers arising from the axillary buds of main shoot leaves 1-11.

fate of individual florets with time from the emergence of the inflorescence to its maturation.

Agronomic studies on the effects of lodging on seed production, where seed yield may be reduced by as much as 60%, have however provided some pertinent data on the capacity of florets to produce harvestable seed (Burbidge et al., 1978). Examination of florets from peak anthesis to harvest has revealed that about 60% of the florets set seed within three weeks (i.e. they are successfully pollinated and fertilized), but that by the final harvest after 4-5 weeks only 40-50% of these yield seed. Thus many more seeds are set than are harvested and the major proportion of this loss can be attributed to the abortion of developing seeds. It is not clear precisely which seeds are most prone to abortion, i.e. their position within the various spikelets.

In general the reduction in the number of seeds that initially develop to a level that can be supported to maturity seems a common feature of the reproductive biology of many species, and may account for the relative constancy of seed size observed in plants growing in a range of stressed conditions (Harper, 1977). Silvertown (1982) has suggested that florets which abort their developing seeds or fruits play an important role in reproduction by acting as 'pollen donors' and thereby maximizing the pollen production of the inflorescence, their female function being redundant. It thus seems probable that the loss of developing seeds by abortion is regulated by some internal control system and Burbidge et al. (1978) suggested that this might be related to a shortfall in the supply of substrates to sustain seed growth, or to the involvement of a hormonal mechanism inhibiting the growth and development of certain seeds within each spikelet.

Within an individual spikelet in ryegrass there is a marked decline in the capacity of florets to set seed from the basal to the distal floret, with basal florets tending to produce heavier seeds than distal ones (Anslow, 1963, 1964; Burbidge et al., 1978). These patterns of development suggest that there may be competition for assimilate or mineral nutrients within the spikelet, with the earlier maturing basal florets developing at the expense of distal florets, i.e. the latter may be more susceptible to seed abortion. There is some evidence that spikelets with relatively few florets have a higher percentage seed set at harvest than spikelets with a higher floret number and this may be explained in terms of reduced competition for resources within the spikelet; for example, the greater seed setting capacity of florets from inflorescences of tillers produced over winter compared with those from tillers appearing in summer, and the observations of Hebblethwaite and Ivins (1978) where the delayed application of nitrogen fertilizer in the spring results in an improvement in seed set in spikelets with fewer florets than those produced by control inflorescences. In general, increasing the supply of nitrogen reduces the percentage seed set in field crops of ryegrass (Spiertz and Ellen, 1972; Hebblethwaite and Ivins, 1977) but this response is confounded by increased lodging. Nevertheless any increase in competition between florets within the inflorescence at the higher nitrogen levels seems likely to reflect the need for assimilate rather than any other substrate for seed development. There is some evidence to support this view in that shading the crop in the spring reduces seed set (Spiertz and Ellen, 1972) but there seem to have been few specific studies on this aspect of development in grasses, whereas in temperate cereals the results of glasshouse and field work show that grain set is greatly reduced by shading during anthesis and the immediate post-anthesis period (Wardlaw, 1975).

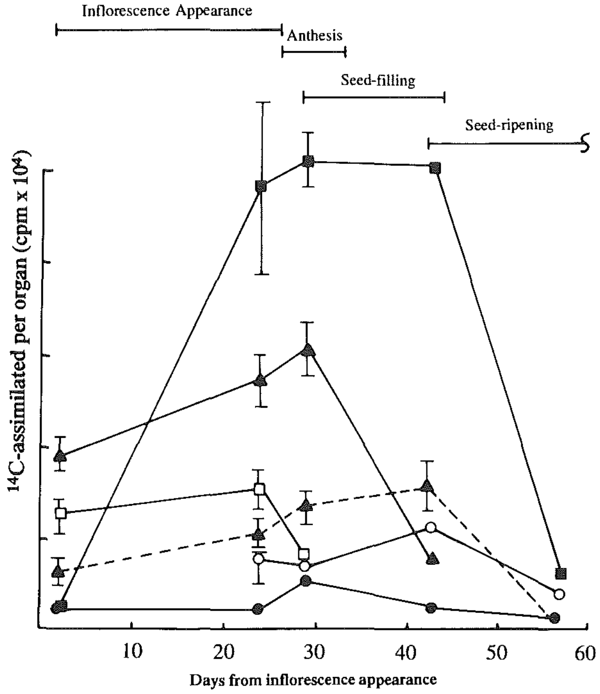

Figure 2. The fixation of $^{14}CO_2$ by the inflorescence and leaves of *L. perenne* with time from inflorescence appearance (+ S.E.). Whole tiller exposed to $^{14}CO_2$ for 10 minutes and then harvested. ■ , inflorescence; —▲—, flag leaf; - - ▲- - , flag leaf sheath; □ , penultimate leaf; ○ , upper internode; ● remaining stem. (From Ong et al., 1978a).

The Assimilate Supply for Seed Growth

The production of assimilate by the various parts of the flowering tiller and its supply to developing seeds can be evaluated by measuring the uptake of $^{14}CO_2$ and following the distribution of ^{14}C-assimilate from source to sink. In a field study of the assimilatory capacity of the inflorescence and leaves of ryegrass, Ong et al. (1978a) found that the inflorescence was the major assimilatory organ of the flowering tiller accounting for almost half of the $^{14}CO_2$ fixed by the tiller during anthesis (Fig. 2). This proportion increased with time as leaf laminae progressively senesced. With the exception of the developing seeds all parts of the inflorescence showed significant photosynthetic capacity, the lemmas and paleas contributed 40% of the $^{14}CO_2$ fixation at anthesis, the glumes 20%, and the rachis the remainder. There was significant export of ^{14}C-assimilate from the inflorescence after 24 hours as also reported in ryegrass by Clemence and Hebblethwaite (1984) and as found for *Poa annua* by Ong and Marshall (1975), but over 70% of the ^{14}C in the flowering tiller was retained by the inflorescence, and the majority of this was probably located in the developing seeds (Fig. 3c). The assimilate supply to seeds was not recorded separately in this experiment but in a similar study with *Poa annua* approximately 70% of the ^{14}C in the inflorescence was recovered from seeds (Ong and Marshall, 1975). During anthesis the terminal internode was the major sink for assimilate exported from the ryegrass inflorescence and this suggests that there may be competition for assimilate between newly developing seeds and the elongating internode. Assimilate exported from the flag leaf and lower leaves was utilized almost entirely by the stem (Fig. 3 a,b) and thus in contrast to most other work on source-sink relationships in grasses and cereals (Ong and Marshall, 1975; Wardlaw, 1975) these leaves did not make a significant contribution to the growth and development of seeds. They did, however, support the development of the inflorescence in the pre-anthesis period.

Although these results suggest that the photosynthetic activity of the inflorescence is wholly adequate to support seed growth, observations in another season revealed that 20% of the ^{14}C in plants four weeks after supplying $^{14}CO_2$ to the entire tiller at anthesis was recovered from the seeds (Fig. 4). Thus the current assimilation of the inflorescence may be supplemented by the mobilization of material previously assimilated by the leaves and temporarily stored in the lower internodes in the post-anthesis period as described for wheat (Austin et al.,1977).

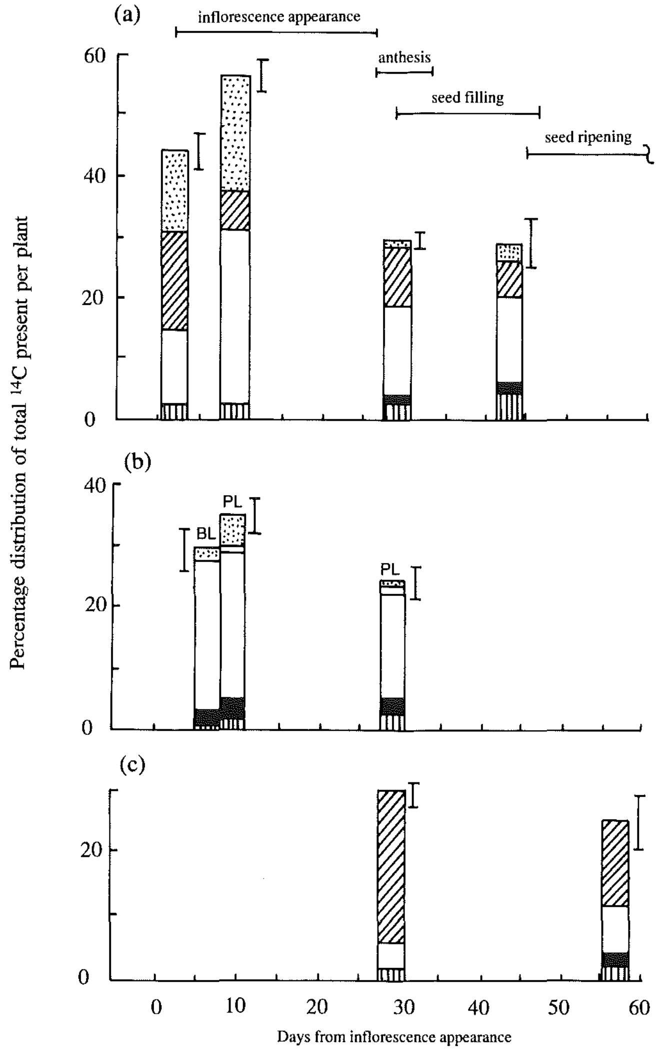

Figure 3. The percentage distribution of ^{14}C-labelled assimilate after 24 hours from (a) flag leaf, (b) penultimate (PL) or basal (BL) leaf, and (c) inflorescence, at different stages of reproductive development (+ S.E.). ░ ,inflorescence; ▨, leaves and upper internode; ☐ , rest of stem; ■ , other tillers; ▥ , root. (From Colvill and Marshall, 1984).

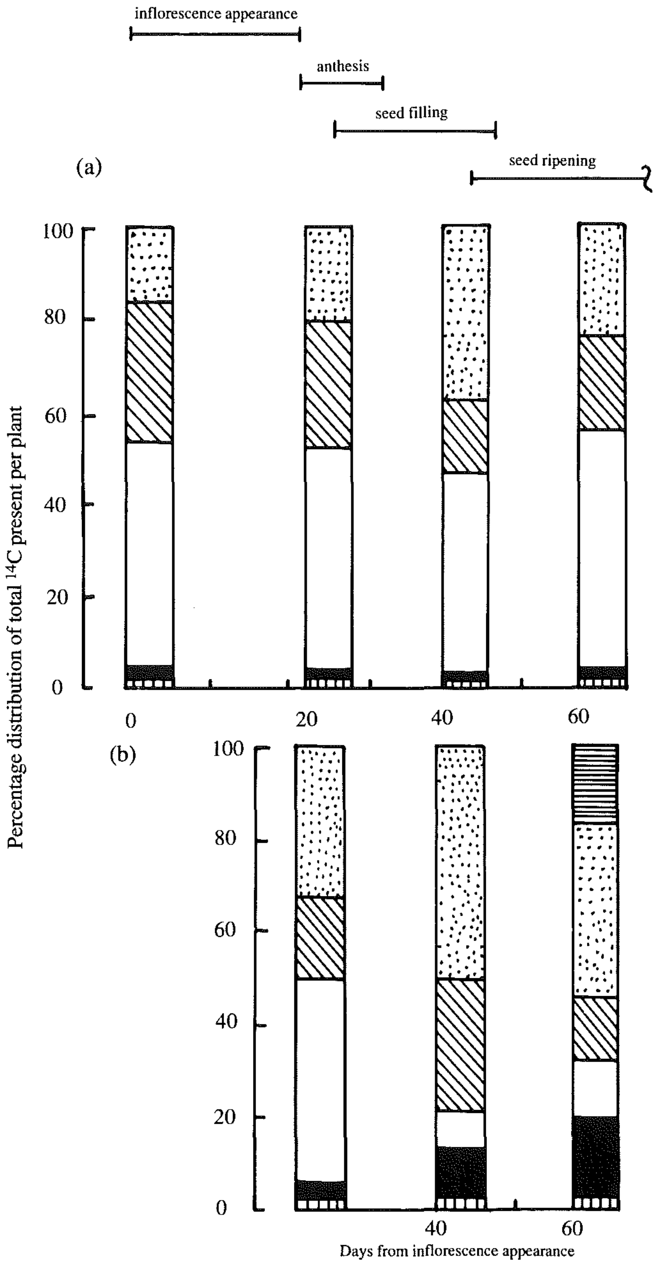

Figure 4. The redistribution of ^{14}C-labelled assimilate with time in *L. perenne*. Main tiller supplied with $^{14}CO_2$ at (a) flag leaf emergence, or (b) anthesis. ░ , inflorescence; ▨ , upper internode; ☐ , rest of stem and leaves; ▤ , seeds; ■ , other tillers; ▥ , root. (From Colvill & Marshall, 1984).

A recently reported field study on ^{14}C-assimilate distriution in *L. perenne* during seed filling by Clemence and Hebblethwaite (1984) shows an interesting additional source-sink link compared with the previously described study of Ong et al. (1978a) and Colvill and Marshall (1984). The latter was conducted on a sward supplied with a relatively low input of nitrogen fertilizer to minimize lodging and observations were made in an unusually dry season, whereas Hebblethwaite and co-workers studied crops well supplied with nitrogen. The higher input of nitrogen fertilizer stimulates tillering as well as causing early and extensive lodging (Hebblethwaite and Ivins, 1977; Hebblethwaite et al., 1980) and so in this situation young tillers which rely on imported assimilate for their development (Colvill and Marshall, 1981) will form a significant sink for assimilate, a demand that can only be met by established flowering tillers. Correspondingly, Clemence and Hebblethwaite (1984) found that ^{14}C-assimilate was readily supplied to developing tillers by the inflorescence and flag leaf during seed filling whereas Ong et al. (1978b) and Colvill and Marshall (1984) recorded only a trace of assimilate moving out of a flowering tiller to subtending tillers at this time. However, in *Poa annua*, Ong and Marshall (1975) also found that young tillers were a major sink for assimilate from the inflorescence. In contrast, Colvill and Marshall (1984) found that developing tillers were supported by the mobilization of reserve materials rather than by current assimilate as one sixth of the ^{14}C in a plant four weeks after supplying $^{14}CO_2$ to the shoot at anthesis was localized in new tillers (Fig. 4). In a lodged ryegrass crop the flag leaf and other leaves thus supply assimilate to two major sinks, developing tillers and the stem, and as a result there is only minor support to growing seeds, but even so both Clemence and Hebblethwaite (1984) and Hampton and Hebblethwaite (1985b) recorded a relatively greater allocation of assimilate from the flag leaf to the inflorescence than that observed by Colvill and Marshall (1984).

It is evident from these ^{14}C-studies that the inflorescence is the principal assimilatory organ of the flowering tiller and supplies the majority of the assimilate utilized by developing seeds. A significant proportion of current assimilate is exported from the inflorescence and in view of this Colvill and Marshall (1984) concluded that the production of assimilate was far greater than that needed for seed growth. This view is supported by experiments where lodging is prevented either by mechanically supporting the crop (Burbidge et al., 1978) or chemically (Wright and Hebblethwaite, 1979; Hampton and Hebblethwaite, 1985b) where the growth and development of many more seeds per inflorescence can be supported, but this response may in part reflect an improvement in the within-crop environment. However, the setting of seeds and their successful early growth is a far more critical developmental stage than their overall growth to maturity and thus if there is some degree of competition between vegetative and reproductive sinks for assimilate (mainly from the inflorescence) then this could perhaps influence the abortion of developing seeds.

Effects of Growth Regulators and Fungicides

Any experimental treatment that modifies source-sink relations to the advantage of reproductive growth and development, for example the application of growth regulators that reduce stem development and thereby reduce lodging, might be expected to enhance floret and seed development. Whilst the results of experiments with growth regulators such as Ancymidol and Paclobutrazol indeed show large increases in seed yield, mainly associated with an increase in seed number per spikelet, the mechanism underlying this improvement is not clear (Hebblethwaite et al., 1982; Hampton and Hebblethwaite, 1985b).

In particular, three aspects need to be resolved. Firstly, whether the number of fertile florets per spikelet at anthesis is influenced by the application of growth regulators: some observations suggest that this is unaltered (Wright and Hebblethwaite, 1979) but others show a significant increase (Hampton and Hebblethwaite, 1985b). Secondly, whether the reduction in lodging of the crop associated with the application of chemicals provides a more favorable environment for the production, release and dispersal of pollen, and so correspondingly results in an increase in the proportion of florets that become fertilized and set seed (Griffiths et al., 1980; Hill, 1980). Thirdly, whether the loss of developing seeds by abortion is reduced by the altered growth pattern of the crop following the application of growth regulators. This has frequently been claimed but is not supported by detailed observations on seed number per spikelet with time. However, in a recent publication Hampton and Hebblethwaite (1985b) provide some evidence that Paclobutrazol application at the time of spikelet initiation significantly reduced the abortion of seeds. This may reflect a direct effect of the growth regulator in suppressing the growth of vegetative tillers that compete with developing seeds for assimilate, or indirectly reflect improved light relations within the crop associated with reduced lodging, i.e. tillers may, by virtue of enhanced photosynthetic capacity, make less demand for assimilate from other parts of the plant.

In general it can be concluded that competition for assimilate between reproductive and vegetative sinks especially during anthesis and the early period of seed growth is important in regulating seed yield. This view is supported by the results of recent experiments in which fungicides have been applied to lodged crops of ryegrass; the crop remains lodged and seed production per spikelet is significantly increased (Hampton and Hebblethwaite, 1984). This increase in seed yield was brought about in the virtual absence of pathogenic fungi and was related to an increase in the leaf area duration of the canopy resulting from delayed leaf senescence. As treatment with fungicide did not influence floret number per spikelet at anthesis and did not alter the structure of the crop canopy, the improvement in seed production per inflorescence must largely be due to a reduction in seed abortion. It can, therefore, be suggested that treatment with fungicide maintained the photosynthetic activity of tillers and resulted in an improved supply of assimilate to developing seeds at a time when they are normally prone to abort. In addition it is possible that fungicides also exert a direct hormonal effect on developing seeds via a cytokinin-like action. This would stimulate the sink activity of developing seeds and sustain their import of assimilate and other substrates, thereby reducing their susceptibility to abortion.

It is clear that precise physiological studies are required to characterize the assimilate requirements of developing seeds. Information on the pattern of assimilate supply with time to individual seeds within a spikelet is needed to identify any differences between those seeds which abort, presumably the youngest and most distal within the spikelet, and those that maintain their growth to maturity. However, as the pattern of assimilate distribution may be markedly influenced by the hormonal relations of the sink (Wareing, 1977, 1979), then the hormonal background of individual developing seeds may be the critical feature that determines their fate. This could form the basis of a mechanism of hormonal inhibition of seed development (Evans et al., 1975) and this possibility needs to be resolved. It is important to note that even where the application of plant growth regulators increases seed numbers per inflorescence the percentage of florets that set seed is at best only about two-thirds of the total (Hampton and Hebblethwaite, 1985b). Thus considerable yield potential remains to be realized.

Seed Size

Seeds that grow to maturity follow a characteristic pattern of rapid increase in size and fresh weight in the first 10 days after fertilization, the period when they are most likely to be susceptible to abortion, and this is followed by a further period of dry weight increase during which reserves are accumulated and the percentage water content of the seed declines (Hill, 1980). The maximum dry weight of seeds is reached at the end of this stage, approximately four weeks after peak anthesis in perennial ryegrass. The final weight of an individual seed depends mainly on its position within the inflorescence, although the earlier appearing inflorescences of tillers produced in the summer tend to produce slightly larger seeds than those of tillers produced later in the year (Anslow, 1964). Basal spikelets produce slightly larger seeds than upper ones, but within a spikelet the basal florets tend to produce much larger seeds than more distal florets. This pattern reflects the relative activity of the individual seed sinks within the inflorescence and may well be related to the onset of fertilization of individual florets. Thus, seeds developing in upper florets within a spikelet compete poorly with those in lower positions for mineral nutrients and assimilate moving into the spikelet; on the other hand, if the lemma and palea associated with each growing seed supply a substantial proportion of the carbohydrate required for growth (Ong et al., 1978a), then differences in the duration of the seed-filling period may be important in accounting for differences in size between adjacent seeds within a spikelet.

The results of field and glasshouse studies show that the level of nitrogen supply, or mineral nutrient regime in general, have relatively little effect on mean seed weight (Hebblethwaite and Ivins, 1977; Ong et al., 1978c). Overall it seems clear that variation in seed size is a minor component of the yield structure of the grass inflorescence, and this follows the general pattern displayed by most plants, namely that seed size tends to be relatively constant in a range of conditions.

CONCLUSIONS

The large difference between potential and actual seed production of the grass inflorescence is due to the poor capacity of florets to yield mature seeds. This under-utilization of floret potential is associated with the lodging of the crop but even when this is reduced there is still a large discrepancy between the numbers of florets and seeds. The physiological factors underlying the poor productivity of florets are not fully understood but the evidence to date suggests firstly, that many florets do not become pollinated or fertilized, and secondly that a high proportion of developing seeds receive insufficient assimilate to sustain their growth at a critical period of their development, and as a result they abort. The latter situation seems to be related to the demands for assimilate elsewhere in the plant and this aspect requires more detailed investigation. There is scope to increase the potential seed yield further, for example by increasing the proportion of high yielding early-appearing tillers with a high number of florets per spikelet, but this approach is unrealistic until its potential can be realized. Currently the use of growth regulators to reduce lodging offers the best approach to improving the productivity of florets in field crops, and also provides a useful physiological tool to analyze the factors underlying this improvement.

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