Floret Site Utilization in Grasses: Definitions, Breeding Perspectives and Methodology[1]

A. Elgersma

ABSTRACT

The seed yield of grasses needs improvement, and seed yield should become a more important selection criterion in grass breeding. Seed yield depends largely on the degree of floret site utilization (FSU). This term is extensively discussed in this paper and several definitions are reviewed. A distinction is made between biological and economical FSU. Causes of variation in FSU and various determination methods are discussed. Suggestion for breeding for increased FSU are also given.

Additional index words: **Seed yield, pollination, fertilization, seed set, seed development, seed harvest, abortion, shattering, harvest losses.**

INTRODUCTION

The success of a herbage cultivar in commercial production not only depends on its forage attributes, but also on its ability to produce seed. In forage varieties, characteristics such as high vegetative production, persistency and quality are of importance to the farmer. The seed producer, however, desires high seed yields of good quality.

There are two alternatives for maximizing seed yields:

1. Cultural manipulation of the grass seed crop to maximize development of flowering stems and fertile florets.
2. Breeding for improved seed production jointly with forage production when developing new varieties.

Breeding perspectives for higher seed production are the focus of this paper.

Floret Site Utilization (FSU), Definitions and Components

Grass seed crops have a high yield potential, but this potential is never fully realized. Griffiths et al. (1973), Hebblethwaite (1977) and Burbidge et al. (1978) found realized yields to be much lower. Based on seed yield components, the theoretical production or potential yield can be calculated as inflorescences m^{-2} x spikelets/inflorescence x florets/spikelet x FSU x average seed weight. Owing to the negative feedback on forage production, it is not desirable to increase the size of the reproductive system, i.e. florets m^{-2}. Instead, the efficiency should be increased (Bean, 1972), which can be achieved by improving the FSU. The meaning of this term, however, is not clearly defined. Bean (1972) defines efficiency of the reproductive system as the percentage of flowers which produce seed, and the size to which these seeds develop. Several other terms have been used to describe FSU. For example, seed set, floret fertility or fertility index have been used. However, some of these last terms are already used for other traits, being components of the total "floret site utilization". For a full understanding of FSU it is necessary to analyze which processes occur from the time of anthesis until determination of the final seed yield. It is important to know how these processes are influenced by environmental and genetic factors, and by genotype x environment interactions.

In a *biological* sense, FSU can be defined as the percentage of florets, present at anthesis, resulting in a viable seed. For seed growers, the percentage and quality of the seeds that can be *harvested* is of interest. After harvesting and cleaning, the commercial seed yield can be expressed as a percentage of the potential seed yield. In an *economical* sense, FSU can be defined as the percentage of florets present at anthesis which contribute to the harvested seed. Economical FSU results from the following processes: pollination, fertilization, seed set, seed development, harvesting and cleaning. During each of these processes losses may occur (Table 1).

Pollination

The term 'pollination' is used to describe processes occurring from the time of anther dehiscence until the pollen reaches the stigma. Pollen grains on the stigma have a mutually stimulating effect on pollen germination. Reduction of the number of pollen grains on the stigma may reduce fertilization. Early lodging limits pollen transport and successful pollination. On the other hand, uniform flowering and high pollen production favor pollination. Pollination is influenced by environmental factors.

Fertilization

In the progamic phase of fertilization, seed set may be reduced due to non-viability of pollen grains or incompatibility. Non-viable egg cells may also reduce FSU.

Pollen grains of grasses have a low retention of viability, especially at low humidity. Jones and Brown (1951) stated

[1]Elgersma, A. Foundation for Agricultural Plant Breeding, P.O. Box 117, 6700 AC Wageningen, the Netherlands. Received for publication 4 November 1985.

Table 1. Processes occurring after anthesis and associated losses that reduce floret site utilization.

Florets at anthesis	Losses
Pollination	Empty florets
Fertilization	Empty florets
Seed set	Empty florets Early abortion
Seed development	
- Early growth stage	Abortion
- Food reserve accumulation stage	Diseases Abortion
- Ripening stage	Diseases Shattering
Harvesting	Shattering Damage
Cleaning	Empty florets Light seeds Heavy seeds
Seed yield	

that the poor seed set observed in some grass species may be due to the susceptibility of stigmas to damage under high temperatures and to desiccation of the pollen. Stigma withering in grasses begins a few hours after pollination. On the stigma, about 60-80% of the grass pollen germinates. The germination percentage increased with greater maturity of pollen and stigma (Watanabe, 1961). Hebblethwaite and Hampton (1981) mentioned that possibly not all florets are potentially fertile, either because of pest damage (Johnston, 1960) or because they are morphologically sterile and incapable of developing seed (Johnston, 1960; Hill, 1980). Johnston (1960) found up to 10% morphological sterility in flowers of *Dactylis glomerata*. Part of the 'sterility' in *Bromus inermis* and *Agropyron* spp. is genetically determined; the environment also strongly influences the percentage of flowers that set seed (Knowles and Baenziger, 1962).

Fertilization may be reduced due to self-incompatibility, which is quite common in grasses. In ryegrass, for example, there is a 2 loci gametophytic system, but under certain conditions some self-fertilization can occur. Probably the absence of other pollen favors self-fertilization. Poor seed set might occur when synthetic varieties are based on a few clones.

Seed Set

According to Hill (1980), the term 'seed set' describes the early growth of the embryo and endosperm. "Set" is indicated by the presence of cell division following successful fertilization.

As shown by Hill (1971) and Burbidge et al. (1978), approximately 60% of all florets are capable of being fertilized. The position of a floret in the inflorescence influences the probability of seed set (Anslow, 1964). In ryegrass, abortion may occur after fertilization up to approximately 21 days after anthesis. Soon after fertilization, cell division can be disrupted resulting in a misshapen ovary. At a later stage, seed development is often resumed. In other cases, cells disintegrate and the entire ovule collapses (Hill, 1980).

It is not clear whether abortion occurs more often after self-fertilization. Burbidge et al. (1978) noticed in *Lolium perenne* that many more seeds were set than were harvested, even when the crop was not lodged. They mentioned two possible reasons for abortion of developing seeds: hormonal inhibition of seed growth and competition for assimilates.

Seed Development

Hyde et al., (1959) distinguished three stages in seed development in ryegrasses:

Stage 1: the growth stage, duration 10 days after pollination. **Characteristics:** rapid increase in seed weight, high seed moisture content and non-viability.

Stage 2: the food reserve accumulation stage, duration a further 10-14 days. **Characteristics:** a threefold increase in seed dry weight. Seeds attain full viability.

Stage 3: the ripening stage, duration 3-7 days. **Characteristics:** dry weight remains approximately constant, but moisture content falls from about 10% to equilibrium with the atmosphere.

The stage of seed development affects three important aspects of seed quality: viability, seedling vigor and storage life (Hyde, 1950). Perennial ryegrass seed harvested 14 days after pollination would be viable, but would give rise to seedlings with poor vigor as high seedling vigor is not present until about 24 days after pollination. Immature seeds deteriorate rapidly in storage.

A study by Hill (1971) with perennial ryegrass has shown that different genotypes may have different patterns of embryo maturation. Furthermore, genotypes differ with respect to dehydration and the time taken to attain harvest ripeness (Hill, 1980). Cultural practices have a major effect on seed development.

During seed development, shedding losses occur. Besides trying to increase seed set, loss of viable seed can also be reduced. Burbidge et al. (1978) did not consider shedding to be a major factor, which contrasts with the results of Stoddart (1964). According to Stoddart (1964), one of the principal sources of yield loss in grass seed crops is the amount of seed shed from the inflorescence. Environmental factors, such as heavy winds, affect shedding. Spread in ripening time also promotes shattering. In *Lolium multiflorum,* genetic variation for seed retention was found between populations (Harun and Bean, 1979). Several authors reported improved seed retention resulting from breeding for this character (McWilliam, 1980; *Phalaris aquatica* (syn. *tuberosa*); Bean, 1969; *Phleum pratense*; Falcinelli et al., 1984; *Dactylis glomerata).*

Seed retention does not affect forage qualities and seems to be a very desirable character in grass seed crops. When growth regulators are introduced into commercial seed production, seed retention will become even more significant.

Harvesting

Not all seed that is produced can be harvested because of spread in ripeness, lodging and harvest losses. Within a seed crop, differences in ripeness exist within and between spikelets, between inflorescences and between plants. The apical florets in the spikelet, the apical part of an inflorescence and the oldest inflorescences ripen fast. The harvest time is a compromise between seed yield and quality. When the crop is harvested too early, many immature seeds are harvested, resulting in:

-drying costs
-increased risk of damage
-cleaning losses (light seed)
-loss of quality (light seed with low seedling vigor)

If harvest is late, many seeds are lost through shedding. At first, apical seeds will shatter which contain light seed. Then, the oldest inflorescences which carry the heaviest and the greatest number of seeds also start to shed. Bonin and Goplen (1963) found that within clones of *Phalaris arundinacea* shattered seeds were heavier than non-shattered seeds. Jensen (1976) found that shed seeds had a lower moisture content than non-shattered seeds. As the time of harvesting differs more from the mean ripeness date, the risk of genetic shift also increases (Davies, 1954).

A lodged crop is difficult to harvest. Morover, new vegetative tillers may grow through the lodged inflorescences and hamper harvesting. Seed quality decreases when the seeds are attacked by fungi. In a lodged crop, shattering is reduced. The harvest method, i.e. combining or swathing, affects seed yield losses. Seeds can be damaged, resulting in decreased quality. Harvest losses are greatly influenced by weather conditions.

Cleaning

After harvesting and drying, the seed is cleaned. Normal or "heavy" seed is separated from dust, sand, stalks, entire spikelets, empty florets, light seed and weeds. The cleaned seed is weighed, providing the final (economical) seed yield. The number of clean seeds can be calculated from the thousand seed weight (TSW).

BREEDING PERSPECTIVES

Possible breeding perspectives for improved FSU, indicated in the above review, are presented in Table 2. More research is needed to investigate which process has the highest correlation with grass seed yield, which characteristic has the largest genetic variation and which trait has the highest heritability.

It is interesting to note that several authors (Knowles and Baenziger, 1962; Ross and Adams, 1955; Lowe and Murphy, 1955; Raeber and Kalton, 1956; Nielson and Kalton, 1959; Ibrahim and Frakes, 1984; Slinkard, 1965 and Davies, 1954) reported FSU to be a fairly stable and highly heritable character. Others, (Mackay, 1960; Bean, 1969; and Bugge, 1981), mentioned large environmental effects on FSU.

A good relationship between "seed set" or "fertility index" and seed production is reported by Knowles and Baenziger (1962), Ross and Adams (1955), Nielsen and Kalton (1959), Slinkard (1965), Davies (1954), Dewey and Lu (1959) and Hearn and Holt (1969). However, the determination method of FSU influences the correlation between FSU and seed yield.

METHODOLOGY

Several studies have been made of FSU, "fertility index" or "seed set" in grasses. The results however, cannot easily be compared, because different characters appear to have been determined in various ways. Three aspects of determining FSU should be taken into account: time of determination, determination method and sampling technique.

The time of determining the number of florets for calculating the potential yield is important. If florets are counted at anthesis, the estimated potential yield is much higher than when counted after the harvest, because florets are lost during development and harvest. The time of determining the number of seeds for calculating the realized yield is also important. If seeds are counted before ripening, realized yield is much higher than when they are counted after harvest, because seeds are shed and lost during ripening, harvesting and cleaning.

Several determination methods have been described previously:

1. **Number ratio between filled and total florets.** This method has been applied quite often to uncleaned seed harvested just prior to ripeness. (Bean, 1969; Davies, 1954; Knowles and Baenziger, 1962). Empty and filled florets were separated by feeling, pressing or by examination over illuminated glass. Developing seeds are included in the seed fraction so this method gives a measure of biological FSU.

Table 2. Prospects of breeding for improved floret site utilization in grasses.

Process:	Selection for:
Pollination	- High pollen production
	- Uniform flowering (heading)
	- Lodging resistance
Fertilization and seed set	- Pollen viability
	- Ovule viability
	- Retention of pollen and ovule viability
	- Disease resistance
	- Lodging resistance
	- Compatibility
Seed development	- Disease resistance
	- Lodging resistance
	- Reduced embryo abortion
	- Uniform ripening
	- Seed retention

2. **Germination percentage.** This method is similar to method 1 in that developing, viable seeds are included. Very young seeds in the early growth stage which do not germinate are not included, however. Biological FSU measured in this way will therefore be lower than FSU as estimated by method 1 (Lewis, 1966; van Wijk, 1985).
3. **Weight ratio between cleaned and uncleaned seed.** This method is easy to apply, but does not give relevant information about FSU. After threshing, seeds are separated from empty florets and light seeds with a wind blower. Cleaned seed is much heavier than light and empty seed, so the percentage of cleaned seed is very high. This results automatically in a high, significant correlation between estimates of FSU and final seed yield (van Wijk, 1985; Raeber and Kalton, 1956).
4. **Volume ratio between cleaned and uncleaned seed.** This method gives a better estimation of the percentage of well-developed seeds than method 3 because seeds and empty florets differ less in volume than in weight (Hearn and Holt, 1969).
5. **Number ratio between cleaned and uncleaned seed.** This method is more precise than the fourth, but is very laborious. After threshing, all potential seeds are counted. Seeds are separated from empty florets and light seeds with a wind blower. Cleaned seeds are counted. Like methods 3 and 4, method 5 underestimates potential seed yield, i.e. the number of floret sites, because losses of floret sites are not included. Estimated FSU based on these methods will, therefore, be too high. Because only cleaned seeds are counted, a measure of economical FSU is given.(Lewis, 1966; Johnston, 1960).
6. **Calculated ratio between realized and potential seed yield:** FSU = yield m^{-2}/(inflorescences m^{-2} x TSW/1000 x florets/inflorescence). This method calculates economical FSU. Number of inflorescences m^{-2} and florets/inflorescence are determined at anthesis to obtain a "realistic" potential yield. FSU-values calculated in this way are much lower than values obtained with the other methods (Meijer, pers. comm.).

Method 1 seems most suitable for determining biological FSU. Shattering losses are not measured when applying these methods. For determination of biological FSU, however, shed seed should also be taken into account. For determination of economical FSU, method 6 seems the best.

The sampling technique for FSU should depend on the purpose. If the aim is to determine the FSU of a crop, inflorescences must be taken at random. If the aim is to detect genetic differences in FSU between genotypes or populations, variation due to age, developmental stage or size of the inflorescence should be reduced. Therefore, spikelets should be taken from similar positions in the infloresences and florets from the same positions in the spikelets.

SUMMARY

The seed yield of grasses needs improvement. Seed yield should become a more important selection criterion in grass breeding. The yield potential, i.e. florets m^{-2} is much higher than the realized yields. Seed yield depends largely on the degree of floret site utilization (FSU). This term is not clearly defined. A distinction should be made between biological and economical FSU. Biological FSU can be defined as the percentage of florets resulting in a viable seed. This characteristic results from several processes, i.e. pollination, fertilization, seed set and seed development. Economical FSU can be defined as the percentage of florets resulting in a harvested seed. This characteristic results from biological FSU, harvesting and cleaning.

In this paper the processes composing FSU in grasses are discussed. During each process losses may occur, resulting in decreased FSU. For several traits, genetic variation has been found which might offer perspectives when breeding for improved seed yield in grasses.

There is no agreement on heritability of FSU. However, results can hardly be compared among experiments because several definitions of FSU and various determination methods have been used. In this paper, three aspects of the methodology of FSU are discussed: time, method and sampling technique. FSU should be determined in a proper way, and methods and terms should be standardized. More research is needed on FSU in grasses to develop better selection criteria for improved seed yields.

ACKNOWLEDGEMENTS

Financial support from the Commodity Board for Arable Products is gratefully acknowledged.

REFERENCES

1. Anslow, R.C. 1964. Seed formation in perennial ryegrass II. Maturation of seed. J. Br. Grassl. Soc. 19:349-357.
2. Bean, E.W. 1969. Environmental and genetic effects upon reproductive growth in tall fescue (*F. arundinacea* Schreb.) J. Agric. Sci., Camb. 72:341-350.
3. Bean, E.W. 1972. Clonal evaluation for increased seed production in two species of forage grasses, *Festuca arundinacea* Schreb. and *Phleum pratense* L. Euphytica 21:377-383.
4. Bonin, S.G., and B.P. Goplen. 1963. Evaluating grass plants for seed shattering. Can. J. Pl. Sci. 43:59-63.
5. Bugge, G. 1981. Genetic variability in the components of seed yield of ryegrass species. pp. 37-41. *In* Breeding high yielding forage varieties combined with high seed yield. Report of the meeting of the Fodder Crops Section of Eucarpia in Merelbeke (Belgium), 8-10 September 1981.
6. Burbidge, A., P.D. Hebblethwaite, and J.D. Ivins. 1978. Lodging studies in *Lolium perenne* grown for seed. 2. Floret site utilization. J. Agric. Sci., Camb. 90:269-274.
7. Davies, E.W. 1954. "Shift" in a late-flowering strain of perennial ryegrass (*Lolium perenne*). pp. 102-106. *In* European Grassland Conference. OEEC.
8. Dewey, D.R., and K.H. Lu. 1959. A correlation and path-coefficient analysis of components of crested wheatgrass seed production. Agron. J. 51:515-518.
9. Falcinelli, M., F. Veronesi, and V. Negri. 1984. Seed dispersal of Italian ecotypes of cocksfoot (*Dactylis glomerata* L.). J. Appl. Seed. Prod. 2:13-17.

10. Griffiths, D.J., H.M. Roberts, and J. Lewis. 1973. The seed yield potential of grasses. Welsh Plant Breeding Station, Annual Report, 1973. pp. 117-123.
11. Harun, R.M.R., and E.W. Bean. 1979. Seed development and seed shedding in North Italian ecotypes of *Lolium multiflorum*. Grass and Forage Science 34:215-220.
12. Hearn, C.J., and E.C. Holt. 1969. Variability in components of seed production in *Panicum coloratum* L. Crop Sci. 9:38-40.
13. Hebblethwaite, P.D. 1977. Irrigation and nitrogen studies in S.23 ryegrass grown for seed. 1. Growth, development, seed yield components and seed yield. J. Agric. Sci., Camb. 88:605-614.
14. Hebblethwaite, P.D., and J.G. Hampton. 1981. Physiological aspects of seed production in perennial ryegrass. pp. 17-32. *In* Breeding high yielding forage varieties combined with high seed yield. Report of the meeting of the Fodder Crops Section of Eucarpia in Merelbeke (Belgium), 8-10 September 1981.
15. Hill, M.J. 1971. A study of seed production in 'Grasslands Rauanui' perennial ryegrass (*Lolium perenne*), 'Grasslands Kahu' Timothy (*Phleum pratense* L.) and prairie grass (*Bromus unilodes* H.B.K.). Ph.D. thesis, Massey University, Palmerston North.
16. Hill, M.J. 1980. Temperate pasture grass-seed crops: formative factors. pp. 137-150 *In* P.D. Hebblethwaite (ed.). Seed production. Butterworths, London.
17. Hyde, E.O.C. 1950. Studies on the development of white clover seed. pp. 12:101-107. *In* Proc. N.Z. Grassl. Assoc.
18. Hyde, E.O.C., M.A. McLeavy, and G.S. Harris. 1959. Seed development in ryegrass and in red and white clover. N.Z.J. of Agric. Res. 2:947-952.
19. Ibrahim, A.E.S., and R.V. Frakes. 1984. Variability and interrelations of seed yield components in tall fescue (*F. arundinacea* Schreb.) Genet. Agr. 38:387-398.
20. Jensen, H.A. 1976. Investigation of anthesis, length of caryopsis, moisture content, seed weight, seed shedding and stripping ripeness during development and ripening of a *Festuca pratensis* seed crop. Acta Agric. Scandinavica 26:264-268.
21. Johnston, M.E.H. 1960. Investigations into seed setting in cocksfoot seed crops in New Zealand. N.Z.J. Agric. Res. 3:345-357.
22. Jones, M.D., and J.G. Brown. 1951. Pollination cycles of some grasses in Oklahoma. Agron. J. 43:218-222.
23. Knowles, R.P., and H. Baenziger. 1962. Fertility indices in cross-pollinated grasses. Can. J. Pl. Sci. 42:460-471.
24. Lewis, J. 1966. The relationship between seed yield and associated characters in meadow fescue (*Festuca pratensis*). J. Agric. Sci., Camb. 67:243-248.
25. Lowe, C.C., and R.P. Murphy. 1955. Open-pollinated seed setting among self sterile clones of smooth bromegrass. Agron. J. 221-224.
26. Mackay, K.H. 1960. Variations in cross-fertility in two xenogamous grasses, *Bromus inermis* Leyss. and *Phleum pratense* L. Doctoral thesis, Univ. Wisconsin.
27. McWilliam, J.R. 1980. The development and significance of seed retention in grasses. pp. 51-60. *In* P.D. Hebblethwaite (ed.). Seed Production. Butterworths, London.
28. Nielson, A.K., and R.R. Kalton. 1959. Combining ability for seed characteristics in *Bromus inermis* Leyss. Agron. J. 51:178-181.
29. Raeber, J.G., and R.R. Kalton. 1956. Variation and inheritance of fertility and its components in *Bromus inermis* Leyss. Agron. J. 48:212-216.
30. Ross, J.G., and M.W. Adams. 1955. The influence of heredity on seed and forage production in smooth bromegrass. Proc. S. Dakota Acad. Sci. 34:16-20.
31. Slinkard, A.E. 1965. Fertility in intermediate wheatgrass *Agropyron intermedium* (Host) Beauv. Crop Sci. 5:363-365.
32. Stoddart, J.L. 1964. Seed ripening in grasses. I. Changes in carbohydrate content. J. Agric. Sci. 62:67-72.
33. Wantanabe, K. 1961. Studies on the germination of grass pollen. II. Germination capacity of pollen in relation to maturity of pollen and stigma. Bot. Mag., Tokyo 74:131-137.
34. Wijk, A.J.P., van 1985. Factors affecting seed yield in breeding material of Kentucky bluegrass (*Poa pratensis* L.) J. Appl. Seed Prod. (in press).