Optimising Seed Production in Kleingrass, *Panicum coloratum* L.

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ABSTRACT

Seed of kleingrass (*Panicum coloratum* L.) matures nonuniformly and shatters readily at maturity. Consequently, many seeds are immature and of poor quality when harvested, and actual seed yields are only a fraction of the total seed produced. Experiments were conducted to determine the optimum time to harvest a seed crop to maximise both quantity and quality of seed. The seed production of genotypes differing in resistance to seed shattering was also evaluated. Genotypes differing in seed retention, including selections from the cultivar Selection-75, were established in a replicated nursery and seed was harvested at four dates in each of two years. Peak seed production was remarkably consistent between years and occurred 20-22 days after anthesis. Seed quality, as measured by mean seed mass, peaked later at 24-26 days after anthesis. An excised-culm, laboratory procedure predicted the relative amount of seed retention observed in whole field plants and will be useful to screen plants for resistance to shattering.

Additional index words: **forage grass, plant breeding, seed shattering.**

INTRODUCTION

Kleingrass (*Panicum coloratum* L.) is a warm-season perennial bunchgrass introduced to the United States from southern Africa in the 1940s. It is utilised for pasture and range, primarily in Texas, where it will tolerate seasonal flooding and long periods of drought. It has also been extensively planted on degraded rangeland (Cox, Martin, Ibarra, Fourie, Rethman and Wilcox, 1987), mostly using cv. Selection-75, released in 1968. A second US cultivar, Verde, released in 1983, was developed primarily as food for gamebirds and has larger seed and improved seedling vigour (Holt, Conrad, Bashaw and Ellis, 1983).

Seed shattering limits the consistent production of adequate amounts of high quality kleingrass seed. The seed shatters readily at maturity or earlier if weather conditions during the final days of seed maturation result in severe disturbance of the inflorescences. Under ideal weather conditions only 19% of the viable seed is harvested (Roe, 1972) with average seed yields only 6% of the potential (Young, unpub. data).

The indeterminate nature of flowering and nonuniform maturation of seed within the same panicle affect the timing of a harvest to maximise both seed quantity and quality. A single, direct heading harvest will invariably consist of a high percentage of immature seed of lower quality, although the exact amount will depend on the timing of the harvest. A quantitative profile of seed production in kleingrass has never been fully described. Such knowledge would provide valuable information needed to schedule an optimum seed harvest.

Recently, a laboratory procedure to quantify seed retention on excised culms of kleingrass was described (Young, 1986), and the inheritance of seed retention in two populations of kleingrass using this technique was reported (Young, 1991). From preliminary observations (Young, unpub. data) genotypes identified with the laboratory procedure as having high resistance to shattering appeared to have superior seed retention when grown in a space-planted field nursery.

The present study was therefore initiated to describe 1) the seed production profile of kleingrass, in general, and 2) the profile of kleingrass plants differing in seed retention as measured with an excised-culm laboratory procedure and determine 3) if the laboratory procedure correctly classified resistance to seed shattering in the field.

MATERIALS AND METHODS

Twenty-three genotypes representing a range of seed retention, as determined visually, were selected from five accessions of kleingrass. Cultivar Selection-75 was included as a control to give a total of 24 entries in the experiment. Plots were established in 1982 and consisted of four, six-plant rows. Rows were 51 cm apart and plants 30.5 cm apart within rows. Plots for the 23 'genotypic' entries contained 24 plants that were vegetatively propagated from a single genotype. Each plot of cv. Selection-75 consisted of 24 different genotypes (a total of 96 genotypes in the four replicates). Therefore, plots of cv. Selection-75 were more variable than those of other entries. It was thought to be important to adequately represent the cultivar even at the risk of introducing a small (only one entry out of 24) additional source of variation into the experiment. The design was a split plot in four replicates with entries as main plots and harvest dates as subplots.

In 1983 and 1985 at each of four harvest dates (16, 22, 27 and 31 days after anthesis), one row from each plot was randomly chosen and all seed was harvested. Within plot variability for true first anthesis was slightly greater for cv. Selection-75 than for other entries. However, even within the clonally propagated plots all plants did not start to shed pollen on the same day. Therefore, the day when anthesis occurred on approximately 10% of the inflorescences was

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used as the 'day of anthesis', rather than true first anthesis within a plot. Seed set was low in 1984, a very dry year, and data were not taken. In addition, the number of inflorescences was counted for one plant in the one remaining row at 28-30 days after anthesis. Average seed mass was determined by counting and weighing 500 seeds at each harvest in each plot for each maturity class. Seed number was determined by dividing total seed mass by the average mass per seed. Seeds per inflorescence were determined from the laboratory procedure for measuring seed retention (SR) (ie seed shattering plus seed retained on the inflorescence).

Seed was cleaned with a wind separator to eliminate those below approximately 0.25 mg seed^{-1}. This produced a seed lot with a visual appearance similar to a typical lot of commercially available kleingrass seed and an average germination of 88.3%. A class of 'mature' seed was then split from the total cleaned seed by removing with a wind separator seed with a mass less than approximately 0.44 mg seed^{-1}. This produced a 'high quality' lot of very dark seed having an average germination of 94.9%.

Percentage SR was determined for all entries using a previously described 'excised-culm' technique (Young, 1986; 1991). Briefly, the protocol was as follows: culms were excised from plants after pollination, placed in water, and the seed allowed to mature in a greenhouse. Each culm was then agitated uniformly with a modified electric toothbrush and the percentage of SR determined by comparing numbers of 'shattered' and 'retained' seed. SR was measured on two culms per plot in each of the two years of the experiment. The ANOVA did not reveal a significant entry x year interaction for %SR. Therefore, entries were then ranked for %SR on the basis of two year means and divided into two categories with 12 entries in each category. The 'high' SR category had a mean SR of 92% and the 'low' SR category had a mean SR of 75%. There was a highly significant difference ($P < 0.001$) between categories when 'entries' in the ANOVA were partitioned into the single degree of freedom contrast 'high' SR vs 'low' SR.

Standard analysis of variance and regression techniques were employed for data analysis. Differences between curves (Figs 1-4) were determined using a regression analysis with indicator variables (Freund and Littell, 1986). P-values associated with differences between two quadratic curves are indicated on each figure.

RESULTS AND DISCUSSION

Seed Production Profile of Kleingrass

The overall ANOVA indicated a significant difference between years for both total seed and mature seed, and quadratic equations gave an excellent fit to the data (Fig. 1). There was also a significant difference among entries ($P < 0.001$) in the overall ANOVA and the entry by harvest interaction was significant. This was anticipated because many different genotypes and multiple harvest dates were used in the study. Regression curves, however, are presented as means over entries. Analysis and inference on a genotype basis would have little practical significance in kleingrass in which plant populations are highly variable.

Curves for total seed production over all entries were different for the two years studied, with total seed production peaking at 22 and 20 days after first anthesis in 1983 and 1985, respectively (Fig. 1). Peak production for total seed was somewhat higher in 1983, and the period of seed production was shorter.

Considerably fewer mature seeds were produced in 1985 compared to 1983 (Fig. 1), and peak production of mature seed occurred at 23 days after anthesis in both years. This was 1 to 3 days later than the peak for total seed production. There was more similarity between the two years in the range of seed production (days after anthesis) for mature seed than for total seed (Fig. 1). This is because immature seed comprised a higher proportion of the 'total seed' class in 1985 (52.1% vs 27.8% in 1983). Mature kleingrass seeds began to abscise at 11-13 days after anthesis (Fig. 1). This agrees with an anatomical study (Burson, Correa and Potts, 1983) that demonstrated a maturing of the abscission layer in kleingrass at about 14 days after anthesis. The slight difference in maturity (2 to 3 days) between the present study and that of Burson *et al.* (1983) is probably due to the presence of a small amount of immature seed in the 'mature' seed class in the current study. This is to be expected and inherent in the use of a wind separator to separate seed by mass.

Extrapolation of the curves are presented as dotted lines to acknowledge the uncertainty associated with extending any curve beyond the data points. However, in this study, extrapolation seems to be justified. The axis intercepts are not very far outside the data points, and more importantly, the intercepts have biological meaning. The projected intercepts are in agreement with previously published studies and observations of kleingrass (Burson *et al.*, 1983; Hearn and Holt, 1969).

Hearn and Holt (1969) reported that kleingrass seeds are virtually all shattered from an inflorescence by 28 days after anthesis. Our results suggest about 35 days using measurements from whole plots. However, the data of Hearn and Holt (1969) were obtained by tagging individual inflorescences and collecting them at intervals rather than utilising data from whole plots. The date when anthesis was first observed within a given plot was used in the present experiment. Continuation of flowering within a plot for 6-7 days is usual for kleingrass, an indeterminantly flowering species. Therefore, the two studies are in basic agreement.

Over all entries, average seed mass peaked 1 and 3 days later than mature seed and 4 days later than total seed in 1983 and 1985, respectively (Fig. 2). The disagreement between the peaks for seed mass and mature seed is due to the mature seed class containing a small proportion of immature seeds for the reasons described previously.

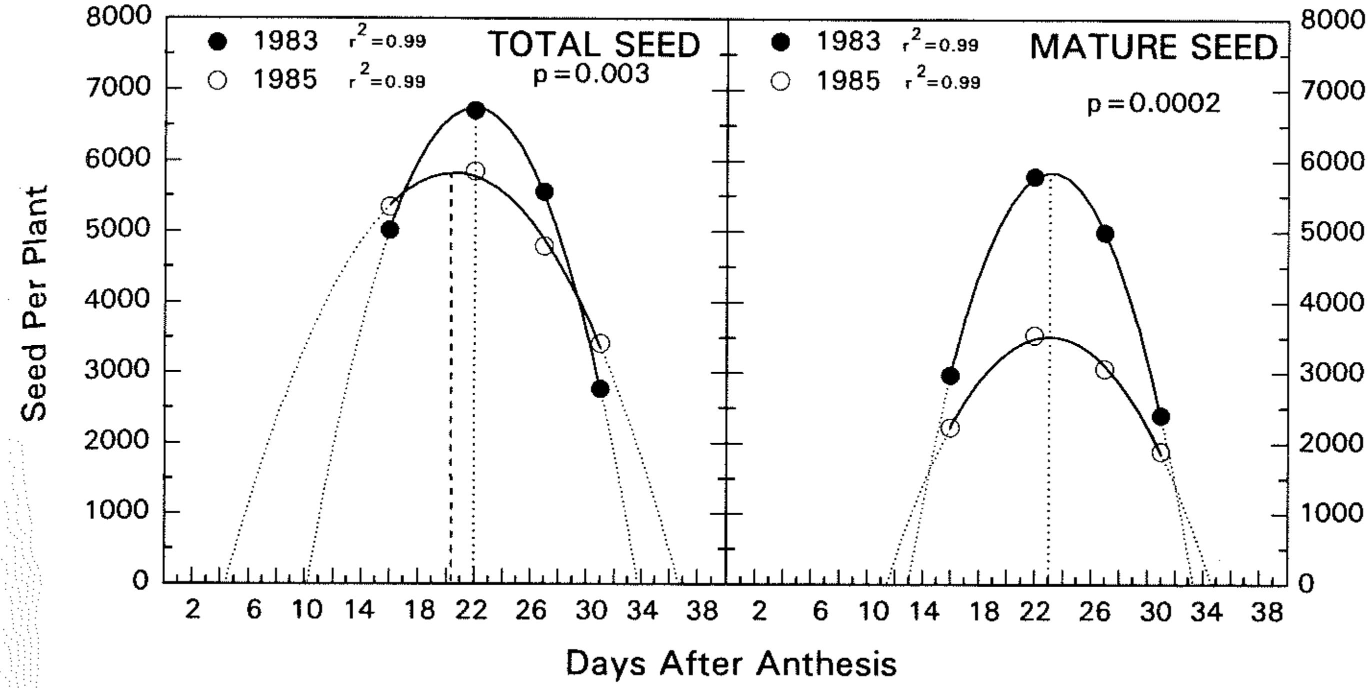

Figure 1.
Spring seed production for total seeds and mature seeds over 24 entries of kleingrass. Regression equations are y = -16695.31 + 2132.59 x -48.52 x^2 and y = -3534.20 + 911.36 x -22.21 x^2 for total seeds in 1983 and 1985, respectively and y = -24222.48 + 2596.84 x -56.08 x^2 and y = -10238.83 + 1195.17 x -25.95 x^2 for mature seeds in 1983 and 1984, respectively.

The seed production profile for cv. Selection-75, the most widely planted US cultivar, was similar to that for all entries. Total seed and mature seed peaked at 22 and 23 days after anthesis, respectively; similar to the profiles for all entries presented together (Fig. 1), although there was less yearly variation in the total seed profile for cv. Selection-75. Average seed mass peaked approximately 3 and 1 days later than mature seed in 1983 and 1985, respectively. Again, this is due to the probable contamination of the mature seed class with some immature seed.

There were significantly fewer inflorescences per plant but significantly more seeds per inflorescence in 1985 than 1983 (Table 1) for cv. Selection-75 and all entries. Thus, the potential total seeds per plant were similar in both years. Actual seed production was slightly higher in 1983 (Fig. 1).

Seed Production Profile of Plants Differing in Seed Shattering

The 'high' SR group retained a greater percentage of its seed compared to the 'low' SR group in both years, but the difference was significant only in 1983 (Fig. 3). This variation was not unexpected because a substantial effect of environmental interactions on the heritability of seed retention in kleingrass had been demonstrated earlier (Young, 1991).

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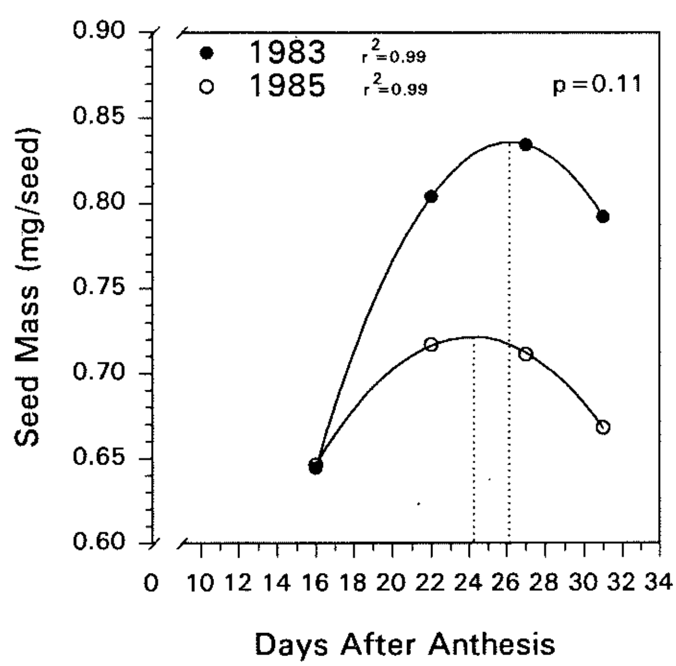

Figure 2.
Changes in mean seed mass during spring seed production over 24 kleingrass entries. Regression equations for 1983 and 1985 are y = 0.437 + 0.097 x -0.002 x^2 and y = 0.059 + 0.055 x -0.001 x^2, respectively.

Table 1. Comparison of inflorescence number, seeds per inflorescence, potential seeds per plant, and % seed retention (SR) between high and low seed shattering categories.

Category	Number of inflorescences	Seeds per inflorescence	Potential seeds per plant	% SR
All entries				
1983	57.2 a	247.3 b	14146 a	78.9 b
1985	41.5 b	447.2 a	18559 a	86.9 a
cv. Selection-75				
1983	72.1 a	216.3 b	15595 a	54.2 b
1985	42.0 b	415.8 a	17464 a	82.9 a
1983				
High %SR	53.8 b	255.3 a	13735 a	91.6 a
Low %SR	58.4 a	243.9 a	14244 a	68.6 b
1985				
High %SR	32.9 a	482.6 a	15878 a	92.4 a
Low %SR	51.6 a	410.8 a	21197 a	80.8 a

For each character within each grouping, means not followed by the same letter are significantly different at $P < 0.05$ (LSD).

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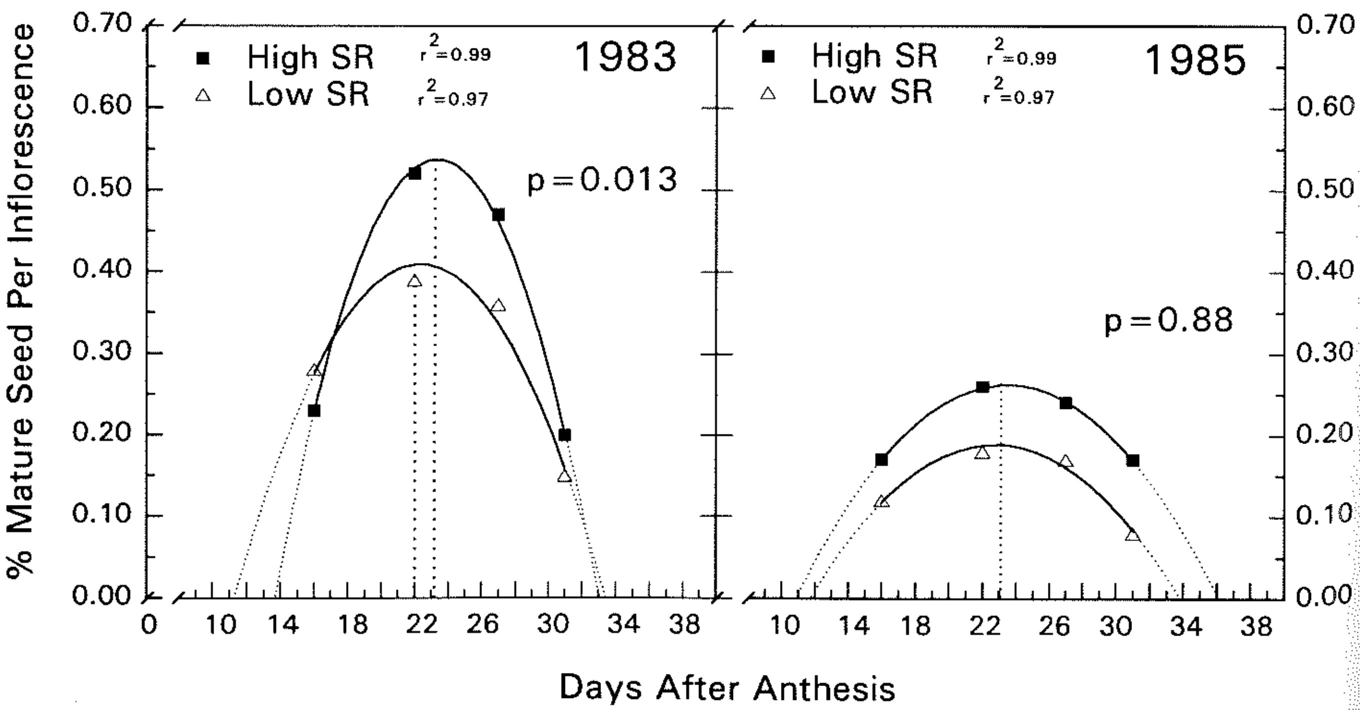

Figure 3.
Field performance during spring seed production of entries differing in laboratory determined SR. Regression equations are $y = -2.581 + 0.267x - 0.006x^2$ and $y = -1.256 + 0.149x - 0.003x^2$ for High SR and Low SR, respectively in 1983 and $y = -0.642 + 0.077x - 0.002x^2$ and $y = -0.610 + 0.070x - 0.002x^2$ for High SR and Low SR, respectively in 1985.

As a group the 'high' SR entries had fewer inflorescences per plant in both years, significantly so in 1983 (Table 1). The number of seeds per inflorescence for the 'high' SR group, while slightly larger, was not significantly different from the 'low' SR group. The lack of association between SR and seeds per inflorescence but negative association of SR and number of inflorescences per plant was also found earlier in a comparison between cv. Selection-75 and an introduction (PI 410177) having superior resistance to seed shattering (Young, 1986). The previous study also found cv. Selection-75 (low SR) to have a higher number of seeds produced per plant compared to PI 410177 (high SR), but fewer seeds harvested due to the differences in SR.

There was a large difference between potential seeds per plant and seed recovered per plant at peak harvest (Table 2). In 1985, the maximum percentage of seed recovered was similar to the previously reported value of 19% (Roe, 1972), while in 1983 the recovery percentage doubled.

Table 2. Seeds recovered at peak seed production as a percentage of total potential seed in kleingrass cv. Selection-75.

Year	Potential seeds per plant[1]	Seeds per plant at peak[2]	Percent of total[3]
cv. Selection-75			
1983	15595 a	5590	35.8
1985	17464 a	3121	17.9
All entries			
1983	14146 a	5845	41.3
1985	18559 a	3511	18.9

[1] Potential seeds = number of inflorescences x seeds per inflorescence. For potential total seeds within each year means followed by the same letter are not significantly different at $P < 0.05$ (LSD).
[2] Determined from the peak of the regression curve (Fig. 1,3).
[3] Percent = 100 x ((Potential seeds/plant)/(Seeds/plant at peak))

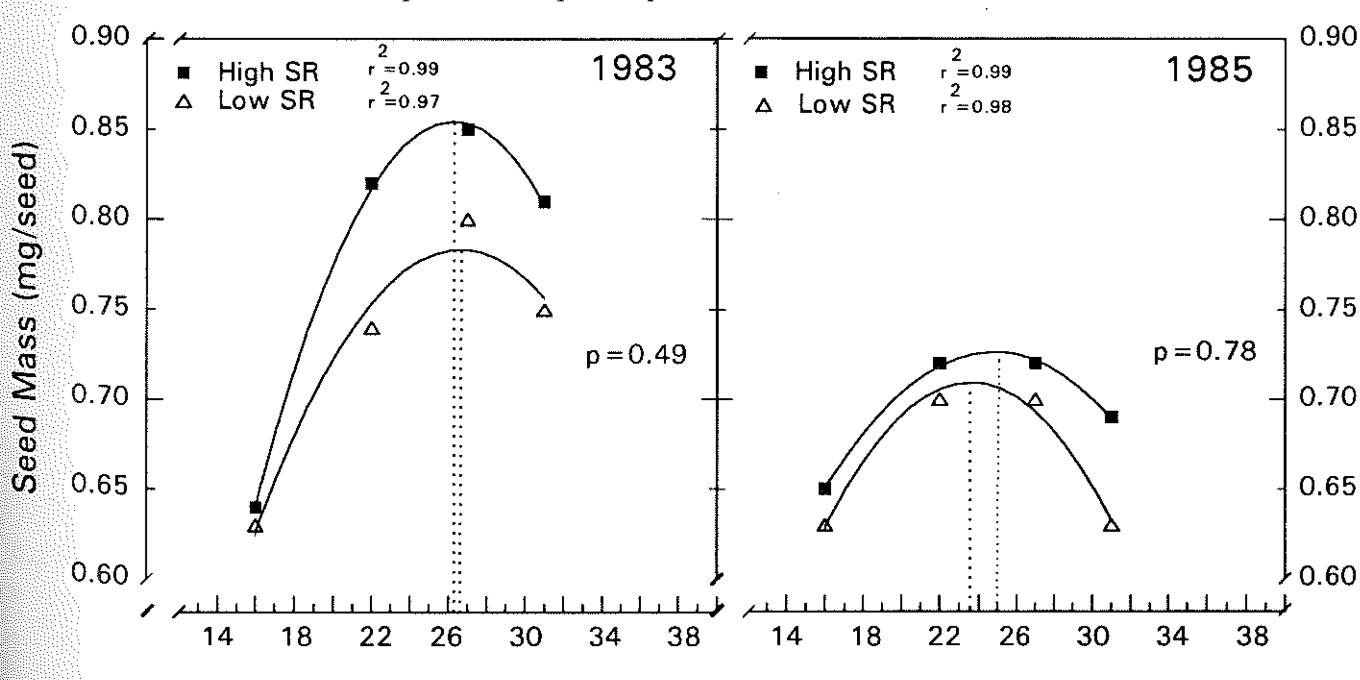

Figure 4.
Seed mass during spring seed production of entries differing in laboratory-determined SR. Regression equations are $y = -0.545 + 0.107x - 0.002x^2$ and $y = -0.203 + 0.074x - 0.001x^2$ for High SR and Low SR, respectively in 1983 and $y = 0.126 + 0.048x - 0.001x^2$ and $y = -0.069 + 0.066x - 0.001x^2$ for High SR and Low SR, respectively in 1985.

There were no significant differences in average seed mass between the high and low SR categories in either year (Fig 4.). However, the high SR category did rank consistently higher in average seed mass at all harvest dates in both years. This can be explained by the greater potential seed mass of the high SR class as measured by weighing seeds from the 'mature' classes (0.879 and 0.868 mg seed^{-1} in 1983 and 1985 and 0.841 and 0.831 in 1984 and 1985 for the high SR and low SR classes, respectively). Thus, no increase in seed mass of harvested seed accompanying an increase in SR was detected.

It is interesting that for plants with high SR a higher percentage of seeds were collected throughout the period of seed production, but the interval during which seed can be recovered was not extended. This is further evidence of the large environmental influence on the expression of the seed retention character in kleingrass (Young, 1991). In this case the environmental influence is probably weather conditions that act to agitate the inflorescence. Only in the total absence of wind will little seed shatter (Young, 1986), and such conditions are not likely to persist for the entire spring seed production period. Evidently, the seed retention character acts to prevent shatter for a short period of time and only under mild weather conditions. It has been proposed from visual observations that resistance to seed shattering may result from either the increased density of spikelets within the panicle or the retention of the glumes (Young, 1991). Differences in inflorescence structure have been related to seed shattering in other grasses (McWilliam, 1980; Falcinelli, Veronisi and Negri, 1984; Whalley, Jones, Nielson and Mueller, 1990).

Field vs Laboratory Evaluation of Seed Shattering

The values for SR as measured with the laboratory procedure (Table 1) do not represent the actual SR which would be observed in seed production under natural field conditions. In other words, an SR percentage of 91.6 does not mean that 91.6% of the seed will be retained on a field-grown plant. However, the relative values for %SR directly translate to field differences in SR. For a given comparison the relationship of %SR to actual field values can be seen by contrasting laboratory-derived %SR ratios with ratios of actual seed production (Table 3). For example, noting that potential total seed production values are similar, in 1983 the ratio of the high to low SR classes for total seed at peak production (from the regression curve) was 1.44 (6709/4651). This was similar to the ratio of %SR of the high SR class to that of the low SR class (91.6/68.6 = 1.34). In 1985 the respective ratios were also similar (1.16 vs 1.14). Thus, the percentage difference seen in the laboratory-derived SR values was comparable to the percentage difference seen under field conditions. The laboratory procedure for determining SR can be considered a relative measure of field performance.

Table 3. Relationship of actual seed production to a laboratory method for measuring resistance to seed shattering (SR).

			Total mature seeds at peak		Laboratory SR	
Year	Category	Potential total seeds[1]	Number[2]	High/Low	%	High/Low
1983	High SR	13735 a	6709	1.44	91.6	1.34
	Low SR	14244 a	4651		68.6	
1985	High SR	15878 a	3717	1.16	92.4	1.14
	Low SR	21197 a	3191		80.8	

[1] Potential total seed = seeds per inflorescence x number of inflorescences per plant. For potential total seeds within each year means followed by the same letter are not significantly different at $P < 0.05$ (LSD).
[2] Number of seeds per plant at peak of regression curve.

Boonman (1973) found the mean 'optimum harvest date for yield of clean seed' to be 6.8 weeks after initial head emergence. However, the yearly range varied from 5.5 to 8 weeks. In the present study there was a yearly difference of only 2 days in time of peak total seed yield when measured from date of first anthesis (Fig. 1,2). Peak yields of the highest quality seed occurred on the same day in both 1983 and 1984 when optimum harvest date was measured from the time of first anthesis. Days after first anthesis would seem to be a more reliable predictor of optimum harvest date than days after initial head emergence

In summary, a seed harvest between 20 and 25 days after first anthesis will produce a yield that will be at least 93% of peak seed production (Fig. 1). Because the number of harvestable mature seeds peaks 1-3 days after the total number of seeds, a harvest between 22 and 25 days after first anthesis should optimise both seed quantity and quality. The *in vitro* laboratory procedure for quantifying seed retention was able to predict relative field performance, and will be useful to screen plants for resistance to seed shattering.

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