environment of the peninsular Florida flatwoods. Once established, individual plants of most accessions proved to be both persistent under moderate grazing pressure and competitive in dense grass swards. Most accessions flowered early enough in the year for seed production prior to normal winter frost. Although plant regeneration of several accessions occurred from natural reseeding for three years, stands of these accessions decreased each year.

Previous evaluation in small plots had indicated that four of the *S. guianensis* accessions and the two native *S. hamata* accessions had potential to persist in this environment. In concurrence with the report of Cameron and Ludlow (1977) that *S. guianensis* var. *guianensis* (robust type) possessed insufficient cold tolerance to persist at temperatures down to $-5°C$, the light frosts encountered each winter were apparently responsible for lack of perennation of the *Stylosanthes* accessions which were perennial types. Late flowering prevented regeneration from seed of only three accessions. Failure of the remaining accessions to persist in adequate stands in the grass sward through annual reseeding was largely due to excessive grass competition by the time the *Stylosanthes* seedlings emerged. The perennial grass sward began growth 3 to 4 months earlier in the spring than emergence of even the earliest *Stylosanthes* accessions.

Even though late emergence and a short grazing season are major limitations in the commercial use of *A. americana* in south Florida, the *Stylosanthes* accessions evaluated were even later than *A. americana* in establishment of grazable stands each year. Value of the species, *S. guianensis* and *S. hamata*, as pasture plants in this seasonally wet, low fertility, subtropical environment is apparently dependent upon development of agronomically acceptable accessions that will perennate.

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FORMATION OF SEED YIELD IN *PANICUM MAXIMUM* CV. GATTON

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ABSTRACT

The components of seed yield were recorded in a seedling crop of Panicum maximum *cv. Gatton grown as an artificial sward in a glasshouse at St. Lucia, Brisbane, Australia. Individual heads emerging over 58 days were dated, time of start of anthesis recorded, and seeds harvested by hand-shaking. Rate of head appearance reached a maximum of c. 12 $m^{-2} day^{-1}$ 11 days after first head emergence and continued at c. 3 $m^{-2} day^{-1}$ thereafter. Branch number per head and 100-seed weight were relatively constant, but number of spikelets per branch decreased sharply with later date of head emergence, and seed setting was also greater on early-formed heads. Shedding of individual spikelets occurred at a*

constant rate on individual heads from 6 to 24 days after commencement of anthesis. However, as the early-formed spikelets on any head had a lower percentage seed set than later-formed spikelets, the curve of weight of filled spikelets shed with time was sigmoid; 50% shedding occurred c. 17 days after commencement of anthesis.

Attention is drawn to the loss of seed yield and decrease in seed quality associated with a single cut harvest.

INTRODUCTION

Seed production of tropical pasture grasses such as *Panicum maximum* (Boonman 1971) is beset with difficulties which are mainly associated with poor synchrony of flowering and with the rapid abscission of ripe seeds (Humphreys 1979). A detailed knowledge of the behaviour of seed head and spikelet populations is a necessary basis for understanding the development of grass seed crops. A number of studies (Favoretto and Toledo 1975; Javier and Mendoza 1976; Nishihira and Nishimura 1977; Kowithayakorn and Moolsiri 1979; Maschietto 1981) have estimated optimum harvest time of the tall types of *Panicum maximum*. Filled spikelets (= "seed") ripen basipetally on the panicle, and Weiser *et al.* (1979) have described the anatomical changes associated with the abscission of the spikelet from the top of the pedicel. There is only one study (Hopkinson and English 1982*a*) which attempts to model the dynamics of inflorescence exsertion and spikelet differentiation, anthesis, maturation and shedding.

This paper reports results of a parallel study to that of Hopkinson and English, conducted also on the shorter guinea grass variety cv. Gatton. It differs in that, the sward being grown in a glasshouse protected from the weather, it was possible to pay detailed attention to the behaviour of individual inflorescences and follow the history of spikelet development and shedding on them. This provides direct records of both new information and details of behaviour that could only previously be inferred.

MATERIALS AND METHODS

Seeds of *Panicum maximum* cv. Gatton (Gatton panic) were sown in trays of soil on September 5, 1979. Seedlings were transplanted at a density of 69 plants m^{-2} on October 8–9 into a bed 2.38 × 0.68 × 0.18 m deep containing a Moggill sandy loam, which was located in a glasshouse at the University of Queensland, St. Lucia. This study formed part of a larger investigation described in detail in Oliveira (1981). The sward was irrigated to maintain good growth. Applications of complete nutrient mixes (which included 100 kg N ha^{-1}) were made on November 21 and December 6, and urea was also applied on December 26 and February 12 to provide a further 48 kg N ha^{-1}. Plants were sprayed to control red-spider (*Tretranchyus* spp.), grasshoppers or caterpillars on December 14, 18, January 16, 20, 22 and February 14.

All tillers with inflorescences just exserting from the flag leaf (except from border plants) were tagged in the afternoon of every second day to date head emergence. These tagged tillers were examined daily and re-tagged to record the commencement of anthesis. Spikelets were harvested by hand-shaking individual heads into paper bags; harvesting began on the sixth or seventh day after the first record of anthesis on that particular head and continued every second day until the tenth harvest of that head, when any remaining spikelets were stripped from the inflorescence. Spikelets harvested from inflorescences commencing anthesis on the same day were bulked, and harvests were made from the inflorescences which began anthesis from December 14 to February 9. The 45 plants from the central datum area were cut at ground level on March 9–10, and dry weight, tiller density, tiller fertility, branch number/inflorescence, and inflorescence length were determined. A General ER Seed Blower was used to separate empty and filled spikelets, and was calibrated at opening 19.9 using a standard Gatton panic seed sample provided by the Standards Laboratory of the Queensland Department of Primary Industries. Number and weight of filled spikelets (= "seed") and of empty spikelets were determined and used to calculate spikelet number per

branch, seed set (ratio of number of filled spikelets to total spikelet number), 100-seed weight, and rate of spikelet shedding.

RESULTS

Climate

The average weekly maximum temperature in the glasshouse during the early seedling phase from October 8 to December 16 ranged from 25.6 to 34.4 °C with a mean of 30.3 °C; minimum temperatures varied from 14.1 to 21.5 °C, with a mean of 17.7 °C. Temperatures increased during the first phase of flowering and seed production; maximum temperatures reached their highest weekly value of 38.2 °C during the third week of January, and were not lower than 30.6 °C during the harvest period. Minimum temperatures of 20–22 °C were maintained from the beginning of February, when maximum temperatures tended to decrease. Relative humidity fluctuated considerably but in the daytime showed a preponderance of higher values ($> 70\%$) in February and March. More detail is available in Oliveira (1981).

Quantum flux density (as PAR) averaged only 59% of outside values. Daily total radiation in the glasshouse (as recorded by a Swissteco Solarimeter to January 21 and an Integrating Pyronometer thereafter) varied greatly. High values of 6400 Wh m^{-2} day^{-1} occurred in the last week of December and from January 7 to February 2, and lower values (*c.* 2500 Wh m^{-2} day^{-1}) predominated in February and early March. Periods of very low radiation (less than 1500 Wh m^{-2} day^{-1}) did not exceed three days duration during the flowering period.

Components of seed yield

The sward made good growth and accumulated a shoot dry weight of 1512 ± 157 g m^{-2} by March 9, with a tiller density of 262 ± 30 m^{-2}. Dissection of border plants indicated that 50% of plants had tillers which had reached floral initiation (double ridge stage) by December 5–6. The rate of head appearance was initially slow. The time from head emergence to the commencement of anthesis was 1.6 ± 0.1 days; in occasional heads this period extended up to 5 days, but there appeared to be no consistent relationship between the duration of this phase and the hierarchical position of the tiller. Tiller fertility was high in this seedling crop, and averaged $91 \pm 3\%$.

The time pattern of inflorescence appearance is presented on the basis of density of heads entering anthesis (Fig. 1). Inflorescence appearance increased to a maximum of 12 heads m^{-2} day^{-1} on December 25 and decreased thereafter to *c.* 3 heads m^{-2} day^{-1} in the latter part of the 58-day tagging period. In Table 1 the data have been recalculated by amalgamating inflorescences produced in 5 key periods. Period 3 covers the phase from when 50% of plants had at least one head emerged to the point where 50% of plants contained one inflorescence with at least 50% of its florets at anthesis. Periods 1 and 2 represent the first and second halves of the interval (between start of head emergence and period 3), whilst periods 4 and 5 equally divide the subsequent phase from period 3 until tagging of heads terminated. Cumulative inflorescences appearance was 42% of the total when 31% (18 days) of the tagging duration had elapsed at the end of period 3.

Number of branches differentiated per head was a stable character (Fig. 1), and decreased only *c.* 5% between the first and last phases (Table 1). On the other hand the number of spikelets per branch decreased by a factor of nearly 5 from early- to late-formed inflorescences (Fig. 1, Table 1). This was accompanied by reducing head length (Fig. 1). The mean seed-set of all florets on a particular inflorescence (Fig. 1) was *c.* 60% for inflorescences reaching anthesis early (by December 29), then decreased to about 20% for mid-season tillers, and showed some recovery to 30–40% for the late-flowering tillers. The change in 100-seed weight was smaller but of similar pattern (Table 1, Fig. 1) and variation associated with time of head exsertion was only *c.* 5%.
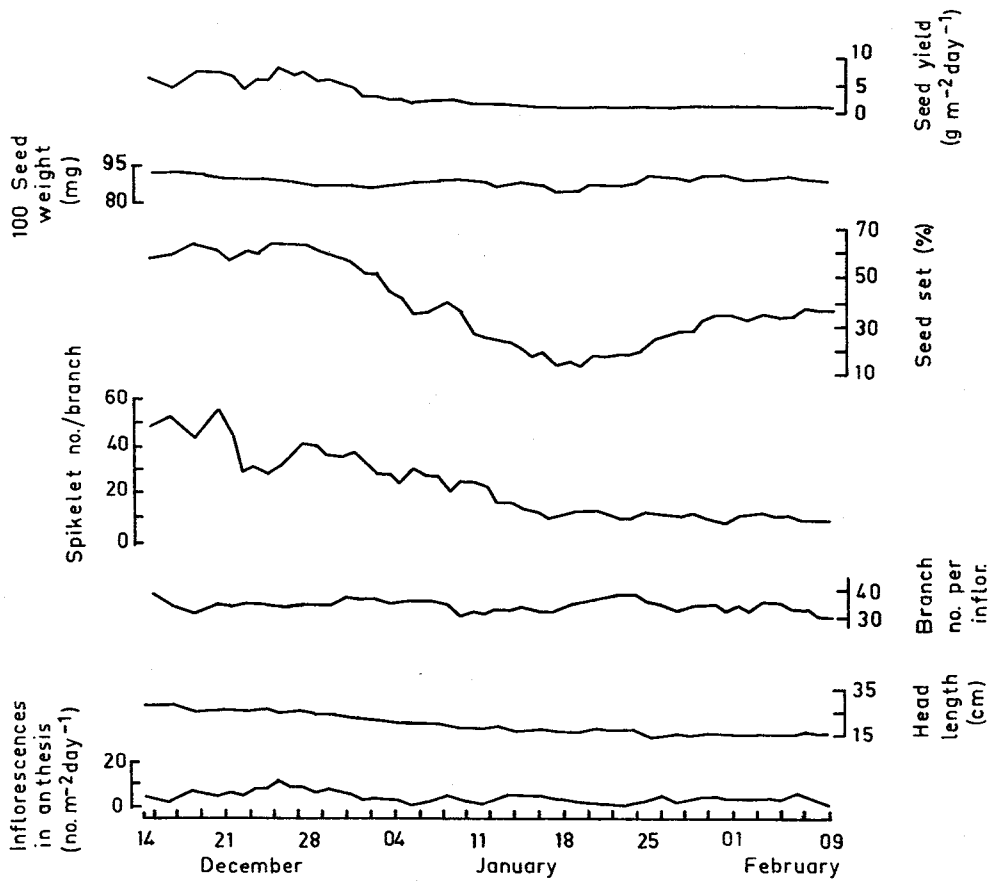
FIGURE 1

Changes in the components of seed yield of *Panicum maximum* cv. Gatton (based on 3-day running means).

TABLE 1

Components of seed yield of P. maximum *for successive periods (1–5)*

Date of first anthesis	1† 14–20/12	2 21–27/12	3 28–31/12	4 1–20/1	5 21/1–9/2	Mean
Rate of head appearance (no. m⁻² day⁻¹)	3.14 ± 0.41*	7.43 ± 1.74	5.50 ± 1.83	3.80 ± 0.31	2.90 ± 0.77	3.97 ± 0.91
Branch no./head	36.1 ± 1.2	35.3 ± 0.50	35.6 ± 0.63	34.8 ± 0.63	34.3 ± 0.62	34.8 ± 0.32
Spikelet no./branch	49.7	34.9	36.9	19.8	10.5	25.4
Seed setting (%)	61.2	62.1	57.2	35.7	31.7	45.2
100-seed weight (mg)	91.4	89.5	87.8	87.1	90.4	88.9
Seed yield (g m⁻² day⁻¹)	3.15	5.05	3.63	0.77	0.30	1.61

*italicised values are S.E. of mean.
†Definition of grouping 1–5 in text.

The daily rate of seed production, which is the product of these components, reached a maximum of *c*. 7.6 g m^{-2} day^{-1} from heads commencing anthesis *c*. December 25, and heads appearing to this point accounted for *c*. 50% of total seed production. However, seed production continued at a relatively steady rate of *c*. 3 g m^{-2} day^{-1} from January 7 to the end of the experimental period. The total pure seed harvest of filled spikelets was 93.4 g m^{-2}, which represented 6.2% of total shoot dry weight.

Seed shedding

The harvest period for each head from the 6th or 7th day after the commencement of anthesis until the 24th or 25th day appeared adequately to cover the seed setting, maturation and shedding phases. Detailed observations of individual heads showed that good spikelet recovery was achieved by hand-shaking every 2 days. The data have been amalgamated in Fig. 2, for heads reaching anthesis in each of the five periods designated earlier, to give the cumulative percentage of total spikelets shed against time (number basis). This showed a highly significant linear relationship, i.e. a relatively constant proportion of spikelets were shed at each harvest. There was a tendency for spikelets appearing on late-formed inflorescences to shed more rapidly, and 50% of the period 5 spikelets had shed at an estimated 12.0 days after start of anthesis on that head, compared to 15.6 days for the period 1 spikelets.
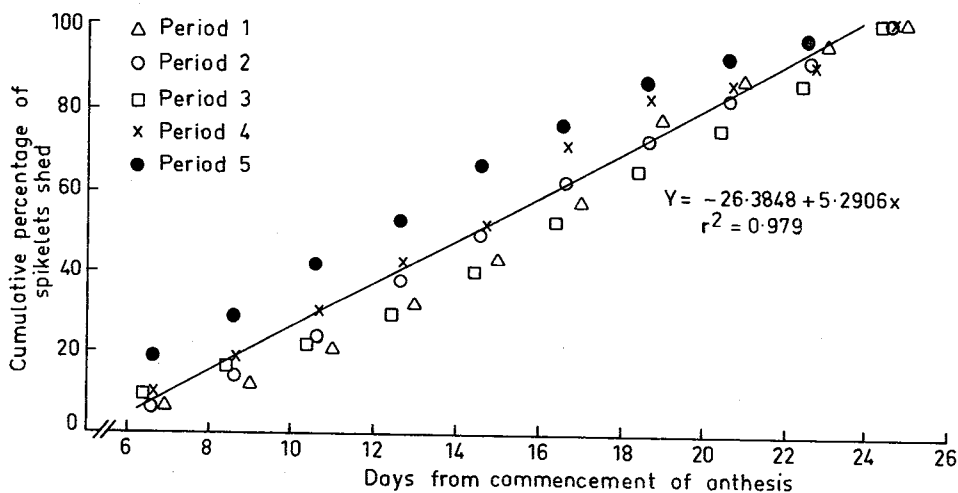

FIGURE 2

Cumulative percentage of total spikelets shed (number basis) against time since commencement of anthesis on single heads, for 5 experimental periods (designated in Table 1).

Seed setting of spikelets on individual heads increased from *c*. 0.3% of the spikelets shed on the 6th or 7th day after commencement of anthesis to 86.7% of the spikelets harvested at the shaking 25 days after anthesis (Fig. 3). The high proportion of empty spikelets shed at the beginning of inflorescence maturation altered the shape of the curve for percentage weight of filled spikelets (= seed) harvested against time (Fig. 3).

The percent weight of filled spikelets shed as plotted against days since commencement of anthesis was considered likely to be a sigmoid curve. In accordance with Finney (1971), the normal equivalent deviate was fitted as a linear function of the log of days from commencement of anthesis. The application of this technique gave a value of 16.9 days from commencement of anthesis for 50% shedding. Thus the shedding data on a filled spikelet weight basis showed a delay relative to the data on a total spikelet number basis. Pure seed content increased with lateness of harvest from an individual head.
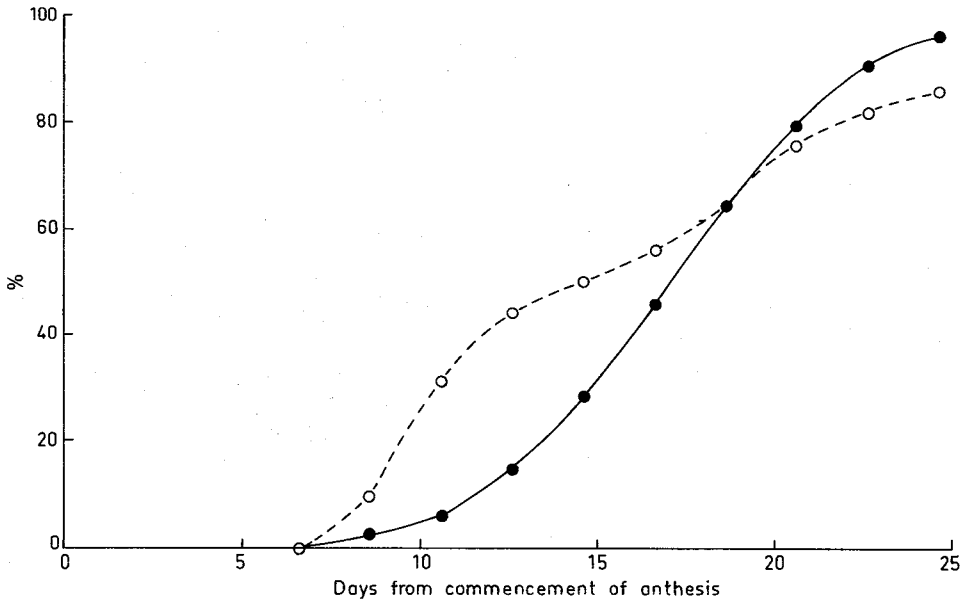
FIGURE 3

Percent seed set (o - - o) and cumulative per cent of total spikelets shed which were filled (●——●, weight basis) against time since commencement of anthesis on single heads.

DISCUSSION

A comprehensive model for the formation of seed yield in Gatton panic has been proposed by Hopkinson and English (1982a), and one of the more useful applications of our study is to consider the extent to which that model is validated and the modifications to it which are suggested by our data. The conditions of our experiment— a seedling artificial sward in a glasshouse were different from the field conditions of Hopkinson and English, but our crop yield components were of a similar order [cf. Tables 1, 2, 3 of Hopkinson and English (1982a)]. Total inflorescence density (230 m^{-2}) was medium relative to their data, spikelet number/head (880) and 100-seed weight (89 mg) were high values, whilst mean seed setting (45%) and duration from commencement of anthesis to completion of seed shedding (25 days) were similar, [but less than in Kowithayakorn and Kanasoot's (1978) study.] The serious dichotomies from the Hopkinson and English (1982a) model were:

(1) Head emergence did not occur at a fixed daily rate and then cease after c. 30 days. In our seedling crop a significant but reduced rate of head appearance (c. 3 m^{-2} day^{-1}) was still evident 58 days after commencement of head emergence. (Fig. 1). This type of behaviour is more in agreement with the four-parameter linear segment model for head emergence of Chloris gayana used by Loch (1983, p. 189). In our experiment continued head emergence was probably stimulated by multiple dressings of nitrogen (Bahnisch and Humphreys 1977), whilst in commercial practice a single fertilizer application at the beginning of the cropping cycle is recommended.

(2) The number of spikelets on each emerging head was not constant, but was highly sensitive to date of head emergence. Spikelet number per head decreased from 1790 in early-flowering tillers to 360 in late-flowering tillers, despite the considerable constancy of branch number per head, an early stage development character which must be under strong genetic control. There was therefore a strong hierarchical effect on spikelet number per branch.

(3) The success rate of seed set (Fig. 1) decreased in the middle of the experiment. This may have been associated with a temporary infestation of red spider about January 16, but successful control with an acaricide applied on January 16, 20 and 22 did not restore seed setting in later-appearing heads to the level recorded in early-appearing heads. These findings should be taken into account in future modelling exercises.

The low level of seed setting and the observed rapid shedding of the early-blooming spikelets at the top of the inflorescence and extremities of the branches agree with the observations of Kowithayakorn and Kannasoot (1978). Hopkinson and English (1982a) suggest that low levels of seed set in early-formed inflorescences are associated with deficiency of pollen and the requirements of psuedogamy, but this phenomenon occurs in late-appearing inflorescences which are surrounded by a high density of earlier-formed heads which are concurrently setting seed well. It is conceivable that more rapid shedding of failed-set spikelets relative to set spikelets could contribute to the sigmoid character of Fig. 3.

Our study with repeated hand-shaking points to the considerable loss of potential seed yield and the reduction of seed quality resulting from a single destructive seed harvest, as was also observed by Kowithayakorn and Moolsiri (1979). Various studies (Javier and Mendoza 1976; Padilla and Febles 1976; Nishihira and Nishimura 1977), have recommended harvesting 18–22, 12–44, and 13 days, respectively, after the commencement of anthesis on an inflorescence. Our data suggest that 58 to 84% of filled spikelets would have been shed by 18 to 22 days, whilst 83% of filled spikelets would not be formed by 13 days after commencement of anthesis. Perhaps seed harvesting by repeated passes over the field with a simple beater-type harvester merits more consideration, especially in view of the inefficiency of seed recovery and the damage to seed quality resulting from header harvesting (Hopkinson and English 1982b).

ACKNOWLEDGEMENTS

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