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EXSERTION, FLOWERING, AND SHEDDING IN *PANICUM MAXICUM* (POACEAE)[1]

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Within-panicle flowering, exsertion, and seed ripening were investigated in four clones of *P. maximum*. Flowering, exsertion, and seed ripening were fast processes (<10 d for each process). Dates and timing were stable within each clone and should allow definition of the harvest date for each genotype and for each harvest method. Clones showed two main flowering patterns differing in the number of flowered spikelets at the date of maximal flowering and in the time of flowering. Seed set was similar to that of allogamous and anemophilous plants. It was nevertheless lower in clones with a high degree of flowering–shedding overlap. In the absence of flowering–shedding overlap, the time for a panicle to flower and to produce seeds was shorter than the time between two emergences of panicles on a tiller. Reproduction timing seemed controlled to minimize competition between panicles on a tiller.

Key words: exsertion; flowering pattern; *Panicum maximum*; Poaceae; ripening time; seed set.

Panicum maximum is a perennial and anemophilous grass probably native to Kenya and Tanzania (Combes, 1975; Pernès, 1975). Most plants are pseudogamous apomicts (Combes, 1975; Pernès, 1975). Apomixis permits clonal multiplication by seeds and pseudogamy means that pollination is necessary to trigger parthenogenesis. The agronomic importance of apomictic varieties of *P. maximum* as forage (Guinea grass) is well known throughout the tropical world (Humphreys, 1975), especially in Brazil where the species covers several million hectares (Serrao et al., 1978). Nevertheless, its seed production is limited by the staggering of its heading and its within-panicle flowering combined with substantial shedding of mature seeds (Boonman, 1971a; Humphreys, 1975; Noirot, 1992; Noirot and Ollitrault, 1992). In the better cases, i.e., harvesting by bagging, seed production is ≈350 kg/ha, which corresponds to 10% of the yield potential (Noirot, 1990). Accurate knowledge of flowering is necessary to improve harvesting methods and breeding.

In *P. maximum*, within-panicle flowering is basipetal (Warmke, 1951; Javier, 1970). The flowering sequence is controlled by the within-sheath spikelet distribution before heading, and the basipetal spreading speed of the flowering after heading (Noirot, 1992). Within-panicle flowering needs ≈7–8 d, and peaks 3–4 d after the first stigma emergence (Noirot, 1992). By contrast, exsertion, shedding, and their relations to flowering are less well known.

In this study, we investigated the development of the panicle from heading to seed shedding in four clones that are morphologically different, especially in their panicle size. Exsertion, flowering of spikelets, and seed ripening were characterized by (1) their intensity (exsertion height, number of flowering spikelets, and number of seeds), (2) their dates (beginning and end), and (3) their duration. Seed set was also observed. Within-clone diversity allowed classification of traits into three groups according to their stability. Within-clone relationships were estimated between all studied traits. In particular, between-clone differences allowed us to distinguish different flowering patterns associated with different seed sets.

We discuss (1) the stability of dates and times and their main practical consequences for the seed harvest, (2) the clonal differences of the flowering patterns in relation to the seed set, (3) the competition between exsertion and flowering, and (4) the relationships between the time of within-panicle flowering and the succession of panicles on a tiller over a 2-mo period.

MATERIALS AND METHODS

Plant material and experimental design—A fertile tiller can produce several panicles by branching (Noirot, 1991). The principal panicle is the first to emerge. Principal panicles constitute the main component of seed production (subsequent panicles are fewer, smaller, and bear fewer spikelets). In our experiments, only the principal panicles were taken into account.

Due to the mode of reproduction, almost 98% individuals of an apomictic variety have the same genotype (that of the female parent), are phenotypically very similar, and can be considered as clones. Rare individuals arise from residual sexuality, but they are easily recognized and eliminated.

Four clones were selected. Clone C1, with narrow leaves and tillers, shows hybrid traits between *P. maximum* Jacq. and *P. infestum* Anders. Its principal panicle is 16–20 cm in length (from the verticil to the top) and bears ≈400 spikelets. Clone 64 has a spreading habit and shows similarities with *P. trichocladum* K. Schum. It produces principal panicles of length close to those of C1, and with a similar number of spikelets. Clone 267 is a well-known type (Common Guinea) of *P. maximum*. Its panicle is medium-sized (28–36 cm in length) and bears ≈2400 spikelets. Clone 2A4 is an apomictic three-way hybrid with C1 as male parent and a tetraploid sexual plant with large panicles as fe-

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male parent (Noirot et al., 1986). Its panicle size is between that of C1 and 267, and its spikelet number is ≈750.

Planting by tuft splitting was done at the beginning of the wet season (June) at the agricultural station of Man (Côte-d'Ivoire). All clones were represented by at least one row of 11 plants. Clones C1, 2A4, and 64 were separated by one row of clone 267. Rows and columns were spaced 1 m apart. Plants were cut monthly from 1 July to 1 September at a height of 15–20 cm. A dressing of NPK fertilizers (100-50-150) was given 15 d before planting, supplying 50 kg/ha nitrogen (urea) a week after every cutting. A net protected the plants against birds.

Notations—Observations were made during the main heading of September-October (6-mo-old plants). Ten randomly selected panicles were tagged at the flag stage on 15 September for clones C1, 2A4, and 267, and on 30 September for clone 64 (the main heading of this clone occurred 15 d later). A mosquito net was put under each panicle to harvest shed seeds. For each panicle, the date of emergence of the first stigma represented the day D_1. Notations were done every morning, just after flowering.

Exsertion is the ultimate step of the internode elongation stage. Exsertion concerns essentially the last sheathed internode under the panicle. Exsertion was characterized by its ultimate height (EXSH) measured in centimeters from flag to verticil, and its duration (EXSEND) expressed in days.

Spikelet flowering begins with the emergence of anthers at ≈0600–0700, followed by that of purplish-blue stigmas. The latter constitute a reference mark, since the stigmas wither during the day, thus avoiding all confusion with the flowering of the day before. The flowering of each panicle was characterized by the number of flowered spikelets (FLONUM), the maximum number of flowered spikelets per day (FLOMAX), and the day by which 95% of spikelets had flowered (FLOTIME).

Glumes and glumelles were removed from shed spikelets. Only mature seeds (easily recognized by size and color) were counted. The shedding sequence was characterized by the number of harvested seeds (SHEDNUM), the initial date of shedding (SHEDT0), and the shedding time (SHEDTIME).

The seed set of each panicle was defined at the end of shedding by SHEDNUM/FLONUM.

Statistical methods—One-way ANOVA (fixed-effect) was used to test between-clone differences. When an effect was significant, the Newman–Keuls test was used for multiple comparison of means.

For each trait, relative within-clone diversity was estimated using the following formula:

$$V_w = \sqrt{MS_r}/\bar{X}$$

where MS_r is the residual mean square of the ANOVA, and $\bar{X}$ is the mean.

One-way ANCOVA was used to test the presence of within-clone regressions and their parallelism. Note that in all cases we checked graphically the assumption of linear regression. The within-clone squared correlation coefficient R^2 was computed to quantify the importance of the relationship. In some cases, the partial squared correlation coefficient was also estimated. All statistics were obtained using Statistica software, except for V_w and the partial squared correlation coefficient, which were estimated using a simple calculator.

RESULTS

Some mosquito nets were destroyed by wind in the case of clones 267 and 64, reducing the panicle number to eight and five, respectively.

Within-clone diversity—Three groups of traits were distinguished from their relative diversity within clones. The first group (middle diversity) included traits related to panicle size, i.e., exsertion height (V_w = 17.4%), number of flowered spikelets (V_w = 17.4%), and maximal intensity of flowering (V_w = 24.7%). The second group (low diversity) included dates and times: exsertion time (V_w = 9.7%), flowering time (V_w = 8.5%), initial date of shedding (V_w = 8.2%), and shedding time (V_w = 12.0%). The last group (high diversity) included seed number (V_w = 36.8%) and seed set (V_w = 43.9%). This high diversity included variation in the number of flowered spikelets, but also random fluctuations in the occurrence of successional events: deposition of pollen, germination of the pollen grain, parthenogenesis triggering, and seed ripening.

TABLE 1. Within-clone relationships in principal panicles. Two statistical tests were realized for each variable combination. The first tested presence of a within-clone regression, the second tested the nonparallelism of the within-clone regression.

	Variable combination	Within-clone regression	Non-parallelism
EXSEND	EXSH	37.5***	0.38 NS
	FLOTIME	0.06 NS	1.35 NS
	FLONUM	1.60 NS	0.32 NS
	FLOMAX	0.28 NS	1.74 NS
	SHEDT0	0.48 NS	1.52 NS
	SHEDTIME	0.00 NS	1.10 NS
	SHEDNUM	0.09 NS	0.41 NS
	SEED SET	0.19 NS	0.21 NS
EXSH	FLOTIME	0.10 NS	1.26 NS
	FLONUM	6.86*	1.20 NS
	FLOMAX	1.60 NS	5.43**
	SHEDT0	0.01 NS	1.58 NS
	SHEDTIME	0.00 NS	2.34 NS
	SHEDNUM	0.07 NS	1.53 NS
	SEED SET	1.33 NS	1.11 NS
	EXSEND-FLOTIME	13.9***	1.82 NS
FLOTIME	FLONUM	0.34 NS	2.01 NS
	FLOMAX	5.23*	1.13 NS
	SHEDT0	0.00 NS	0.77 NS
	SHEDTIME	0.16 NS	0.77 NS
	SHEDNUM	2.12 NS	0.38 NS
	SEED SET	1.29 NS	0.46 NS
FLONUM	FLOMAX	26.2***	5.76**
	SHEDT0	0.16 NS	0.52 NS
	SHEDTIME	0.04 NS	0.24 NS
	SHEDNUM	0.36 NS	1.18 NS
	SEED SET	1.24 NS	0.29 NS
	SHEDT0-FLOTIME	0.49 NS	0.26 NS
FLOMAX	SHEDT0	2.41 NS	0.10 NS
	SHEDTIME	0.30 NS	0.37 NS
	SHEDNUM	3.02 NS	2.35 NS
	SEED SET	0.09 NS	1.32 NS
	SHEDT0-FLOTIME	0.18 NS	0.38 NS
SHEDT0	SHEDTIME	37.0***	2.08 NS
	SHEDNUM	9.97**	5.80**
	SEED SET	6.71*	2.75 NS
SHEDTIME	SHEDNUM	10.9**	5.72**
	SEED SET	8.60**	5.01**
SHEDNUM	SEED SET	82.6***	0.77 NS

NS: $P > 0.05$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

Within-clone relationships—Table 1 summarizes all within-clone relationships. The exsertion time was only related to the ultimate height (R^2 = 57%). More interesting was the exsertion time's independence of other dates and times (flowering and shedding). Independence

TABLE 2. Mean comparison. Index letters indicate results of the Newman–Keuls test.

		C1	64	2A4	267	$F_{3,29}$	Significance
Exsertion	EXSH	41.0^b	10.3^a	50.8^c	55.2^c	55.6	***
	EXSEND	10.9^b	8.4^a	10.6^b	13.0^c	20.0	***
	EXSH/EXSEND	3.76^b	1.19^a	4.78^d	42.4^c	87.1	***
Flowering	FLONUM/EXSH	7.7^a	49.2^b	12.4^a	10.6^a	19.6	***
	FLOTIME	7.60^a	8.60^b	10.7^c	11.4^c	40.6	***
	FLONUM	311.9^a	392.2^a	627.4^b	576.3^b	29.0	***
	FLOMAX	84.2^a	117.4^a	105.4^a	104.5^a	2.41	NS
	FLOMAX/FLONUM	0.272^b	0.292^b	0.170^a	0.180^a	23.7	***
Shedding	SHEDT0	10.1^b	11.0^{bc}	8.8^a	11.3^c	15.2	***
	SHEDTIME	8.40^a	8.40^a	9.90^b	10.4^b	6.63	***
	SHEDNUM	60.9^b	95.0^c	30.4^a	76.6^{bc}	11.4	***
	SEED SET	0.194^c	0.248^c	0.051^a	0.135^b	14.2	***
Discrepancies	EXSEND-FLOTIME	3.30^c	−0.20^a	−0.10^a	1.63^b	13.9	***
	SHEDT0-EXSEND	−0.80^a	2.60^b	−1.80^a	−1.75^a	15.8	***
	SHEDT0-FLOTIME	2.50^c	2.40^c	−1.90^a	−0.13^b	29.1	***

NS: $P > 0.05$; ***: $P < 0.001$.

means that the end of exsertion did not trigger the end of flowering and the beginning of shedding.

The exsertion height was positively related to the number of flowered spikelets (R^2 = 20%), but this relationship could simply express differences in panicle size. The second relationship with the exsertion height concerned the time between the end of exsertion and the end of flowering: the larger the exsertion, the greater the discrepancy (R^2 = 33%). The exsertion height also influenced the flowering maximum, but only in clone 64.

The flowering time of panicles did not depend on the number of their flowered spikelets. This explains why the maximum of the flowering peak (FLOMAX) was positively related to FLONUM (R^2 = 43%). Within-clone regressions were parallel, showing a similar increase in the flowering peak per flowered spikelet for all clones. By contrast, a longer flowering time led to a lower flowering peak (R^2 = 16%), indicating a trade-off effect. The relationship became more marked when FLONUM was considered as constant (R^2_{xyz} = 44%). Within-clone regressions were parallel, meaning a similar decrease in the flowering peak for all clones when flowering time increases.

No flowering traits were correlated with those of shedding. In particular, the flowering time affected neither the date of the beginning nor the time of shedding, and the number of flowering spikelets was independent of the number of seeds.

A delayed beginning of shedding shortened shedding time (R^2 = 57%) and lowered seed set (R^2 = 25%) in all clones. Within-clone regressions were parallel, meaning a similar decrease in seed set for all clones when the delay increased. The delay also led to a decrease in the seed number, but only in clones 64 and C1 (R^2 = 60%).

The shorter the shedding time the lower the seed set (R^2 = 24%), but this relationship can be expected from the effect of delay on shedding time and seed set. A shorter time of shedding led to a smaller number of seeds, but only in clones 64 and C1 (R^2 = 46%).

The seed number was related positively to seed set in all clones. Within-clone regressions were parallel, indicating a similar increase in seed production for all clones when seed set increased.

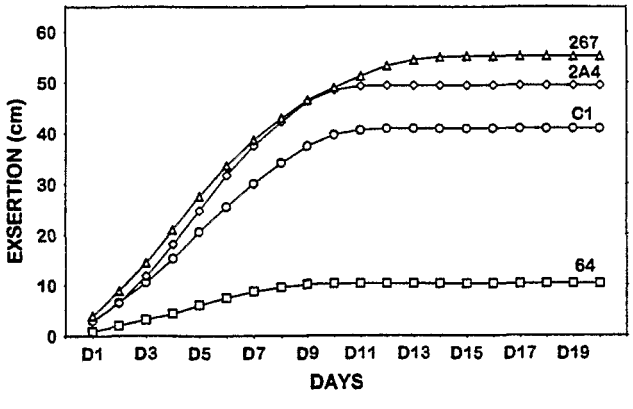

Fig. 1. Averaged exsertion of principal panicles of clones 64, C1, 2A4, and 267. Each point is the mean of eight to ten observations.

Between-clone differences—The observed means and their comparisons are given in Table 2. The exsertion height distinguished clone 64 (10 cm) from the others (Fig. 1). Its low exsertion was a trait originating from *P. trichocladum*. The exsertion time showed large differences, contrasting clone 64 (8.4 d) with clone 267 (13.0 d). Clones C1 and 2A4 had an intermediate time of exsertion (10.6–10.9 d) significantly different from the former. The average speed of exsertion, estimated by EXSH/EXSEND, distinguished clone 2A4 (4.8 cm/d) from clone 64 (1.2 cm/d). Clones C1 (3.8 cm/d) and 267 (4.2 cm/d) were significantly different between themselves and from clones 2A4 and 64.

Flowering showed a maximum 3–5 d after D_1 (Fig. 2) for all clones. By contrast, its duration differed between clones. Clone C1 had the shortest flowering (7.6 d), followed by clone 64 (8.6 d) and clones 2A4 and 267 (11 d on average).

The number of flowering spikelets also showed clonal differences. Clones C1 and 64 produced, on average, 312 and 393 flowered spikelets, respectively. This number was almost doubled in clones 2A4 (627 spikelets) and 267 (576 spikelets). By contrast, the maximum of the flowering peak was similar for all clones. This explains why the relative intensity of the peak (FLOMAX/FLONUM) contrasted clones C1 and 64 (peak with

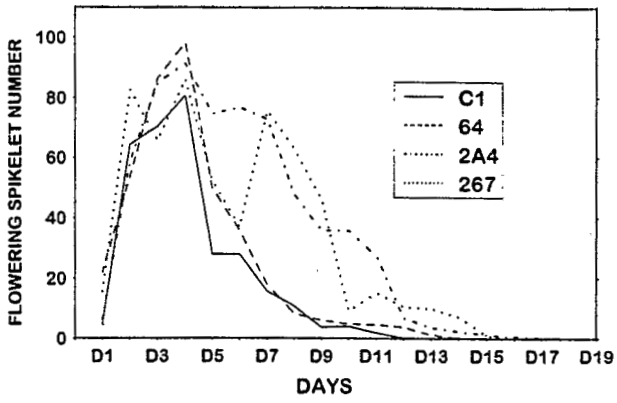

Fig. 2. Averaged flowering in principal panicles of clones 64, C1, 2A4, and 267. Each point is the mean of eight to ten observations.

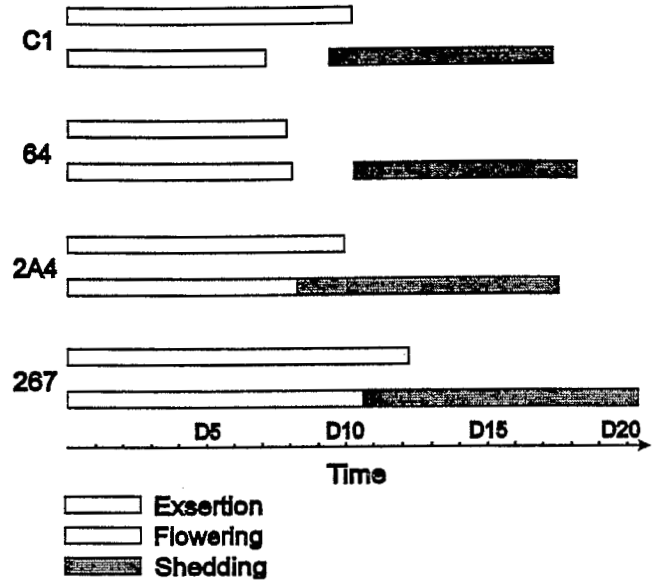

Fig. 3. Timing of exsertion, flowering, and shedding in clones 64, C1, 2A4, and 267. Shedding clearly overlapped flowering for clone 2A4, and slightly for clone 267.

28% flowered spikelets) with clones 2A4 and 267 (staggered peak with only 17.5% flowered spikelets). To summarize, two types of flowering pattern were evident, differing in the flowered spikelet number, the flowering time, and the relative intensity of the flowering peak.

Clonal differences appeared in shedding. In particular, shedding began 8.8 d after D_1 in clone 2A4, i.e., 1.3–2.5 d earlier than in other clones. The shedding time again contrasted clones 2A4 and 267 with clones C1 and 64. The more staggered the flowering the more staggered the shedding. The seed number contrasted clone 64 (the highest production with 95 seeds per panicle) with clone 2A4 (30 seeds). Seed set was low (<25%), but it differentiated clones: 2A4 (5.1%), 267 (13.5%), C1 (19%), and 64 (24.8%).

Clonal differences were emphasized for the "flowering end–shedding beginning" (F–S) discrepancy. Flowering ended 3.3 d, on average, before exsertion in clone C1. This discrepancy was halved in clone 267, and became nil for clones 64 and 2A4. When the discrepancy was corrected using EXSH as covariate, flowering ended 3.1 d, on average, before exsertion in clones C1 and 64, whereas it was almost simultaneous in clone 267 (−0.2 d) and delayed (−1.4 d) in clone 2A4. This ranking, which corresponded to that of seed set, was also that of the F–S discrepancy. Between-clone correlation between F–S and seed set was high and significant (r = 0.956). In clones C1 and 64, flowering ended ≈2.5 d before shedding (Fig. 3). In clone 267, flowering was achieved when shedding began, whereas the two processes partially overlapped (2 d) in clone 2A4. Clonal differences existed also for EXSEND-SHEDT0. Shedding began 1–2 d before EXSEND, except for clone 64 (2 d later). Note that clonal differences disappeared ($F_{3,28}$ = 0.56 NS) when EXSH was used as covariate.

DISCUSSION

Dates and timing: stability and rapidity, practical consequences—Within a clone and in a well-defined environment, the stability of dates and times characterized the three processes—exsertion, flowering, and shedding. In addition, dates and times were independent of the flowered spikelet number, and the result is consistent with our previous studies (Noirot, 1992). Dates and times were also independent (except for time and date of beginning of shedding). Thus, the end of flowering was not controlled by the end of exsertion. In addition, the beginning of shedding was neither related to the end of flowering nor to that of exsertion.

Dates and times reflected mainly fast processes. Within-panicle flowering lasted 8–11 d. In comparison, within-inflorescence flowering lasts 7 and 2 wk in *Setaria sphacelata* and *Choris gayana* (two other tropical grasses), respectively (Boonman, 1971a). Seed ripening, estimated by the date of shedding of the first seed, lasted 9–11 d. This is a relatively short time in Poaceae.

In a practical approach, knowledge of flowering and shedding discrepancies are of great importance for the harvest. In *P. maximum,* panicle branching leads to several heading waves, which are less and less intense, and which are constituted by panicles with fewer and fewer spikelets (Noirot and Ollitrault, 1992). Consequently, it is advisable to harvest on the first heading wave. Several methods can be used: bagging, reaping followed by ripening in hay, or the combine harvester. Whatever the method, knowledge of the seed ripening time permits the definition of the harvest date. In the first case, for example, bags must be established when most principal panicles just end their flowering, and then must be harvested ≈10 d later. As there are differences in behavior between varieties, the dates of harvest must be defined for each variety.

Clonal differences in flowering behavior—Two main flowering behaviors were emphasized and contrasted: 2A4 and 267 vs. C1 and 64. The principal difference concerned the number of flowered spikelets, which was larger in 2A4 and 267. The difference can be partially explained by panicle size variation. Nevertheless, for 267, the number of flowered spikelets was clearly smaller than its averaged number of spikelets per panicle (≈2400

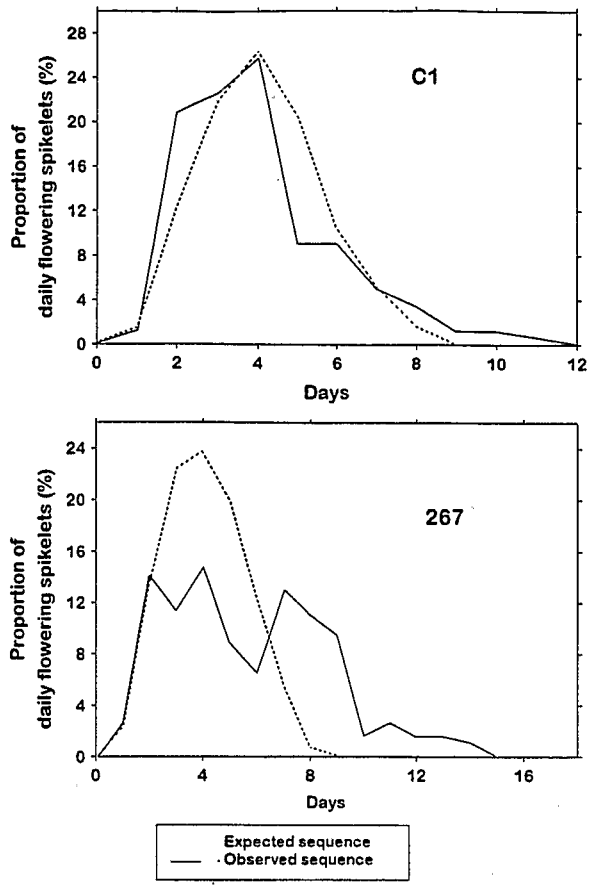

Fig. 4. Expected and observed flowering sequence in principal panicles of clones C1 and 267. The expected sequence was computed from Noirot's (1992) data for C1 and 267. The observed sequence corresponds to data of the current study.

spikelets). This suggests no flowering for many spikelets in this clone. Similar observations were described in *Lolium perenne* (Anslow, 1963), and in many other Poaceae by Jones and Brown (1951).

The second difference concerned the relative intensity of the flowering peak and the flowering time. A peak intensity proportional to the spikelet number and a 7- to 8-d flowering time independent of panicle size (Fig. 4) are expected (Noirot, 1992). This behavior was indeed observed in clones C1 and 64. By contrast, the two other clones showed a lower relative intensity of flowering peak and a longer flowering time (11 d). A panicle shape difference could explain, through a change in the spikelet distribution in the sheath, the difference in flowering behavior, but this hypothesis can be easily rejected by a simple visual observation. A lowering of the spreading speed of flowering could also lead to a reduction in the number of flowered spikelets at the date of maximal flowering and to a staggered time of flowering. This hypothesis is consistent with the within-clone correlation we observed between peak intensity and the flowering time, even in clones C1 and 64. A delay in within-inflorescence flowering was also recorded by Jones and Brown (1951) in various Poaceae. According to these authors, this trade-off in the flowering behavior, as well as the absence of flowering of some spikelets, may be related to the presence of some unfavorable conditions.

Seed set, seed production, and flowering behavior—In our experiments, seed set was defined as the "seed number / flowered spikelet number" ratio. In the case of clones C1, 64, and 2A4, this definition is close to the classical definition "seed number/spikelet number" (seed set s.s.). Our parameter should, nevertheless, strongly overestimate seed set s.s. in clone 267 for which some spikelets did not flower. Nonetheless, our observations on seed set (5–22%) are consistent with those (4.5–48.7%) observed in *P. maximum* in Puerto Rico (Warmke, 1951), although they are in the lowest part of this range.

Within clones, seed set did not relate to flowering traits. In particular, it did not depend on the number of flowered spikelets. By contrast, a between-clone relationship was emphasized between the seed set and the degree of flowering–shedding overlap. The lowest seed set characterized the 2A4 clone with the largest overlap. This overlap occurred not only due to a later end of flowering, but also because of faster seed ripening in this clone.

A low seed set could explain the lower seed production (on a farming scale) of the clone 2A4 at Man (50 kg/ha) than at Bouaké (250 kg/ha). The production components (heading intensity and panicle size) were similar for the two regions (personal observations). In addition, we showed that within panicles, the number of flowered spikelets was independent of the seed number.

Seed set could be one of the main limitations to the seed production of *P. maximum.* Indeed, bagging, which is the most efficient harvest method in terms of yield per hectare, only allows harvesting of 10% of the flowering potential (Noirot, 1990). We infer that an averaged seed set of 20% explains 50% of the discrepancy. This shows clearly that improvement of seed set constitutes one of our major aims.

Competition between exsertion and flowering: a hypothesis—The sigmoidal shape of the exsertion curves (Fig. 1) shows that exsertion virtually began with flowering, and that the two processes overlapped considerably. The processes also concern a mode of growth by auxesis (internode elongation, stigma and stamen exsertions). The importance of the competition appeared through the within-clone relationships between the height of exsertion on the one hand, and the number of flowered spikelets and the "end of exsertion-end of flowering" discrepancy on the other. References to this type of relationship are scarce in the literature. Nevertheless, a study on water stress applied to *Sorghum* (Santamaria, Ludlow, and Fukai, 1990) showed that varieties with low osmotic adjustment had a later and lower flowering, whatever the earliness of their heading. These results are consistent with a hypothesis of water competition between exsertion and flowering. The stressed *Sorghum* varieties with low osmotic adjustment also produced fewer seeds.

Flowering time and inflorescence branching—Branching consists of panicle emergence at regular time intervals from the second and third node located under the principal panicle. Such a process, called inflorescence branching, was recorded in barley (*Hordeum vulgare*) by

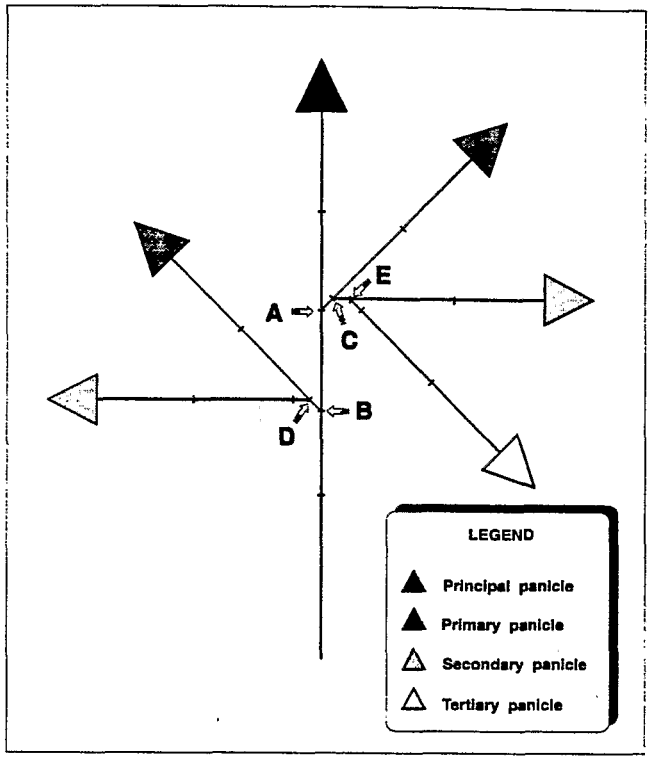

Fig. 5. Diagram of a fertile tiller of the C1 clone at the six-panicle stage. The alphabetical order A, B, C, D, and E of the branching node symbolizes the chronological order of panicle emergence (from Noirot, 1991).

Aspinall (1961) and in *Panicum coloratum* and *Setaria sphacelata* by Boonman (1971b). This phenomenon was also studied in *P. maximum:* a first primary panicle emerges at node A, then a second one at node B (Fig. 5). These are followed by a first secondary panicle at node C, etc. The process is theoretically indeterminate with, in this case, 10 d of between-panicle time discrepancy. In practice, the process is limited (up to six panicles were observed in C1 on <1% of fertile tillers) and the shortest discrepancy was 12 d. In fact, branching stops when the discrepancy exceeds 20 d (delay > 10 d) (Noirot, 1991).

Timing of flowering, exsertion, and ripening appear to be integrated into the process of inflorescence branching. The emergence of a new panicle on a fertile tiller happens when the exsertion and the flowering of the former panicle end, avoiding between-panicle competition.

Similarly, shedding generally began when panicle flowering ended, except in clones 267 and 2A4 for which we observed slight overlap at Man. On a fertile tiller there are never two panicles simultaneously in the seed ripening phase. The competition for nutritional elements necessary to elaborate the seed are thus limited to the within-panicle competition.

To summarize, the timing of flowering, seed ripening, and panicle branching seems to minimize competition processes between panicles produced by a tiller. Several points corroborate this hypothesis: (1) the arrest of branching, when discrepancy between two panicle emergences exceeds 20 d, avoids overlap of the three processes; (2) within a plant, the most vigorous tillers have the most marked branching; and (3) between clones, the lower the intensity of branching, the larger the panicles (Noirot, 1990).

Two reproductive patterns can be recognized. In one case, the reproductive investment of a tiller is essentially in a large principal panicle (clones 267 and 2A4, for which panicle number per fertile tiller is two times lower than in C1) and lasts 2–3 wk (Noirot, 1990). In the other case, the reproductive investment of a tiller is several smaller panicles (clones C1 and 64) and lasts up to 2 mo. All intermediate behavior exists, but the presence of this polymorphism within the species shows that these two patterns have either a similar fitness or an environment-dependent fitness. Further studies on this subject appear of great interest in relation to the mode of reproduction.

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