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The within-panicle flowering sequence in *Panicum maximum* 1. A well-determined process

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Abstract

The total number of spikelets in a panicle is related quadratically to panicle size. Spikelet distribution along the panicle axis, before exsertion, is the same, between small and large panicles, within or between clones. The speed of the basipetal spread of flowering is proportional to the mean size of the panicles of the clone. The daily number of flowering spikelets can be predicted every day. Its relation to panicle size is also quadratic. Consequences for the requirements of water and energy are also quadratic. The multiplicity of the reproductive strategies (small or large panicles) is discussed in relation to culm branching (NOIROT, 1991) and adaptation to variable rainfall in a tropical environment.

Keywords: *Panicum maximum*, panicle size, flowering sequence, spikelet distribution, requirements

Résumé

Le nombre total d'épillets d'une panicule est une fonction quadratique de la taille de l'inflorescence. La répartition des épillets le long de l'axe paniculaire, avant l'exertion, est la même, au facteur de taille près, entre petites et grandes panicules, à l'intérieur, comme entre les clones. La vitesse de propagation basipète de la floraison diffère entre clones et est proportionnelle à la taille moyenne de la panicule. Le nombre d'épillets en fleur chaque jour peut être prévu. Il suit aussi une fonction quadratique de la taille de l'inflorescence. Les conséquences sur les besoins en eau et énergie sont du même ordre. La multiplicité des stratégies reproductives (grandes ou petites panicules) est discutée en relation avec l'apparition successive de panicules par ramification (NOIROT, 1991) et l'adaptation aux fluctuations de pluviométrie en milieu tropical.

INTRODUCTION

Panicum maximum is an apomictic and perennial grass from Kenya and Tanzania (COMBES, 1975; PERNES, 1975). Cultivated as fodder throughout the tropical regions, its commercialization is often hindered by its low seed production (HUMPHREYS, 1975). As with many other tropical grasses, staggering of the flowering, and shedding at maturity constitute the main problem (BOONMAN, 1971).

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The sources of the staggering of flowering are varied. Thus, panicles of a plant are not synchronous, due to heterogeneity of tillers with respect to the inductive conditions (NOIROT & OLLITRAULT, 1992), and culm branching (NOIROT, 1991). An other source of staggering derives from the flowering sequence of spikelets within a panicle. WARMKE (1951, 1954) and JAVIER (1970) have shown that: 1°/ the complete exsertion of the panicle lasts three days; 2°/ the flowering begins with the first spikelets located at the top of the panicle, and spreads downwards; 3°/ flowering occurs every day at the same time, which differs between varieties and lasts 80 min to 3 hours or more; 4°/ half of the spikelets have flowered 9 days after the beginning of exsertion.

Within a panicle, spikelets located on different racemes flower simultaneously. Manually bringing together of all racemes along the panicle axis restores the spikelet to the position they occupied in the sheath before exsertion and it is then easy to verify that the flowered spikelets are grouped together (NOIROT, pers. obs.). This led us to the following hypothesis: the flowering date of a spikelet is determined by its pre-exsertion location along the panicle.

The panicle is a structure with ramifications. According to FRANQUIN (1972, 1985), the number of ramifications of each order at any time can be derived from a Pascal triangle. The number of nodes of the order r ramifications is quadratically related to the number of nodes of the order r-1 ramifications. Thus, a relation of type $y = n^{2r}$ should exist between the number of spikelets (y) and the number of nodes (n) of the axis of panicle (r is the order of the spikelet considered as ramification). In addition, all nodes of same physiological age should flower simultaneously.

Panicle size is known to be highly variable in *Panicum maximum* (WARMKE, 1954; JAVIER, 1970; PERNES, 1975). Node number and internode length should explain such diversity. According to the previous model, differences in node number imply that a polynomial relation should exist between spikelet number and the panicle size. These differences are determined as early as the stage of branching *primordia* (GILLET, 1980) and are due to differences of vigour of the tiller at the induction stage as in *Phleum pratense* (BEAN, 1970).

In this paper, the flowering sequence of spikelets is determined. The relation with the first stages of floral development are emphasized. The consequences of the relation between spikelet number and panicle size on instantaneous requirements during flowering are discussed.

MATERIALS AND METHODS

The following definitions were used:

– the flag stage was characterized by the emergence, at the flag level, of the first spikelet from the sheath;

– the first inflorescence of a fertile tiller was a principal panicle;

– the panicles, occurring at the second and third node under the principal panicle, were primary panicles (NOIROT, 1991);

– the culm branching was the process, which led to the emergence of primary panicles under the principal panicle of a fertile tiller.

In *P. maximum*, the spikelet showed two flowers, the first to flower being hermaphrodite. According to the variety, the second flower was either male or sterile. In our experiment, we only took into account the flowering of the hermaphrodite flower.

Three apomictic accessions – C1, 267 and T58 from the live collection maintained at the Research Station of Adiopodoumé (Côte-d'Ivoire) – were selected as being representative of the range of wild-type diversity. The C1 variety had narrow tillers and leaves, and produced small panicles (about 16 cm). Accession 267, growing at the roadside in the low coastal region of Côte-d'Ivoire, was also called Common Guinea. Its panicle was medium size (about 28 cm). The T58 variety was a type with a large panicle (about 40 cm). Owing to their mode of reproduction, these varieties were clones.

The main aim is to explain the number of daily flowered spikelets in a panicle of each of these varieties. Two experiments were made. The first studied the distribution of spikelets in the sheathed panicle, the second examined the flowering date of spikelets in relation with their pre-exsertion location in the sheathed panicle. This latter provided information on the spreading speed of flowering along the panicle. The experiments took place during heading in September-October, with five-year-old plants of the collection.

In the first experiment, for each accession, ten principal panicles were simultaneously sampled at the flag stage. Each panicle was cut into 2cm segments. These segments were numbered from the top of the panicle, and their spikelets were counted. For each accession, a 10-line table (the panicles) was obtained, where the different segments each constituted a variable (see table I). The sum of these variables gave the number of spikelets of the panicle. Correspondence analysis (Benzecri, 1973) was applied to each of the three tables in order to identify factors of variation.

Table I. – *Data used for correspondence analysis. This table corresponds to the C1 Variety. Columns represent the different 2 cm-length sector. The upper sector of the sheathed panicle is the sector 0-2 cm, the lower is the sector 18-20 cm (in many panicles, this last sector is located under the panicle and does not contain any spikelet). Each line corresponds to a panicle.*

0-2 cm	2-4 cm	4-6 cm	6-8 cm	8-10 cm	10-12cm	12-14 cm	14-16 cm	16-18 cm	18-20 cm
18	13	47	44	25	14	4	0	0	0
13	28	45	50	49	28	18	8	3	0
20	35	53	58	50	31	21	13	5	0
20	38	53	54	43	28	20	8	2	0
18	37	48	44	21	11	3	0	0	0
15	36	47	51	38	24	14	5	1	0
16	35	43	54	50	25	21	8	3	0
23	43	64	70	59	37	26	15	4	1
15	35	45	52	57	29	19	13	6	0

In the second experiment, for each clone, four samples of five principal panicles at the flag stage, corresponding to different treatments, were tagged the same day. Except for the reference sample, the treatment involved cutting the sheath (and hence the panicle) at a given distance from the flag (and so from the top of the panicle) related to the mean size of the panicle. For the C1 variety, for example, the different cut levels were 4, 8 and 12 cm. For accessions 267 and T58, they were respectively 6, 12, 18 cm, and 8, 16, 24 cm. This topping led to the exsertion of truncated panicles. On each panicle, the date of emergence of the first stigma was noted. The experiment was repeated about 15 days later (heading date factor), but also on primary panicles (panicle order factor). Thus, there were 15 inflorescences per clone and per treatment. Heading dates were different between clones (they had not the same precocity) and between panicle order. A three-way analysis-of-variance was applied to test effects of clone, heading date, panicle order and interaction on the date of first flowered spikelet; heading date was a random-effects factor, nested to the fixed-effects factors clone and order. Expected mean squares were calculated

using the method of BENNETT and FRANKLIN (1954) (see SCHEFFE, 1959; p. 284-289). Thus, clone effects, order effects and clone·order effects were tested against the heading date mean square, whereas heading date effects was compared to the residual mean square. A second three-way analysis-of-variance tested the same effects on the parallelism of the regression lines between time (date of the first flowered stigma) and pre-exsertion location on the sheathed panicle (cutting treatment). Mean coefficients of regression b_{xy} were estimated when the parallelism hypothesis was not rejected; they gave the speed of spreading of flowering according to the pre-exsertion location of the spikelet on the sheathed panicle.

RESULTS

Spikelet distribution on the principal panicle at the flag stage

The number of spikelets per panicle varied within a clone. It could be estimated knowing the spikelet number of a definite sector ($R^2 > 96\%$). In the C1 variety, this sector was located between 7 and 9 cm from the top of the panicle. In the varieties 267 and T58, it was located respectively at 12-14 cm and 16-18 cm from the top. This roughly corresponds to the mid-panicle.

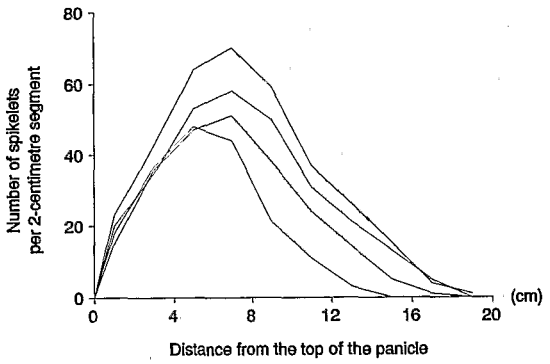

FIG. 1. – Spikelet distribution on four panicles of the C1 variety, sampled at the flag stage. The curves are mathematically similar.

The spikelet distribution on the sheathed panicle also showed within-clone variability (fig. 1). For each of these three accessions C1, 267 and T58, more than 70% of this variability was explained by a single factor, contrasting the small and the large panicles.

Analysis of between-clone diversity gave approximately the same results: the observed differences between distributions were related to size variations. Figure 2 shows the mean distribution of spikelets. The triangular form and the asymmetrical appearance were common to the three accessions. The spikelet distribution of T58 seemed to be defined by direct analogy with the spikelet distributions of 267 or C1.

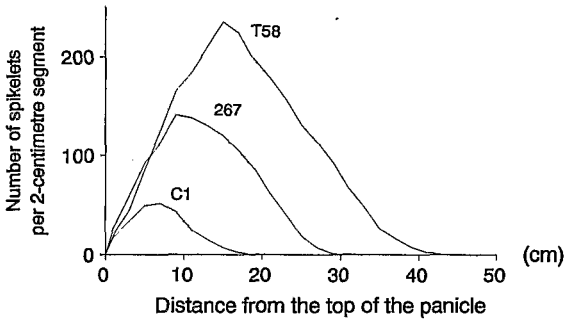

FIG. 2. – Mean distribution of spikelets in the sheathed panicle for three clones of different sizes.

Modelling of the spikelet distribution in the sheath

The model is designed to explain the relation between spikelet distribution and panicle size. The spikelet distribution in the sheath depends on the overlapping of panicle racemes, when these are grouped together along the axis.

Figure 3a shows a simplified model of an inflorescence. Simple torsion of the axis is sufficient to generate the panicle in space. This model contains some simplifying hypotheses:

– the racemes are equally spaced along the axis;

– the spikelet distribution is uniform on the raceme.

The exserted inflorescence (fig. 3a) is characterized by an angle α such that tan (α) = AB/BE = 2/3. This corresponds to the mean form observed in *P. maximum*. The second scheme (fig. 3b) shows the successive overlapping of racemes in the sheathed panicle. This leads to the theoretical distribution of spikelets in the sheath (fig. 3c). The resemblance to figure 2 is striking. This shows how the spikelet distribution of a large panicle (AB) is defined by direct analogy with a smaller panicle with 4 racemes (AC) or 7 racemes (AD).

According to this model, a doubling of panicle height results in a four-fold increase in spikelet number.

Progress of flowering on the panicle

In the C1 variety, the first stigma occurred at a mean of 2.6 days after the flag stage. This interval was 2.5 days in 267 and 3.7 days in T58. Nevertheless, these variations between clones were not significant (risk $\alpha > 20\%$) (see table II). Effects of panicle order, interaction and heading date were also not significant, although heading date effects were nearly significant (risk $\alpha = 5.2\%$).

The speed of spread of flowering was greater as the clone produced large panicles (fig. 4):

C1: 1.95 cm/day (r=0.98) (*)
267: 4.08 cm/day (r=0.98)
T58: 5.92 cm/day (r=0.99)

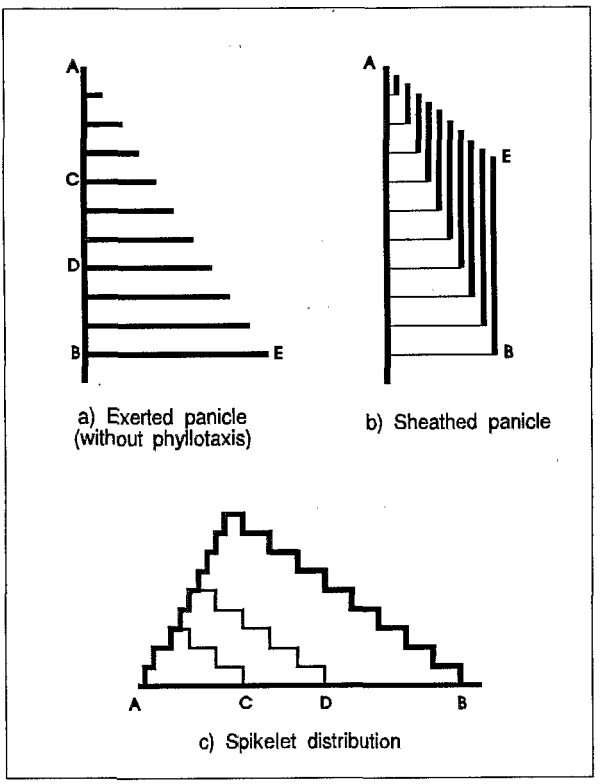

FIG. 3. – Schematic representations of the spread or sheathed panicles: a) spread panicle without phyllotaxis; b) the same panicle, but sheathed, with its racemes represented in a parallel direction to the axis (fine lines show the projection of the raceme insertion points); c) the spikelet distribution, expected from raceme overlapping, for three panicles of different sizes.

TABLE II. – *ANOVA of the trait "Date of the first flowered spikelet in the untruncated panicles". Factors were clone, order and heading date. Heading date was nested to clone and order. Clone and order were fixed-effects, whereas heading date was a random-effect.*

Source of variation	SS	df	MS	F	Significance
Clones	7.244	2	3.122	0.800	NS
Order	0.011	1	0.011	0.003	NS
Clone.Order	1.356	2	0.678	0.174	NS
Heading date\Clone.Order	11.700	3	3.900	2.832	NS
Residual	49.600	36	1.377		
Total	69.911	44			

(*) These estimations were computed using the means of each treatment (see Fig. 4).

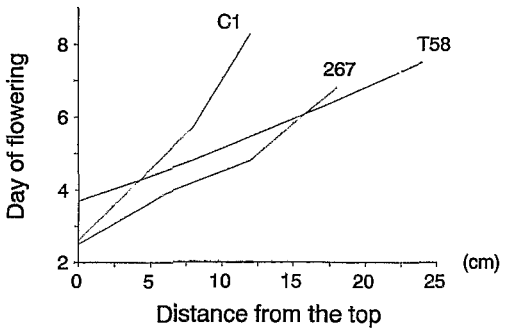

FIG. 4. – Time course of spikelet flowering in relation to its location into the sheathed panicle. The lowest slopes correspond to the shortest times, i.e. to the greatest speeds.

TABLE III. – *ANOVA table for testing effects of clone, order, clone. order and heading date on the parallelism of the regression lines between time (date of the first flowered stigma) and pre-exsertion location on the sheathed panicle (cutting treatment). Heading date was nested to clone and order.*

Source of variation	SS	df	MS	F	Significance
Linear regression	358.905	1	358.905	227.85	***
Clone	38.854	2	16.427	10.43	***
Order	4.258	1	4.258	2.70	N.S.
Clone.Order	0.415	2	0.208	0.13	N.S.
Heading date\Clone.Order	11.807	3	3.936	2.50	N.S.
Residual	229.98	146	1.575		
Total	638.219	155			

TABLE IV. – *Mean times (in days) of the maxima and the end of flowering in three clones C1, 267 and T58. The time origin T0 is given by the beginning of the flowering. Mean times of each clone were computed knowing the mean distribution of spikelets and the mean speed of spreading of the flowering.*

	Time of maximal flowering	Time of the end of flowering
C1	3.08	9.2
267	2.45	7.1
T58	2.53	6.8

These speeds remained approximately constant along the panicle. In addition, the speed of spreading was not changed either by the heading date of panicle or by the panicle order (principal or primary) or by interaction clone order (see table III).

Knowing the spikelet distribution in the sheathed panicle and the speed of spreading of the flowering, in reference to the pre-exsertion location of the spikelet, the expectation of the daily number of flowered spikelets became possible. Table IV gives the mean expected times needed to reach the maximum and the end of flowering of a panicle. In the three accessions, the maximum was reached three days after the appearance of the first stigma. The flowering of a panicle lasted about 7 to 9 days according to the clone.

DISCUSSION

The flowering sequence: a process determined from the first stages of floral development

The simultaneously flowering spikelets, distributed on many different racemes, arose from the same sector of the sheathed panicle. Every day, successive sectors flowered. Prediction of the daily number of opened spikelets depends then on the speed of spreading of flowering along the panicle. This speed was constant and characterized the clone. It did not depend on either the heading date or on the order of the panicle (principal or primary). The expected dates of the maximum of flowering (3 days after the flag stage) and of the end of flowering (7 to 9 days after the first opened spikelet) were compatible with the data of the literature (JAVIER, 1970; WARMKE, 1951; WARMKE, 1954). This shows three points:

– firstly, under normal conditions of flowering, the spread of flowering was a well-determined process;

– secondly, cutting treatment had no (or little) effect on the speed of flowering;

– thirdly, the speed of spreading of the flowering was proportional to the panicle size. Thus, the flowering duration (7 to 9 days) was similar whatever the panicle size.

The number of spikelets in a panicle was highly correlated with the number of spikelets in the mid-panicle before exsertion. This median location was also the one of the "double-ridges" at the outset of floral development (BLONDON, 1968). This was not the only relation with the beginning of the floral morphogenesis. Within or between clones, variation in spikelet distribution was due to size variation of panicles. A single factor explained this variability: vigour of mitosis in the floral meristem resulting in the final size of the inflorescence, as in *Phleum pratense* (BEAN, 1970). This factor determined the number of tiers of the panicle as early as the stage of branching *primordia* (GILLET, 1980). Thus, the number of spikelets per inflorescence and their distribution are controlled by a single process, determined during the earliest stage of floral development.

The simplified model of panicle structure and its relation to FRANQUIN's model

Our simplified model of panicle structure explains the similarity of spikelets distribution between small and large panicles, despite some limiting assumptions, such as the equal spacing of the racemes along the axis. In fact, such a hypothesis is incompatible with the presence of a verticil on the panicle of *P. maximum*. This implies that the insertion location of the raceme on the axis is independent of spikelet distribution. A lower insertion is equivalent to adding a spikelet-free sector at the bottom of the raceme. This additional hypothesis fits well with the panicle structure, observed since the lower part of racemes did indeed lack spikelets.

This panicle model implies a quadratic relation between inflorescence size and the number of spikelets. This relation follows from FRANQUIN's model of structure in higher plants (1972, 1985). According to this author, the total number of nodes located on all primary branches is a quadratic function of the number of nodes on the principal stem. With our hypothesis of a constant number of spikelets at each

raceme node, the number of spikelets in a panicle is then a quadratic function of the node number of the axis, and thus of panicle size.

The spread speed of flowering and its consequences

According to FRANQUIN's model (1972), nodes occurring simultaneously should bear spikelets with synchronous flowering. Thus, this model implies that the flowering date of a spikelet is determined during the early stages of floral development, when spikelets are forming. A constant speed of branching of the *primordia* corresponds then to a constant speed of flowering along the panicle. Different flowering speeds in clones corresponded to different intensities of cellular division of the initiated meristem. The effect of vigour on the panicle size observed by BEAN (1970) in *Phleum pratense* is comparable.

The speed of flowering was greater in larger panicles, such that the flowering time within a panicle was almost equal for all clones. Thus, the daily number of flowered spikelets will also be related quadratically to panicle size. In *P. maximum* with large panicles, each inflorescence will have much larger instantaneous requirements (quantities of water, phosphorous, light, etc. *per* day).

To avoid such instantaneous requirements, some accessions exhibit culm branching (NOIROT, 1991): a vigorous fertile tiller can produce a new panicle every 12 days. This interval is greater than the time needed for panicle flowering (7 to 9 days). This avoids overlapping of the flowerings of two panicles borne by the same tiller. The fact that the process of culm branching is more frequent in the types with small panicles emphasizes the multiplicity of the reproductive strategies in *P. maximum*. The production of a given quantity of seeds can be reached either by producing a single large panicle, or by generating four simultaneous, half-sized and principal panicles without change on the sequence of the requirements of water and metabolites. Alternatively, culm branching allows the sequential emergence of half-sized panicles with change on the instantaneous requirements. The role of culm branching as an adaptive strategy to environments with highly variable rainfall (NOIROT, 1991) was confirmed. This suggested also the importance of water requirements in the flowering (anthesis and stigma dehiscence).

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