Evidence for a periodic component in the heading in a tropical grass: *Panicum maximum* Jacq

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Abstract

In *Panicum maximum*, the staggering of heading over two months or more, occurs frequently. A culm branching process is one of the main causes, a periodic process largely regulated by branching aptitude of tiller. Culm branching is greater for late sowings. This control in the staggering of reproductive investments may constitute an adaptation to variations in rainfall in the tropical environment.

Keywords: *Panicum maximum*, heading, culm branching, periodicity, dephasing

Résumé

Chez *Panicum maximum*, l'étalement de l'épiaison sur deux mois, voire plus, est un comportement fréquent. Un processus de ramification paniculaire en constitue une des causes principales. Il s'agit d'un phénomène périodique régulé en majeure partie par l'aptitude à ramifier de la talle. Cette aptitude est plus intense chez les semis tardifs. Cette régulation dans l'étalement des efforts reproductifs pourrait constituer une adaptation aux fluctuations pluviométriques en milieu tropical.

INTRODUCTION

Panicum maximum is a perennial grass probably native from Kenya and Tanzania (COMBES, 1975; PERNES, 1975), cultivated as fodder throughout the tropical world. The main hindrance to commercialization of the *P. maximum* fodder varieties is often their low seed productions. The staggering of heading over two months or more, and shedding at maturity are the causes (BOONMAN, 1971 *a*; HUMPHREYS, 1975).

The presence of aerial tillers, growing from axillary buds located above ground, is well-known among the Graminae and *P. maximum* is no exception. Nevertheless, two types of aerial tillers are distinguished, depending on their node number and origin. The first, studied by COMBES (1975), is particularly developed among the accessions with a spreading habit. This tillering type produces aerial tillers from nodes located near the ground following an acropetaly sequence. It is a classical

tillering for which the aerial location is due to a greater internode length than in accessions with a tufted habit. At heading, these tillers show more than two nodes. Such an aerial tillering is frequent in accessions genetically introgressed by *P. trichocladum*. In return, the second type of aerial tillering is very common among the accessions with narrow leaves. In this case, branching occurs from the second and third node under the inflorescence (fig. 1). Such tillering has been noticed in barley by ASPINALL (1961) and in *Panicum coloratum* and *Setaria sphacelata* by BOOMANN (1971 *b*), and is called culm branching. These branchings show only two nodes and a very short first internode (NOIROT, pers, obs.). This process is very interesting in terms of its relations to the chronology of heading.

LEGEND

▲ Principal panicle

◮ Primary panicle
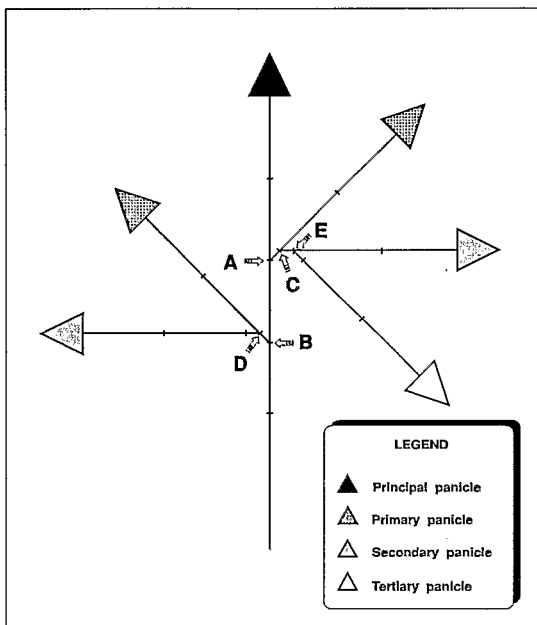
△ Secondary panicle

△ Tertiary panicle

FIG. 1. — Schematic representation of a headed tiller of the variety C1 at the 6-panicle stage. The alphabetic order of the letters A, B, C, D and E (of the branching node) symbolizes the chronological order of emergence of the panicle.

In this paper, I show how the heading of the culm branchings constitutes a periodic process. Comparison with an oscillatory process with damping is propounded. The relation between the branching aptitude and the vigour of tiller, and the effects of this process on the staggering of the heading are discussed in relation to the climatic adaptation.

MATERIALS AND METHODS

The following definitions were used (fig. 1):

— The heading stage is characterized by the emergence of the first spikelet at the flag level.

— The principal panicle is the terminal inflorescence of a fertile tiller.

— The primary panicle is the terminal inflorescence of a culm branching under the principal panicle.

— The secondary panicle is the terminal inflorescence of a culm branching under the primary panicle, and so on.

The observations were made at the Research Station of Adiopodoumé (Ivory Coast). The C1 variety with narrow and numerous tillers was selected for its pronounced ability to produce panicles during two, even three, months.

The first experiment used a plant sown in April. Every day, from September 1 to November 4, the inflorescences were tagged at the heading stage with bits of wool of different lengths and colours. Then, the plant was up rooted and each tiller was separated. Thirty-seven were randomly selected for detailed observation of culm branching. The results allowed 1° the establishment of the sequence of emergence of panicles on a fertile tiller; 2° the list of observed configurations; and 3° the estimation of time intervals between two emergences.

In a second experiment, two lots with respectively 1,118 and 1,033 tillers ([1]) were sampled simultaneously in the first week of November from two different seed-bearer yield. The first lot corresponded to a March sowing, the second to a June sowing. For each lot, the tillers were classified into nine types according to their culm branching (intensity and mode). Frequencies of these nine types were estimated for each sowing date.

The data of this latter experiment were processed by correspondence analysis (BENZECRI, 1973). This statistical method looks for independent factors that explain the observed variability of a contingency table or a frequency table.

RESULTS

Culm branching: a theoretically boundless oscillatory process

A culm branching has only two nodes, only the lowest of which produces a branch. Thus, a primary panicle can produce only one secondary panicle, only one tertiary panicle, etc. (fig. 1).

The process of culm branching can be compared to a pendulum that is swinging between two levels: the second node (node A) and the third node (node B) located under the principal panicle. The process always begins with the development of a primary panicle at level A. The process continues with the development of a primary panicle at level B, a secondary panicle at level A (node C), then at level B (node D), etc. Theoretically, this is a boundless process.

In practice: a great diversity of configurations

Practically, no tiller with 7 panicles was observed among the 2,151 studied tillers, and tillers with six panicles appeared at a very low frequency (0.2%). Some tillers stopped their development, others followed different sequences (fig. 2). Finally, nine configurations were observed: six for classical development (P1, P2, P3, P4, P5 and P6) and three for the diverging sequences (P2.1, P2.2 and P3.1).

([1]) For constituting each lot, plants were up rooted at random on the yield, until more than 1,000 tillers were sampled. That corresponded respectively to 3 and 4 plants.
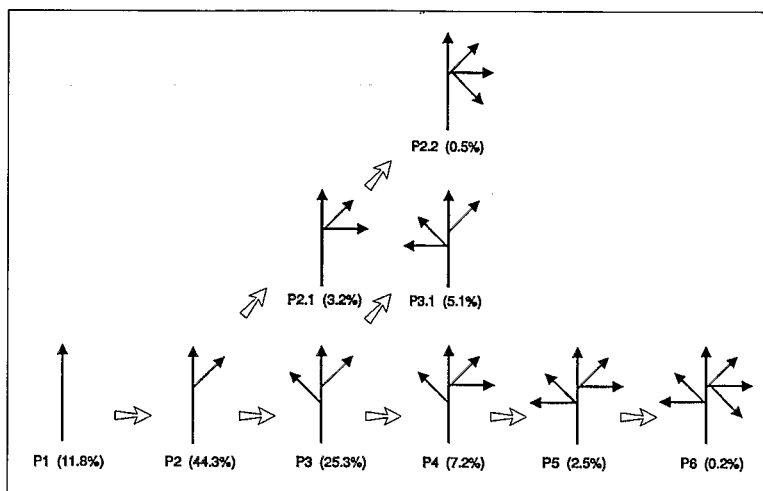
FIG. 2. — Schematic representation of culm branching diversity and its developmental sequences in the variety C1. The normal sequence is P1 to P6. The configurations P2.2 and P3.1 are the results of divergent sequences.

Some significant differences between sowing dates

All the evidence is that the emergence of a secondary panicle at node C depends on the previous development of the primary panicle at node A. On the other hand, the absence of the primary panicle at node A is not relayed by the bud of node B. Table I shows the different observed values of conditional probabilities of emergence of panicles. For each node, there was a marked influence of sowing date ($P < .001$). The June sowing showed more P1 configurations with only one panicle, but finally gave more panicles per fertile tiller.

TABLE I. — *Conditional probabilities for emergence of culm branching as a function of the sowing dates. For example, $P(C \backslash (A + no \, B))$ means probability of the emergence of panicle C when panicle A has emerged and panicle B is absent.*

	March sowing	June sowing
P (A)	0.894	0.868
P (B\A)	0.391	0.514
P (C\(A + B))	0.296	0.198
P (C\(A + no B)	0.053	0.102
P (D\(A + B + C))	0.140	0.420
P (D\(A + B + no C))	0.051	0.242

A decrease in the probability $P(A)$[2] in June was correlated, in the normal sequence, with an increase in $P(B\backslash A)$, with a decrease in $P(C\backslash(A \text{ and } B))$, and with a large increase in $P(D\backslash(A \text{ and } B \text{ and } C))$. Thus, a small change in the initial probability had repercussions by oscillation on all the other conditional probabilities.

Source factors of configuration diversity

The different factors are given by correspondence analysis applied to a Burt table (see appendix):

    — The first factor explains, in the statistical meaning, 61% of the variability. It symbolizes the general aptitude of the tiller to branch.

    — The other factors explain some dominance conflict between buds. The second factor (17% of the variability) is at the origin of the higher frequencies of the configurations P1 and P5 in the June sowing. It shows the increased dominance for the level B. The third factor (15% of the variability) brings out a dominance relation between the buds C and D; it opposes the configurations P2.1 and P3.1 and thus explains the diverging sequences.

Timing of the process

The interval between the headings of the principal panicle and of the primary panicle A shortens as the total number of panicles of the tiller increases. This relation explains 41% (in the statistical meaning) of the interval variability. It is not linear and the data fit well with a hyperbolic model (fig. 3), which shows two interpretable asymptotes:

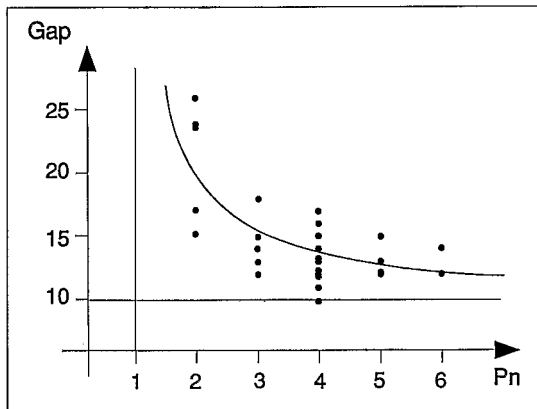FIG. 3. — Branching aptitude (Pn as panicle number) and interval between principal panicle and primary panicle A. The interval unit is one day.

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[2] $P(A)$ is the probability of emergence of the panicle A. $P(B\backslash A)$ is the probability of emergence of the panicle B, when the panicle A emerged. $P(C\backslash(A \text{ and } B))$ is the probability of emergence of the panicle C, when panicles A and B emerged. Etc.

— The interval tends to infinity when the panicle number is near to one (absence of branching).

— The interval is near to 10 when the panicle number tends to infinity. This interval constitutes the half-period of this periodic process.

TABLE II. — *Expected interval between the heading of the principal panicle and the heading of the first primary panicle as a function of the total panicle number of a tiller. Expected values were computed by the fitted hyperbolic function.*

Final number of panicles	2	3	4	5	6
Delay in days	21.2	15.5	13.5	12.7	12.1

Table II gives the expected values with the hyperbolic fitting within the studied scale (2 to 6 panicles). The interval varies between 12 and 21 days and this amplitude (9 days) is close to half-period. The continuation of culm branching with the development of the second primary panicle took place a mean 11.3 days later. This interval depended neither on the configuration, nor on the branching intensity. When the axillary bud of the level B was not developped, the secondary panicle C took over and emerged 19.8 days after the heading of the primary panicle A. Whether the panicle C was emerged or not, panicle D appeared a mean 15.5 days after B. Interval BD was shorter than the interval AC, a feature of the process: the interval between two successive headings decreases when culm branching increases.

The branching intensity in relation to the heading precocity of the tiller

The number of panicles per fertile tiller was uncorrelated with the heading date of the principal panicle when all observed configurations were considered ($r = .171$). Significant correlation was noted when the configuration P1 was excluded from the calculation ($r = -.398$). Thus the configuration P1 depends essentially on a dominance relation irrelevant to the emergence date of its single panicle. In return, late tillers exhibited greater opposition to branching.

DISCUSSION

Culm branching has been noted in barley (ASPINALL, 1961), *Panicum coloratum* and *Setaria sphacelata* (BOONMAN, 1971 *b*), but has never been examined in full detail. In *P. maximum*, it is a general process, related to the flowering, and particularly marked for types with narrow tillers. Two nodes are involved in this branching: the second and the third nodes under the top panicle of the tiller. The process is periodic, and theoretically boundless, with, in this extreme case, emergence of a new panicle every ten days.

Culm branching and tiller vigour

In practice, not all induced tillers exhibit the same degree of branching. This degree varies between 0 and 6 panicles per fertile tiller. Branching aptitude is the principal source of the observed diversity of branching. Poor branching aptitude characterizes late headed tillers, which in *Lolium* and *Phleum* are the least vigourous (ANSLOW, 1963; BEAN, 1970). Thus, branching aptitude could be in relation to the vigour of the tiller.

Culm branching: an oscillatory process with damping

If we consider the nodes A and B as a two-pole, levels A and B appear as being of opposite polarity. Thus, we obtain figure 4, where oscillating curves of
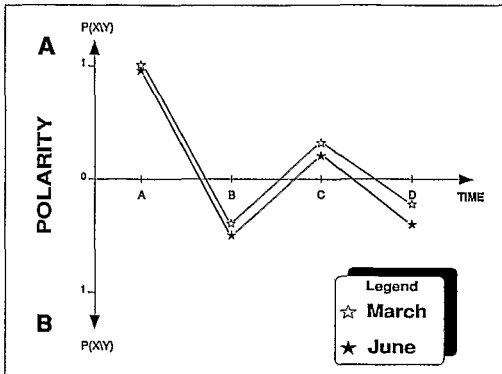

FIG. 4. — Changes in conditional proba-
bilities as a function of the polarity
and of the sowing dates (March or
June). Time is expressed by the
chronology of the emerged panicles
A, B, C and D.

conditional probabilities are drawn for the March and June sowings and for the normal sequence. There was damping with time. The June sowing differed from the March one by an increasing polarity for level B. Note that it is also possible to draw the curves for the absence of bud development. In this case, the point symbolizing the probability P (no A) would have a polarity of type B. In fact, the transition from absence to presence should be considered as a polarity change. This hypothesis of a different polarity between the two levels fits well with the chronological observations. The presence of such a damped process implies, as in the physical sciences, the notions of resistance and feed-back with dephasing. Thus, the opposite of the branching aptitude — the resistance — appears to be at the origin of the damping.

Dephasing as source of panicle absence

In figure 4, time is represented by chronobiological units: the buds. If there is a direct relation between this chronological scale and real time, the setting up of such a swinging system should correspond to the establishment of an internal clock. This clock might control the emergence of panicles in the time, and the buds should develop only when they are in phase with their polarity.

In theoretical conditions — branching aptitude is infinite —, the half-period of the process is near 10 days. The correspondence between the real time and the biological clock has a tolerance close to the half-period. A greater delay produces a dephasing of the bud A with its polarity: the panicle A is missing. Likewise, the heading of panicle C occurred when it was in phase with its polarity. In the normal and the P2.x sequences, the time interval between emergences of A and C was identical, and corresponded approximately to the period. The behaviour of the secondary panicle D was similar.

Culm branching at the origin of the staggering of heading. Relation to rainfall

The regulated emergence of culm branching leads the narrow-leafed varieties to produce panicles over a period of two months at least. This floral behaviour is completely opposite to that of temperate and perennial grasses, and probably represents an adaptation to a climate characteristic of the tropical environment.

The importance of the rainfall on reproduction by seed is known in an other african Graminae: *Sorghum bicolor*. A water stress before anthesis decreases panicle exsertion and the seed number (SANTAMARIA *et al.*, 1990). For this species, there is also a regulating process, which allows fitting of the heading date to the end of the wet season (CURTIS, 1968). For *Panicum maximum*, personnal observations showed sudden stoppings of heading on the early presence of the Harmattan − a dry northern wind − in October.

In the wild, a period of dormancy of 5-6 months allows seed germinations as early as March, if the wet season has just come on. Late germinations, corresponding to experimental late sowings, give rise from a delay in the wet season, which is often associated with a scarcity of water in Africa. Such a relation exists along a Northern-Southern gradient in Ivory Coast as in Kenya.

On average, culm branching is more marked for late sowings. It is a partially compensatory process, the late sowings showing fewer induced tillers than early sowings. In particular, this compensation in seed number is characterised by more pronounced staggering in time. Such behaviour avoids excessive instantaneous development of panicles at anthesis or at the internode elongation stage, for which water requirements are higher. For this reason, the control of culm branching is likely to be an adaptation to rainfall.

ACKNOWLEDGEMENTS

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APPENDIX

The correspondence analysis was applied to table III. The sub-table in bold type constitutes a Burt table. This sub-table is involved in the computation of the factors. The columns E0 and E1 and the lines MA0 to P3.1 (in italics) are not involved in this computation. They are only projected, as points, on the graphs and need interpretation.

TABLE III. — *Data used in correspondence analysis. The identifier BO means, for example, absence of panicle B. The identifier MD1 means presence of panicle D in March sowing. The identifier P2 is the name of the configuration P2.*

	A0	A1	B0	B1	C0	C1	D0	D1	E0	E1
A0	256	0	256	0	256	0	256	0	256	0
A1	0	1895	1034	861	1611	284	1728	167	1881	14
B0	256	1034	1290	0	1212	78	1290	0	1280	10
B1	0	861	0	861	651	210	694	167	857	4
C0	256	1611	1212	651	1867	0	1757	110	1867	0
C1	0	284	78	210	0	284	227	57	270	14
D0	256	1728	1290	694	1757	227	1984	0	1974	10
D1	0	167	0	167	110	57	0	167	163	4
E0	256	1881	1280	857	1867	270	1974	163	2137	0
E1	0	14	10	4	0	14	10	4	0	14
MA0	109	0	109	0	109	0	109	0	109	0
MA1	0	924	563	361	787	137	896	28	920	4
MB0	109	563	672	0	642	30	672	0	668	4
MB1	0	361	0	361	254	107	333	28	361	0
MC0	109	787	642	254	896	0	883	13	896	0
MC1	0	137	30	107	0	137	122	15	133	4
MD0	109	896	672	333	883	122	1005	0	1001	4
MD1	0	28	0	28	13	15	0	28	28	0
JA0	147	0	147	0	147	0	147	0	147	0
JA1	0	971	471	500	824	147	832	139	961	10
JB0	147	471	618	0	570	48	618	0	612	6
JB1	0	500	0	500	397	103	361	139	496	4
JC0	147	824	570	397	971	0	874	97	971	0
JC1	0	147	48	103	0	147	105	42	137	10
JD0	147	832	618	361	874	105	979	0	973	6
JD1	0	139	0	139	97	42	0	139	135	4
P1	1	0	1	0	1	0	1	0	1	0
P2	0	1	1	0	1	0	1	0	1	0
P3	0	1	0	1	1	0	1	0	1	0
P4	0	1	0	1	0	1	1	0	1	0
P5	0	1	0	1	0	1	0	1	1	0
P6	0	1	0	1	0	1	0	1	0	1
P2.1	0	1	1	0	0	1	1	0	1	0
P2.2	0	1	1	0	0	1	1	0	0	1
P3.1	0	1	0	1	1	0	0	1	1	0