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Staggering of heading in *Panicum maximum* Jacq. Origin and regulation

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Abstract

In *Panicum maximum*, staggering of heading over 2 months or more occurs frequently. Initiation of tiller over one month gives rise to the first wave of heading. Following waves derive from culm branching. Two main control systems operate during heading: 1. a fast control that alternates overheading and underheading days; 2. a monthly control that decreases or increases the intensity of the third wave as a function of the first wave intensity. These controls in the staggering of reproductive investments may constitute an adaptation to variations in rainfall in the tropical environment.

Keywords: *Panicum maximum*, heading, culm branching, control, initiation, timing

Résumé

Chez *Panicum maximum*, l'étalement de l'épiaison sur 2 mois, voire plus est un comportement fréquent. L'initiation des talles sur 1 mois est à l'origine de la première vague d'épiaison. Les vagues suivantes sont le résultat d'un processus de ramification paniculaire. Deux principaux systèmes de régulation interviennent durant l'épiaison: 1. une régulation rapide qui alterne les jours de sous-épiaison et de sur-épiaison; 2. une régulation mensuelle qui diminue ou augmente l'intensité de la troisième vague en fonction de l'intensité de la première vague. Ces régulations dans l'étalement des investissements reproductifs peuvent constituer une adaptation aux variations de pluviométrie en milieu tropical.

INTRODUCTION

Panicum maximum is a perennial and apomictic grass of the Panicoideae family. Kenya and Tanzania are its centre of origin (Combes, 1975; Pernes, 1975), but it is geographically distributed throughout the tropical world. Cultivated as fodder, its low seed production greatly hinders the commercialization of varieties. Staggering of heading over 2 months or more, coupled with shedding at maturity, constitute the main causes (Boonman, 1971; Humphreys, 1975).

A process of branching is partly responsible for this staggering (Noirot, 1991). A fertile tiller can produce new panicles at relatively regular intervals. Indeed, all fertile tillers are not synchronous. This trait contrasts with the situation in temperate grasses (Boonman, 1971). This lack of synchronization may be explained by differences between induction dates and heterogeneity within the periods needed for each stage of floral development.

Floral development of a grass comprises four main stages, defined in *Festuca, Lolium, Dactylis* and *Phleum* (Bean, 1970; Blondon, 1968; Gillet, 1980; Ikegaya, 1984; Ryle, 1964): 1. the emergence of "double ridges" at the middle of the apex is the first sign indicating a morphogenetic change. This stage constitutes the initiation. It results from an induction that has generally occurred 8 to 10 days before; 2. racemes emerge at the following stage (primordia). These two first stages occur over a few days; 3. floral development continues with spikelet differentiation (glumes and glumellas). The apex size is 3 to 7 mm; 4. lastly, from 8 to 30 mm, floral pieces emerge. At this moment, reproductive structures are created and subsequent events are already implicated in reproductive functioning or internode elongation by auxesis.

Internode elongation of tillers occurs during floral development and continues afterwards. It is physiologically independent of floral development (Gillet, 1980). This caulescence puts floral structures over the leaves at a moment (end of the gametogenesis) favourable to reproduction. The emergence of the top spikelet out of the sheath is the flag stage. This stage is more visual than physiological and marks the beginning of heading. It practically coincides with the end of panicle growth. Only the elongation of the last internode continues and causes panicle exsertion out of the sheath.

In this study, we examined floral development and internode elongation in order to establish the staggering of heading. The relative importance of the regulated and programmed processes is discussed in relation to adaptation for seed production in the tropical environment.

MATERIALS AND METHODS

The studied plant material was the CI variety, with numerous narrow tillers. It was selected for its profuse heading staggered over 2 months. In this apomictic accession, plants from sowing or from vegetative multiplication theoretically have the same genotype, mutations apart.

First, the caulinary apex was observed from initiation to heading, in a meadow used for seed production at the agricultural station of Man (Côte-d'Ivoire). Planting took place in the first week of June 1982 by tuft splitting. The development of the tiller population was monitored from July 27 to September 14, 1982.

Every week, ten plants were randomly selected, and five tillers were removed from each, without taking into consideration their position on the tuft or their order (principal or primary). The sample comprised 50 tillers representative of the meadow which were dissected, if necessary, under a binocular microscope. The apices were classified into 6 groups:

1: vegetative meristem,

2: floral meristem less than one millimetre in length; this class corresponds to the "double-idges" stage,

3: floral meristem of 1 to 2 mm, corresponding to the stage of branching *primordia*,

4: inflorescence apex of 2 mm to 2 cm, with differentiation of spikelets,

5: panicles of 2 to 10 cm,

6: and lastly, panicles of more than 10 cm, headed or sub-headed.

A second experiment, involving chronological observation of heading, was carried out at the research centre of Adiopodoumé (Côte-d'Ivoire). Two plants of the CI variety were studied. The first was obtained from sowing in Petri dishes on March 15. The seedling was planted in a flower pot under shaded conditions one week later. The second was obtained from one field tiller removed on April 1 and planted immediately in a flower pot under shaded conditions too. A 15-day interval separated the two implantations in order to give approximately the same vegetative growth at the moment of field implantation, on May 1, at the beginning of the wet season. Plants were cut monthly at a height of 15 cm from June 1 to September 1.

Panicles at the flag stage were tagged daily, from September 1 to November 3 inclusive, with wool of different colours and lengths. On November 4, the two plants were uprooted and each tiller was separated. Vegetative and headed tillers were counted. Tagging allowed reconstitution of the calendar of panicle emergence, called the chronological sequence of heading. Since fertile tillers are able to produce many panicles, these were classified on the basis of their order of emergence on each tiller: first, second, third, and so on (Noirot, 1991). Thus, the chronological sequence of emergence of all panicles was divided into sub-series or waves: first wave, second wave, and so on (fig. 2). For the three first waves, mean, standard deviation, skewness and kurtosis were estimated. These parameters described respectively the precocity, the staggering and the shape of waves.

Smoothing of the sequence by polynomial and mobile regression (Lejeune, 1985) with a window of 14 days emphasized the trend (fig. 1 A) and the deviations (background noise) (fig. 1 B). An autocorrelation study was applied to the background noise to verify if noise is a purely random process. Spectral analysis was used to reveal a possible periodic process in noise.

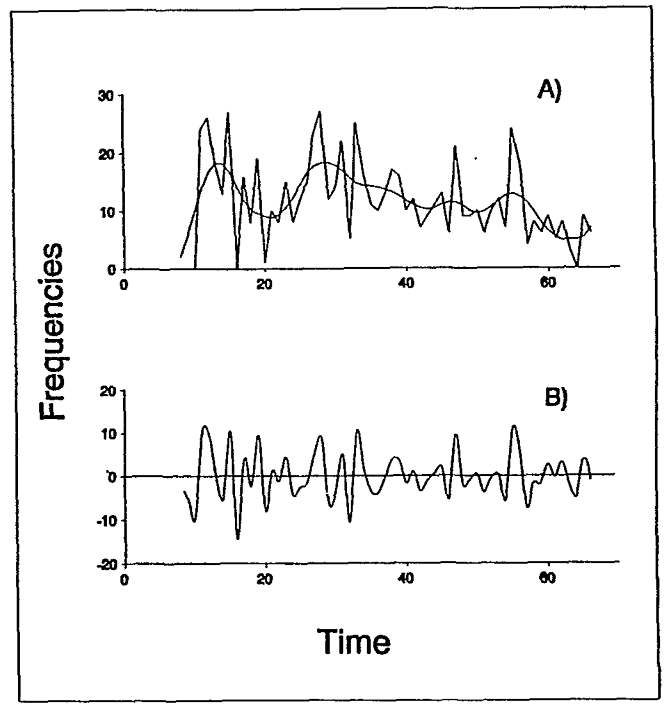

Fig. 1. – Trend (A) and background noise (B) of the heading sequence of the sowing plant.

RESULTS

Floral development from initiation to heading

Table I shows the progression of the tiller population. The first changes appeared on July 27. The first headed panicles emerged one month later during the last week of August. A transitory stage of the floral meristem of 1 to 2 mm (class 3) was always present on August 31, thus implying initiation on July 24. Thus, initiation of all fertile tillers also lasted one month.

TABLE I. — *Development of the caulinary apex in the C1 variety between July 27 and September 14. Numbers are percentages, estimated every week on a sample of 50 tillers.*

	07/27	08/03	08/10	08/17	08/24	08/31	09/07	09/14
Vegetative meristem	98	84	46	18	6	8	4	6
Floral meristem up to 1 mm	2	14	44	22	0	0	0	0
Floral meristem 1 to 2 mm	0	2	6	8	8	4	0	0
Floral meristem 2 mm to 2 cm	0	0	4	34	22	12	2	0
Panicle 2 to 10 cm	0	0	0	18	58	48	8	2
Panicle greater than 10 cm	0	0	0	0	6	28	86	92

Progress of heading

The absence of heading in the first week of September was the first trait of the heading sequence (fig. 2). Our results on floral development clearly indicate that the sub-headed or headed tillers on September 1 had been beheaded. This demonstrates the speed of internode elongation (one-metre growth in about one week).

The chronological sequences of the two plants were highly similar. Some likenesses should be emphasized: 1. the first wave lasted barely more than one month, approximately the time necessary for initiating all headed tillers; 2. panicle emergence was a very irregular process. The number of panicles emerging per day varied from 0 to 25; 3. the means and the maxima (¹) of the first two waves were separated by 17 days; 4. the waves had approximately the same staggering, but were increasingly flattened (table II); 5. the waves overlapped considerably; 6. lastly, there was a general trend towards a decrease in the mean number of emerged panicles.

The two plants showed some differences too (table III): 1. tillering and fertile tiller number were markedly greater in the sowing plant; 2. the mean number of emerged panicles per fertile tiller was 30% greater for the plant produced by vegetative multiplication.

(¹) Estimated after smoothing.

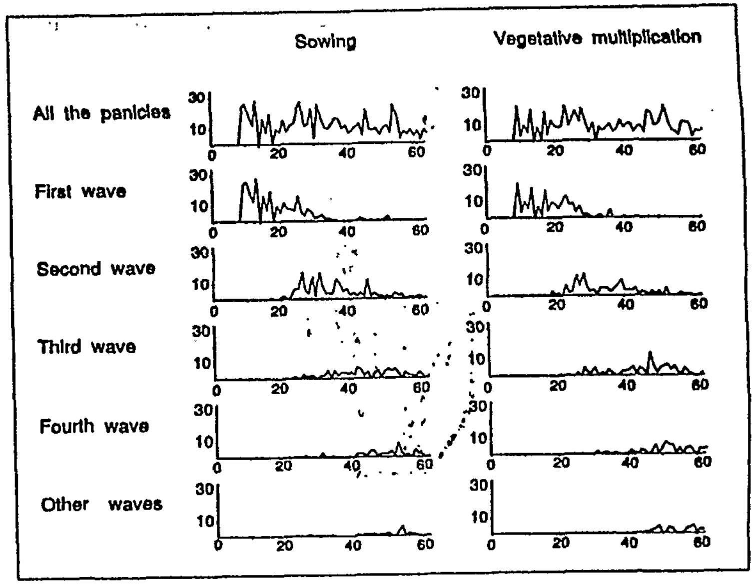

FIG. 2. — The heading pattern and its splitting into successive waves in the C1 variety. Panicle number is indicated on the ordinate, and time (days) on the abscissa.

TABLE II. — *Main characteristics of the three first waves. Mean and standard deviation are respective estimations of precocity and staggering. Skewness and kurtosis (Fisher's coefficients g_1 and g_2) describe their shape.*

	Mean	Standard deviation	Skewness	Kurtosis
First wave	16.8	8.0	0.915	0.90
Second wave	33.1	10.0	0.340	−0.10
Third wave	42.3	9.9	−0.132	−0.65

TABLE III. — *Main differences between C1 variety plants produced by sowing and tuft splitting.*

	Tuft splitting	Sowing
Total number of tillers	525	901
Number of fertile tillers	179	275
Panicle number/fertile tiller	3.21	2.49

Origin of the daily variability within heading sequences

Deviations from the general trend (fig. 1 A) accounted for the background noise (fig. 1 B), which explained 67% of the daily variability and did not depend on the trend values ($r=0.032$ and $r=0.059$ for respectively sowing plant and tuft splitting plant). For the two noise sequences (sowing and tuft splitting), heading at t time was significantly and negatively correlated with heading at t-1 time and there was no other correlation. Spectral analysis showed a periodic process with wave length equal to 2 days, which explained 25% of noise. These two results can be explained by a first order Markov's process (days with overheading were followed by underheading and vice versa).

DISCUSSION

Staggering of heading and duration of initiation

In grasses, the interval between initiation and heading varies from 30 to 50 days according to the species and the environmental conditions. Thus, in *Phleum pratense*, heading occurs 40 to 50 days after initiation (Bean, 1970). In Nigeria, Curtis (1968) noticed in *Sorghum* an interval of 40 days, under natural conditions. Ikeda (1970) showed that 33 days are necessary, under optimal conditions of short days, to obtain heading of rice. In the C1 variety of *P. maximum*, the observed interval is one month.

This interval corresponds to the time necessary for induction of all fertile tillers and also for the first heading wave. Thus, staggering of initiation constitutes one of the sources of the spreading of seed reproduction over two or more months. In the C1 variety, more than 200 fertile tillers emerged during one month, with peaks of 20 panicles per day. Growth of these tillers was very fast (one week was enough for panicle growth of more than one metre). Thus, staggering of initiation avoids excessive emergence of simultaneous caulescent tillers, and allows distribution of the water requirements for emergence of all fertile tillers.

Heading with running waves and its regulation

The second source of staggering is culm branching, observed by Aspinall (1961) in barley and by Boonman (1971) in *Setaria sphacelata* and *P. coloratum*. In *P. maximum*, this process leads a fertile tiller to produce a new panicle every two weeks (Noirot, 1991). The number of emerged panicles, limited to six in the C1 variety, varies between tillers as a function of vigour (Noirot, 1991). Culm branching is therefore likely to reproduce the first wave, with decreasing intensity.

Heading did show in fact many maxima. A first peak appeared on September 10, corresponding to the maximum of the first wave. The second peak emerged 2 weeks later, and comprised 50% of principal panicles and 50% of primary panicles. There was marked overlap of the waves: each wave lasted about one month, but they were consecutive and separated by an interval of 16 days. The general trend for all panicles was indeed a decrease in the mean number of panicles and the consecutive waves preserved approximately the same staggering, but were increasingly flattened. The change in the shape of consecutive waves shows that each wave was not the simple scaling down of the preceding wave with a scale equal to the branching probability.

This flattening and the skewness change of the peaks could be explained by a lower branching probability of fertile tillers pertaining to the same peak. Such a hypothesis is, however, unlikely since the heading date of the principal panicle does not influence the emergence probability of the first primary panicle (Noirot, 1991). Moreover, the second peak appears 5 days late. Within a heading peak, competition between fertile tillers contributes to an increase in the time interval between the principal panicle and the primary panicle. This results in a shifting of the peak of the second wave. This peak is then largely constituted by fertile tillers, for which branching will stop due to lack of vigour; whence the observed lowering of the peak of the third wave. In this way, variety C1 controls its temporal pattern of heading. This explains why the late sowings with lower heading intensity exhibit greater and partially compensatory branching (Noirot, 1991). In our experiments, the same effects differentiate plants produced by sowing or tuft splitting: branching intensity was greater for the plant with fewer fertile tillers.

Control of heading is not of one type. First order Markov's control allows daily adjustment: days with overheading are followed by days with underheading. The main characteristic of such control is to be related to the heading intensity of the genotype (Noirot, unpublished). This emphasizes the role of caulescence in the adjustment of the heading dates (Curtis, 1968) and the role of competition for water between tillers in the internode elongation stage. This competition changes the heading pattern by modifying the speed of caulescence and the bud inhibition. The heading process, with successive waves and its control types, appears to be an adaptation related to the water reserves of the soil, which fluctuate markedly in the tropical environment.

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