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Inheritance, distribution and biology of andromonoecy in the agamic complex of the *Maximae* (Panicoideae)

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Abstract *Panicum maximum* belongs to the agamic complex of the *Maximae Panicoideae* which includes two other species, *P. infestum* Anders., *P. trichocladum* K. Schum., and several morphologically intermediate types. Andromonoecy and hermaphroditism have been recorded in this complex, but their distribution depends on the species, the level of ploidy, the mode of reproduction and the geographical origin. In particular, hermaphroditism appears to exist only in polyploid apomicts of the species *P. maximum* and was more frequent in maritime regions. Andromonoecy showed a monogenic and recessive inheritance. In andromonoecious plants, flowering of the male flower occurred later than that of the hermaphrodite flower within the spikelet. This flowering discrepancy varied between clones in respect of both mean and variance. All results are discussed in terms of the evolutionary process involved.

Key words *Panicum maximum* · Andromonoecy · Hermaphroditism · Apomixis · Sexuality · Temporal dioecism

Introduction

Panicum maximum belongs to the agamic complex of the *Maximae (Panicoideae)* which includes two other species, *P. infestum* Anders., *P. trichocladum* K. Schum., and several morphologically intermediate types. The center of diversity of this agamic complex is

located in Tanzania and in Kenya (Combes 1975; Pernès 1975) and includes a polyploid and apomictic pool as well as diploid and sexual ones. The apomictic pool represents 93% of the genotypes in the centre of diversity and 100% elsewhere. In *P. maximum* Jacq., each spikelet contains two flowers: one hermaphrodite and one male. Nevertheless, in many plants, the male flower is vestigial, and the plant is then effectively hermaphrodite. In addition, some plants have both hermaphrodite and andromonoecious spikelets (personal observation), and are called partial hermaphrodites.

P. maximum is an economically important species, and its apomictic varieties are cultivated as forage throughout the tropical world (Grof and Harding 1970; McCosker and Teitzel 1975; Pernès et al. 1975; Noirot 1983; Savidan et al. 1989). Their use is nevertheless limited by their relatively low seed production (Boonmann 1971; Humphreys 1975; Pernès et al. 1975), partly due to a low seed-set (20%) (Noirot and Ollitrault 1996). One way to improve seed-set in the absence of resource limitation is to increase pollination efficiency by the selection of andromonoecious varieties. This approach is realistic because: (1) pollination is necessary to trigger parthenogenesis (pseudogamy) (Warmke 1954), (2) andromonoecy should improve pollen donation (Janzen 1977; Willson and Burley 1983; Sutherland and Delph 1984), (3) pseudogamous apomicts of *P. maximum* are self-compatible (Noirot et al. 1997), and (4) male investment is analytically related to seed-set in pseudogamous and self-compatible apomicts (Noirot et al. 1997). In addition, our best varieties for seed production in Côte-d'Ivoire are andromonoecious. Here we report our studies on the inheritance of andromonoecy.

There are many ways to improve pollen production, the simplest being to increase pollen number per stamen and stamen number per flower. In fact, andromonoecy appears to split pollen production. Interpretation of the advantages of andromonoecy depends

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on the discrepancy between the opening of male and hermaphrodite flowers in relation to the within-panicle flowering time. This is why the discrepancy between male and hermaphrodite flower opening is also presented in this paper.

Otherwise, it is important to estimate the hermaphroditism/andromonoecy ratio and its variation according to the species (*P. maximum*, *P. infestum*, and *P. trichocladum*), the mode of reproduction (sexuals vs apomicts), the ploidy level (diploid vs tetraploid), and the region (maritime vs continental, Kenya vs Tanzania) in order to understand the simultaneous presence of hermaphrodites and andromonoecious plants.

Materials and methods

P. maximum is a perennial grass. Each accession was vegetatively multiplied by tuft splitting. Accessions were therefore clearly identified as different clonal lines.

Opening dates of male and hermaphrodite flowers

Plant material

The timing of andromonoecy was studied in 14 accessions: one *P. trichocladum*, one *P. infestum*, three apomictic *P. maximum*, three wild hybrids *P. maximum* × *P. infestum*, three diploid sexuals, and three tetraploid sexuals obtained by colchicoidization of diploid sexuals.

Notations

Opening dates of the male and hermaphrodite flowers were recorded for 50 spikelets per clones. This permitted the calculation of the difference between opening dates.

Statistical analysis

Data on flowering timing were analyzed using a one-way ANOVA with a fixed effect. When the effect was significant, the Newman and Keuls test was used for a multiple comparison of means. The multiple comparison of variance was done using the Levine test (for the global test, but also for the 2 × 2 tests) and the Ryan correction of the risk I for each 2 × 2 test.

A sub-table was obtained by: (1) dropping *P. infestum* and *P. trichocladum* which were represented by only one clone each, and (2) re-grouping other clones into four groups – G1: the C types, G2: the apomicts, G3: the tetraploid sexuals, and G4: the diploid sexuals. A nested ANOVA with two factors (groups and clones within groups) was then applied to the sub-table.

Inheritance of andromonoecy

Plant material

The inheritance of andromonoecy was studied using four tetraploid clones: two sexuals (1S18 and 2S87) and two apomicts (1A48 and

C1). Clones C1 and 1S18 are andromonoecious, whereas 2S87 and 1A48 are hermaphrodite. In addition, 1S18, C1, and 1A48 are self-compatible, whereas 2S87 is completely self-incompatible. Clone C1 is an intermediate type between *P. maximum* and *P. infestum* (Combes 1975; Pernès 1975).

Four crosses were studied: 1S18 × 1S18, 2S87 × 1S18, 2S87 × 1A48, and 2S87 × C1, with 150, 130, 30, and 22 hybrids, respectively.

Notations

Five principal panicles were sampled per hybrid, and 20 spikelets were dissected per panicle. The absence of partial hermaphrodites among these progenies allowed a classification of the descendants into either the hermaphrodite group or the andromonoecious group.

Statistical analysis

The χ^2 test was used to fit data to a Mendelian hypothesis, except when the results were obvious (i.e. 100% or an exactly 1:1 ratio).

Distribution of andromonoecy in *Maximae*

Plant material

The distribution of andromonoecy in the tribe *Maximae* was studied in wild accessions from Kenya and Tanzania. The studies included 19 sexual *P. maximum*, 262 apomictic *P. maximum*, two apomictic *P. infestum*, one apomictic *P. trichocladum*, two intermediate types *P. maximum* × *P. trichocladum*, and 18 intermediate types *P. maximum* × *P. infestum*, also called C types (Pernès 1975).

Notations

Two principal panicles were sampled per clone, and 25 spikelets were dissected per panicle. Clones were classified according to their frequency of andromonoecious or hermaphroditic spikelets: (1) andromonoecious when 100% spikelets were andromonoecious; (2) partly hermaphrodite when 1–99% of spikelets were hermaphrodite; and (3) hermaphrodite when 100% spikelets were hermaphrodite.

Statistical analysis

The χ^2 test was also used here.

Regional distribution of andromonoecy in apomictic *P. maximum*

Plant material

The regional analysis of andromonoecy related only to the 262 *P. maximum* apomictics.

Notations

See distribution of andromonoecy in *Maximae*.

Statistical analysis

Log-linear analysis was used to highlight factors explaining the regional distribution of andromonoecy in the center of diversity.

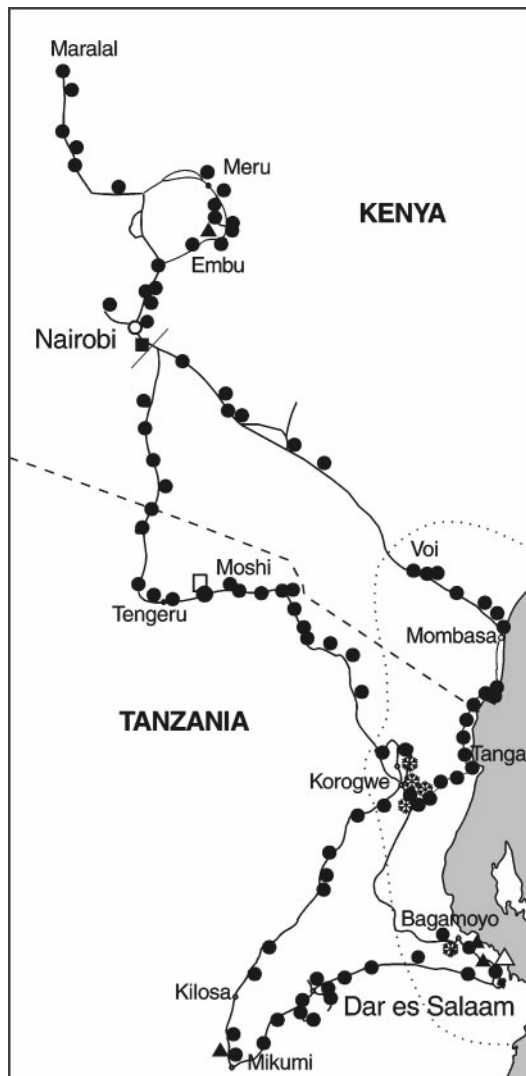


Fig. 1 Distribution of *Maximae* accessions in Kenya and Tanzania (from Combes 1975; Pernès 1975). A line separates maritime regions (Voi, Mombasa, Tanga, Korogwe, Bagamoyo and Dar es Salaam) from continental regions. ●: polyploid apomicts of *P. maximum*; *: diploid sexuals of *P. maximum*; △: *P. infestum*; □: *P. trichocladum*; ▲: C types (wild hybrids *P. maximum* × *P. infestum*); ■: wild hybrids *P. maximum* × *P. trichocladum*

Four contrasts were defined: F1: andromonoecy vs hermaphroditism; F2: Kenya vs Tanzania, representing a North-South gradient; F3: maritime region (including Voi, Mombasa, Tanga, Korogwe, Bagamoyo, and Dar es Salaam) vs continental region (Fig. 1); and F4: regions with sexuals (Korogwe and Bagamoyo) vs other regions.

The log-linear analysis includes two steps:

- (1) We look for the simplest and best models explaining data variation in a four-entry table. A good model was one for which discrepancies between the theoretical table (calculated from the model) and the observed table were not significant (χ^2 test).
- (2) Except in the case of independence between all contrasts, models include interactions. Only interactions comprising the first contrast (which we wanted to explain) were taken into account. To test an interaction, we dropped it from the model and observed the effects on “observed-expected” discrepancies. When discrepancies became significant, this means that the first contrast (andromonoecy/her-

maphroditism) is related to the other contrast present in the interaction. For example, a significant F1-F2 interaction indicates that F1 depends on F2. Similarly, a significant F1-F2-F4 interaction means that F1 is affected by the interaction F2-F4.

Statistica software from StatSoft was used for all analyses.

Results

Opening dates of male and hermaphrodite flowers

In each spikelet, the male flower always opened after the hermaphrodite flower. The difference between the two dates constitutes the opening-date difference (ODD). The ODD was not stable within clones, but stability depended on the clone ($F_{13, 686} = 21$; $P < 0.000$) (Table 1). The ODD range varied from 2 days to 5 days in T54 and K211, respectively. ODDs differed also between clones in their averages ($F_{13, 686} = 23.1$; $P < 0.000$) from 1 day to 3 days.

No differences in ODDs were noted between *P. maximum* apomicts, C types, 4x-sexuals and 2x-sexuals ($F_{3, 8} = 1.26$; $P = 0.35$), showing that neither the mode of reproduction, the level of ploidy nor the interspecific origin influences the ODD.

Inheritance of andromonoecy

Self-fertilization of the andromonoecious sexual 1S18 gave only andromonoecious plants: 1S18 was therefore homozygous for this trait. The cross between the hermaphrodite 2S87 and 1S18 gave 55% of andromonoecious hybrids, and the result did not differ from a 1 : 1 ratio ($\chi^2 = 1.108$; $P > 0.05$). This suggested a monogenic inheritance (one locus with two alleles: *H* for hermaphroditism and *h* for andromonoecy),

Table 1 Differences of opening date between male and hermaphroditic flowers of the same spikelet in 14 accessions (A = apomict; DS = diploid sexual; TS = tetraploid sexual). Letters indicate results of the multiple comparison of means or standard deviations

Accession		Means	SD
G24	<i>P. trichocladum</i> (A)	2.5 ^{bc}	0.74 ^{cd}
TT1	<i>P. infestum</i> (A)	2.3 ^b	0.45 ^b
C1	C type (A)	2.5 ^{bc}	0.65 ^c
T2	C type (A)	2.9 ^c	0.81 ^{cde}
T112	C type (A)	2.5 ^b	0.93 ^{def}
K211	<i>P. maximum</i> (A)	2.7 ^{bc}	1.23 ^e
K212	<i>P. maximum</i> (A)	2.2 ^b	1.03 ^{fg}
K195	<i>P. maximum</i> (A)	3.0 ^c	0.59 ^b
T26	<i>P. maximum</i> (DS)	1.3 ^a	0.45 ^b
T40	<i>P. maximum</i> (DS)	2.1 ^b	1.00 ^{ef}
T54	<i>P. maximum</i> (DS)	2.2 ^b	0.42 ^a
1S17	<i>P. maximum</i> (TS)	2.7 ^{bc}	0.99 ^{ef}
1S18	<i>P. maximum</i> (TS)	1.1 ^a	0.42 ^a
2S24	<i>P. maximum</i> (TS)	2.6 ^{bc}	1.05 ^{fg}

where 2S87 would be *Hhhh* and 1S18 *hhhh*. Hermaphroditism is dominant over andromonoecy. These results were confirmed by a similar cross (2S87 × 1A48), where 50% of hybrids were andromonoecious. Nevertheless, the cross 2S87 × C1 revealed a highly significant discrepancy in this model ($\chi^2 = 8.91$; $P = 0.003$) in favor of andromonoecy (4 hermaphrodites vs 18 andromonoecious plants).

Distribution of andromonoecy in the tribe *Maximae*

All diploid sexuals were andromonoecious. Clones of *P. infestum*, *P. trichocladum*, and all their natural interspecific hybrids with *P. maximum*, were andromonoecious. By contrast, apomictic clones of *P. maximum* were polymorphic. In this case, the percentages of hermaphrodite, andromonoecious, and partly hermaphrodite clones were 41.6%, 55.3%, and 3.1%, respectively. Hermaphrodite and partly hermaphrodite clones were therefore re-grouped because of the genetic dominance of hermaphroditism. The percentages then became 44.7% and 55.3%, and did not differ from a 1:1 ratio ($\chi^2 = 2.58$; $df = 1$; $P = 0.10$).

Regional distribution of andromonoecy in *P. maximum* apomicts

The log-linear analysis with four factors: andromonoecy/hermaphroditism (F1), Kenya/Tanzania (F2), maritime/continental (F3), and presence of sexuals/absence of sexuals in the neighborhood (F4) led to two models which both fitted the data well (model 1: $\chi^2 = 1.34$; $df = 6$; $P = 0.97$, and model 2: $\chi^2 = 1.90$; $df = 6$; $P = 0.90$).

The first included the interactions F2-F3-F4 and F1-F3. Dropping F1-F3 from the model increased the discrepancies significantly ($\chi^2 = 7.03$; $df = 2$; $P = 0.03$). The maritime region showed a higher andromonoecy rate than the continental region (Table 2).

The second model included the interactions F2-F3-F4 and F1-F4. Elimination of F1-F4 from the model, increased the discrepancies significantly ($\chi^2 = 6.47$; $df = 2$; $P = 0.04$): andromonoecy was more frequent in regions of Korogwe and Bagamoyo, where sexuals were present (Table 2).

Table 2 Regional distribution of andromonoecy in apomictic *P. maximum*. Interspecific hybrids and sexuals, which were not polymorphic, are not included

Contrast	% Andromonoecy
Kenya vs Tanzania	50 vs 59
Continental vs Maritime	51 vs 66
Non sexuals vs sexuals	52 vs 69

There was no effect *sensu stricto* of the Kenya/Tanzania contrast on andromonoecy (Table 2).

Discussion

Inheritance of andromonoecy

The hypothesis of Mendelian, monogenic and recessive inheritance should be accepted in *P. maximum*. Indeed, this hypothesis fitted well with most of the studied crosses. In addition, this type of inheritance has already been observed in *Cucumis ficifolius* (Visser and Nijs 1984), *Lagenaria siceraria* (Singh et al. 1996) and *Asparagus officinalis* (Loptien 1979). For the cross using C1 as parent, the andromonoecy rate was lower than expected. This could be due to some distortion of segregation, which is frequent in crosses using a C type (wild hybrid *P. maximum* × *P. infestum*) (Assienan and Noirot 1995).

Absence of hermaphroditism in diploid sexuals

Hermaphroditism seems to be absent in the diploid sexuals despite gene flow between the two pools (Savidan and Pernès 1982; Assienan and Noirot 1995). Several hypotheses can explain this result. Some diploids could be genetically hermaphrodite *Hh*, but hermaphroditism would not be expressed at the diploid level. Nevertheless, the genealogy of the tetraploid and sexual hybrids (1S17, 1S18, 2S24, 2S87) we used as parents in this study is consistent with their sexual colchiploidized parent being *hhhh*.

Absence of hermaphroditism in diploid sexuals could also result from an overrunning of diploid populations by andromonoecy. Overrunning should occur if the advantage due to the presence of more stamens in andromonoecious plants than in hermaphrodites is not outweighed by some trade-off with other reproductive traits; for example, the number of pollen grains per stamen.

Absence of hermaphroditism in diploid sexuals could be compared to the absence of apomixis in these plants. In apomixis, fertile diploids are *aa* (the rare *Aa* diploids are sterile, but show apomictic embryo-sacs), whereas apomicts are *Aaaa*. Absence of *Aaaa*, *AAAA*, and *AAAA* apomicts and sterility of *Aa* diploids lead us to suppose that an allelic dosage would trigger sterility when the proportion of the *A* allele is higher than 0.25 (Noirot 1993). To-date, only *Hhhh* genotypes have been recorded among andromonoecious apomicts, whereas all diploids were *hh*. The similarity is striking, although further studies are necessary to complete our genetic identification of andromonoecious apomicts. Screening of haploids in progenies from andromonoecious and sexual tetraploids may indicate whether *Hh* plants are

sterile. Similarity does not imply linkage. Indeed, at the tetraploid level, andromonoecy concerns both sexuals and apomicts.

Absence of hermaphroditism in *P. infestum* and *P. trichocladum*

Only three clones belonging to the two species were studied here. Although they were all andromonoecious, direct observations were not sufficient to extend this conclusion to all plants of these species. Nevertheless, information can be acquired indirectly. For example, all intermediate types with *P. maximum* are F₁ hybrids arising from the pollination of unreduced female gametes of diploid sexuals by *P. infestum* or *P. trichocladum* (Assienan and Noirot 1995). Diploid sexuals being andromonoecious, this suggests that all *P. infestum* and *P. trichocladum* parents of these wild F₁ hybrids were also andromonoecious, implying that hermaphroditism is absent in the two species.

Distribution of hermaphroditism in *P. maximum* apomicts

By contrast with diploids, apomicts included hermaphrodites in a ratio close to 1:1. This ratio concerns genotypes, not plants. Indeed most genotypes belonged to monomorphic populations (Combes 1975; Pernès 1975), in which plants were therefore either 100% andromonoecious or hermaphrodite. In polymorphic populations, genotype frequencies are unfortunately unknown.

The similarity between the 1:1 ratio observed in the apomict pool and in progenies of the *hhhh* × *Hhhh* cross may be a coincidence. Indeed, this implies that new apomictic genotypes would arise from the fertilization of unreduced female gametes of diploid sexuals only by pollen of hermaphrodite apomicts. If pollen of andromonoecious apomicts participates in the fertilization of unreduced *hh* gametes, andromonoecy would overrun the apomictic pool. Regional differences in the hermaphroditism/andromonoecy ratio illustrates the expected trend of andromonoecy overrunning. Indeed, although a “maritime effect” and a “sexuality effect” were correlated, we can consider the presence of sexuals in the maritime region as the causal effect of the higher proportion of andromonoecious plants in maritime regions.

The overrunning speed of andromonoecy is low. In agamic complexes, the genotypic composition of the apomictic pool at equilibrium is reached more slowly when the proportion of apomicts is high (Marshall and Weir 1979). These expectations have been verified in the *Maximae* complex for isozymic traits showing segregation distortion (Assienan and Noirot 1995). This could also be true for hermaphroditism, which should

disappear in the long term. Continuous gene flow of the *H* allele could counter-balance this trend, but this hypothesis leads to the problem of the origin of such gene flow. Conversely, we can suppose a frequency dependent function favoring hermaphroditism in apomicts. An evolutionary stable strategy (ESS), such as defined by Maynard-Smith (1976), would be necessary to explain: (1) how the apomictic pool reached the equilibrium, and (2) the further stability of the apomictic pool.

Differences of opening dates between male and hermaphrodite flowers within spikelets

In the spikelet, the male flower always opened about 2.5 days after the hermaphrodite flower. In contrast, the interval between stigma and stamen emergence of the hermaphrodite flower did not exceed 2 h (unpublished data). Andromonoecy appears to be a means of splitting pollen donation. In *P. maximum*, the within-panicle flowering begins at the top of the panicle and spreads basipetally. Seven to eight days are necessary for the full flowering of a panicle and the peak of receptive stigma occurs about 4 days after the beginning of flowering (Noirot 1992). The peak of male flowering does not exactly coincide with the peak of female flowering, thus favoring allogamy. Andromonoecy is then equivalent to temporal dioecy (Cruden 1988) and its evolutionary advantage could result from an increasing investment in male function (Spalik 1991). This would explain why all diploid sexuals are both allogamous and andromonoecious.

Conversely, the evolutionary advantage of the splitting of pollen production should not exist in andromonoecious apomicts. Other facts must be taken into account to explain the advantage of splitting, if indeed there is an advantage. In particular, ODD avoids simultaneous flowering within the spikelet and decreases instantaneous requirements. This could decrease competition between anthesis and exertion, leading to a staggering of within-panicle flowering and to a lower seed-set when it happens (Noirot and Ollitrault 1996). The observed between-clone differences in ODD variance may be explained by this hypothesis. T58 contrasted with K211 in ODD variance, but also in drought adaptation. Unfortunately, this example is currently too small to be generalized. Further studies comparing apomictic accessions from a dry region (Maralal) to those from wet regions (Korogwe) for ODD average and variance could prove interesting.

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