Size Variations of Flowering Characters in *Arum italicum* (Araceae)

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ABSTRACT

In *Arum*, bigger individuals should proportionally invest more in the female function (number or weight of female flowers) than the male. The aim of this paper is to quantify variations in reproductive characters (size of the spadix parts, number of inflorescences) in relation to plant and inflorescence sizes. The appendix represents 44% of the spadix length. The female zone length represents 16.5% of the spadix length and is much longer than the male zone (6%). Moreover these three spadix zones increase with plant vigour indicating an increasing investment into reproduction and pollinator attraction. It appears that the length of appendix increased proportionally more than the lengths of the fertile zones. On average an inflorescence counts 156 male flowers and 61 female flowers which result in a male-biased floral ratio in *A. italicum*.

The numbers of male and female flowers increased significantly with the spadix size but differently according to the gender, the number of female flowers increasing faster than male: on the other hand this effect was marginally significantly ($p = .08$). This relative gender difference of flower number increase is visualised by a significant decrease of the maleness floral ratio with spadix size.

KEY WORDS

Flower numbers, resource allocation, sex ratio, size-advantage model.

INTRODUCTION

An extreme form of flowering character variations according to the size is gender modification, which occurs in several species of *Arisaema* (Clay, 1993). Individual plant gender changes from pure male, when small, to monoecious (*A. dracontium*) or pure female (*A. ringens*) when large (Gusman & Gusman, 2003). This gender change is reversible, damaged female individuals will flower as male the following year (Lovett Doust & Cavers, 1982). These changes are related to change in plant size and are explained by the size-advantage model. The size-advantage model postulates a sex change when an increase in body size is related to differential abilities to produce or sire offspring (Policansky, 1981). For entomophilous plant species, as Aroids, the size-advantage model predicts a female-biased gender expression with increased size (Klinkhamer *et al.*, 1997).

In *Arum* species, inflorescences are monoecious (e.g. hermaphrodite) bearing both male and female flowers and such dramatic gender change does not exist. But the size-advantage model should also apply and thus bigger plants should produce more female-biased inflorescences. This should be represented in *Arum* by a proportionally bigger increase of the female function (number or weight of female flowers) than for male flowers.

Interestingly the only study on *Arum* related to this topic gave contradictory results (Méndez, 1998). In Spanish populations of *Arum italicum*, the number and size of inflorescences increase with plant size, estimated by the dry weight, as well as the total of flowers (Méndez, 1998). The numbers of male & female flowers were positively correlated to the inflorescence size but with the same relation (i.e. slope). Finally the floral sex ratio (66–72% of male flower) was not correlated to the plant size or the number or size of inflorescences (Méndez, 1998). Thus the reproductive effort is related to the plant vigour but with no differences among gender and thus no female bias in bigger inflorescences. A complementary study showed that in terms of biomass, male and female flowers each represented only 6% of the spadix biomass but when considering a range of different flower biomasses there was a disproportionate allocation to the male part versus female (Méndez, 2001), which is a result contrary to the size-advantage model. In *Arum* the pattern is expected to be complicated because an individual can produce several inflorescences and in fact the last-produced (and smaller) inflorescence showed a female-biased floral ratio compared to the first and larger one (Méndez, 1998), which is a result in accordance to the size-advantage model.

The aim of this paper is to characterize the reproductive characters of *Arum italicum* in the south of France and to quantify variations in reproductive characters (size of the spadix parts, number of inflorescences) in relation to plant and inflorescence sizes. Do more vigorous plants produce more and bigger inflorescences? Do bigger inflorescences bear more flowers? Does the floral sex ratio change according to the inflorescence size?

MATERIALS AND METHODS

During the spring of 2001, 90 inflorescences of *Arum italicum* Miller were harvested in order to measure the spathe length and different parts of the spadix, i.e. fertile male and female zones and appendix length. Plant vigour was estimated by counting the number of inflorescences produced and by measuring the height of the longest petiole, and the limb length and width of leaves (at the level of the petiole). Leaves were approximated as a triangle with respect to their surface. For some of these inflorescences, the number of male and female flowers per inflorescence ($n = 67$) were also counted. The floral sex ratio (number male flowers/(number of male + female flowers)) was calculated for some of these inflorescences ($n = 64$). The floral sex ratio varies from 0 (pure female) to 1 (pure male).

Data analyses consisting of linear regression analysis and slopes were compared with an ANCOVA analysis. Mean size differences between inflorescences were tested with a t-test. A distribution test to assess if the floral sex ratio was non-biased (equal to .5) with a Kolmogorov-Smirnov one sample test using a normal distribution (mean: .50, standard deviation: 1). All these analyses were performed using Systat 11 (2004) software.

RESULTS

Morphology and plant vigour

The mean sizes of the different parts of the inflorescences are shown in Table 1. The appendix appears to be an important part of the inflorescence as its length represented 43.1 ± 8.2% of the total spadix size (66% when considering only the fertile zones). The female zone is about 2.5 times longer than the male zone.

A positive relationship was found between leaf size and spathe length ($R^2 = .33$, $F_{1,67} = 33.1$, $p < 10^{-5}$). Moreover, the mean appendix size increased with spathe size ($R^2 = .24$, $F_{1,62} = 20.27$, $p < 10^{-5}$). For plants producing two inflorescences, the size of the second appendix was smaller than that of the first ($t = 2.28$, $df = 29$, $p = .03$). But there was no difference in spadix sizes between the inflorescence of plants flowering once and the first inflorescence of plants flowering several times ($t = .26$, $df = 33.3$, $p = .79$). Finally an inflorescence produced an average of 155.6 ± 42.7 male flowers and 60.8 ± 19.2 female flowers. Thus as an overall, the floral ratio in *A. italicum* was male biased (.72 ± .04) and

Table 1. Reproductive morphological measures (mean ± SD) in millimetres of *Arum italicum* inflorescences in south-western France (n = 90). The sum of the lengths of the appendix, the male zone and the female zone are not equal to the spadix length, as the appendix stipe and the two sterile zones were not measured.

Spadix	Appendix length	Appendix diameter	Male zone	Female zone
101.7 ± 29.7	44.8 ± 17.2	10.6 ± 3.4	6.4 ± 1.5	16.8 ± 5.4

statistically different from .5 ($p < 10^{-5}$). In average, male flowers were 2.5 times more numerous than female flowers.

Intra-plant relationships

Both the sizes of the appendix and of the two fertile zones were positively correlated with the spadix size, which is logical due to the autocorrelation of these traits. But interestingly, when comparing the slopes, it appears that the appendix (slope = .51) increased proportionally more than the fertile zones (Fig. 1). In the same way, both the fertile male (slope = .03) and female (slope = .15) zones increased with the spadix size, with the female zone increasing proportionally more than the male zone (Fig. 1).

The number of male and female flowers increased significantly (respectively: $R^2 = .28$, $F_{1,62} = 19.73$, $p = 4 \times 10^{-5}$; $R^2 = .39$, $F_{1,60} = 37.68$, $p < 10^{-5}$) with the spadix size (Fig. 2). The two slopes on log-transformed data were marginally significantly different ($F_{1,124} = 2.28$, $p = .08$), the number of female flowers (slope = .76) increasing faster than for male flowers

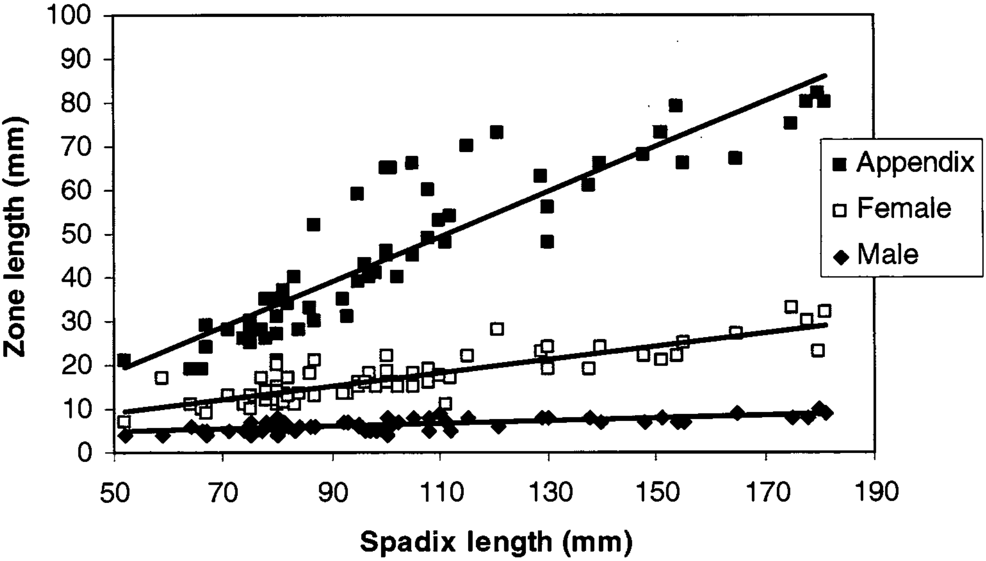

Fig. 1. Relationships between the lengths of the spadix and the appendix, the male flower zone, and the female flower zone. Each of the measured parts increases with spadix length (appendix: $R^2 = .81$, $F_{1,87} = 373.85$, $p < 10^{-5}$; male zone: $R^2 = .48$, $F_{1,87} = 83.95$, $p < 10^{-5}$; female zone: $R^2 = .73$, $F_{1,87} = 226.39$, $p < 10^{-5}$). But the slope for the appendix regression is higher than for any of the fertile zones ($F_{1,175} = 75.50$, $p < 10^{-5}$). In the same way, the fertile female zone increases more than the fertile male zone ($F_{1;175} = 69.45$, $p < 10^{-5}$).

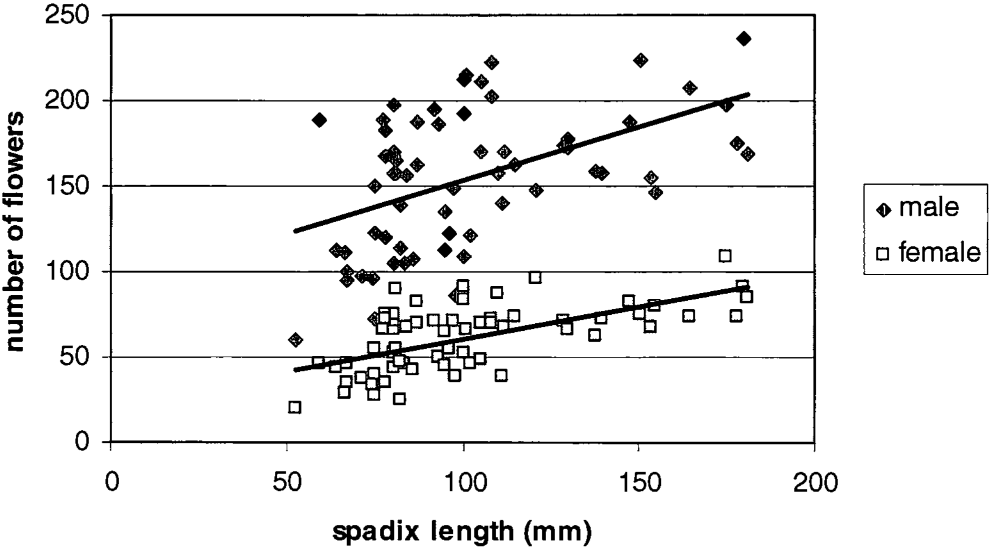

Fig. 2. Relationships between the length of the spadix and the number of male and female flowers.

(slope = .52). This gender difference of flower number increase is visualised by a significant decrease of the maleness floral ratio with spadix size (Fig. 3). But the floral sex ratio remained male biased, i.e. superior to .5.

DISCUSSION

Morphology and plant vigour

A positive relationship was found between leaf size and inflorescence number (Albre & Gibernau, 2008). It appears that

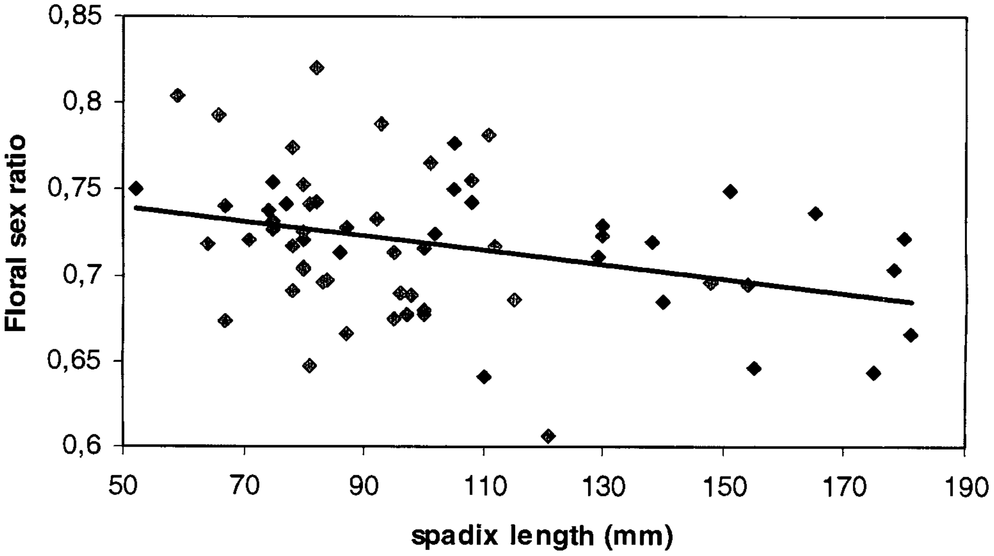

Fig. 3. Relationships between the length of the spadix and the floral sex ratio ($F_{1,62}$ = 7.47, P = 8×10^{-3}, R^2 = .11).

the number of inflorescences increases with the mean plant or leaf size, i.e. with plant vigour (Méndez, 1998). A previous study has shown that *A. italicum* cannot produce an inflorescence until the tuber mass has reached a determined weight. But afterwards, larger *Arum* produce more numerous inflorescences than smaller ones (Mendez and Obeso, 1993). So, a plant may increase its pollination probability by increasing their flower number. In fact, one third of the inflorescences of *A. italicum* do not reach the pollination stage because of accidents (rot, predation) occurring during their development (Albre & Gibernau, 2008).

Intra-plant Relationships

In terms of biomass or size, there is a disproportionate allocation of the spadix to the appendix versus fertile parts. In terms of biomass, considering only the spadix (1.5 g in average), the appendix represents 45% of the mass while the male and female flowers represent 6% each (Méndez, 2001). A comparable result was found in term of lengths as the appendix represents 44% of the length of the spadix and the male zone 6%. The only difference is about the female zone, whose length represents 16.5% of the spadix length and is much longer than the male zone. It thus appears that appendix length, and thus inflorescence size, increases with plant vigour. The main role of the appendix is to attract pollinator insects by emitting heat and volatile compounds (Meeuse, 1978; Uemura *et al.*, 1993; Kite, 1995). Moreover, the number of attracted insects generally increases with appendix length (Mendez & Obeso, 1992). So, large plants also increase their pollination probability by increasing their appendix size. In Spain, Mendez & Obeso (1992) noted that only 40% of the inflorescences which lost their appendix when heating also initiated fruit development. These authors suggested that the appendix was not an indispensable structure for fruit initiation. Nevertheless, cross-pollination by insects is obligatory for *A. italicum*, because of the protogyny and the particular morphology of its inflorescences. In fact, as the insect visitors are attracted only by the volatile compounds emitted by the appendix (Knoll, 1926; Lack & Diaz, 1991; Mendez % Obeso, 1992), this structure appears to be necessary for fructification.

The numbers of male and female flowers were positively correlated to the inflorescence size confirming that the reproductive effort is related to the plant vigour (Méndez, 1998). But contrary to a previous study suggesting no female bias in bigger inflorescences with a floral sex ratio (66–72% of male flower) not correlated to plant size or the number or size of inflorescences (Méndez, 1998), our data showed that a proportionally higher investment in terms of number of female flowers can occur in *Arum italicum* leading to increase the femaleness of the inflorescence in relation to its size. Such result is in accordance to the size-advantage model.

Surprisingly, a complementary study showed that in terms of biomass, male and female flowers each represented only 6% of the spadix biomass but when considering a range of different flower biomass there was a disproportionate allocation to the male part versus female (Méndez, 2001), which is a result contrary to the size-advantage model. In *Arum* the pattern is expected to be complicated because an individual can produce several inflorescences and in fact the last-produced (and smaller) inflorescence showed a female-biased floral ratio compared to the first and larger one (Méndez, 1998), which is a result in accordance to the size-advantage model. Difference of result between flower masses and numbers (Méndez, 1998, 2001) probably reflect that an increase in inflorescence size entails an increase in flower size, rather than in number.

In fact despite a weak increase of both fertile zones, the female zone shows a greater growth than the male zone. Nevertheless, the factors responsible for such increases are not the same according to the fertile zone. In fact, the increase of the female zone may be due more to an increase in the size of the female flowers.

On the contrary, the increase of the male flower zone is mainly due to an increase in the number of male flowers. So, large inflorescences increase the number of gametes, and thus their reproductive capacity. On the other hand, it is not known if the increase in the number of both male and female gametes is similar or different. But further studies are needed to test whether sex ratio variations can occur at the gamete level, ovules vs pollen grains, in relation to plant/inflorescence size variations.

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