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AGE-SPECIFIC SEX RATIO IN A MONOECIOUS SPECIES *CROTON BONPLANDIANUM* BAILL

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SUMMARY

The ratio of male to female flowers (sex ratio) in the monoecious *Croton bonplandianum* Baill decreased as plants aged in three habitats. Two major forces, male and female gametic success and intra-sexual selection, have been invoked to explain the decrease in sex ratio. While increasing female gametic success at successive stages of growth might be responsible for the enhanced allocation of resource to the females and hence for the absolute increase in number of female flowers at a later age, increasing male gametic success does not change the absolute number of male flowers but merely causes an increase in the number of pollen grains deposited on the stigma. Differences in the sex ratio between habitats was influenced by the differential fitness gained by the two sexes in the various habitats.

Key words: Age-specific sex ratio, gametic success, sexual selection, pollen grains.

INTRODUCTION

In the limited number of studies on the evolution of sex ratio in monoecious species (defined here as the ratio of male to female flowers), the discussions pertain to the average life-time sex ratio with little reference to the age-specific sex ratio (Lloyd, 1975; Bawa, 1977). Age-specific sex ratios are important in view of their role in increasing life-time reproductive success (Emmel, 1976) and in shaping the average life-time sex ratio. We are not aware of studies examining factors responsible for the evolution of such temporal shifts in sex ratio. However, two main theories are generally accepted in explaining the evolution of sex ratios, namely the reproductive resource allocation theory (Fisher, 1958; Charnov, Maynard Smith & Bull, 1976; Maynard Smith, 1978; Bawa, 1980; Bawa & Beach, 1981) and the sexual selection theory (Charnov, 1979; Wilson, 1979).

Here we report variations in sex ratio with age in a monoecious species, *Croton bonplandianum* Baill (Euphorbiaceae). We show that factors influencing male and female success as well as available resources shape the sex ratio of the plants through the reproductive season. In addition, we document differences in sex ratio among habitats in response to availability of resources and the success of pollination.

MATERIALS AND METHODS

The plant

Croton bonplandianum was introduced to India during the late 1890's from Paraguay (Kaul, 1967). In little more than 50 years, it was reported from all over

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Table 1. *Age, numbers of branches and percentage distribution of 'Stages' of* Croton bonplandianum

'Stage'	Age (d)	Number of branches		Percentage of population
		Range	Mean	
0	—	—	—	8·3
I	20–25	—	1·00	12·3
II	35–40	3–6	3·52	13·9
III	50–65	10–22	15·32	35·8
IV	65–75	40–85	52·20	24·9
V	80 and above	90–260	113·00	4·8

India. It now occurs widely along roadsides, railways, abandoned fields, in wide open ravines, etc. Interestingly and probably related to its pollination by wind, this species is seldom found in areas enclosed by shrubs and trees where free movement of air is hindered.

Croton bonplandianum produces a terminal raceme at an age of 20 to 25 d after which, at intervals of 15 to 20 d, three to four polychasial branches develop, each ending in a terminal raceme. We refer to termination of each order of branches in an inflorescence as a 'Stage'. Thus, the plant at 20 to 25 d with a single inflorescence is referred as 'Stage I'. The first set of polychasial branches arising after 'Stage I' is referred as 'Stage II' and so on. Plants with more than four polychasial branches, i.e. after 'Stage V', were rarely found.

Table 1 records the approximate age, the number of branches of each 'Stage' and the frequency of plants at these 'Stages' for a representative population containing some plants over 80 d old.

The inflorescence

The inflorescence is a terminal protogynous raceme with female flowers at the bottom and male at the top. Both male and female flowers open acropetally. While there is only one female flower per axil, there are usually three, and rarely four, male flowers per axil. The opening of male flowers occurs in three acropetal phases, with only one flower of an axil opening at each phase.

The study site

The habitats occupied by *Croton* included the following: (i) favourable conditions for growth with sufficient moisture, for example, shallow channels along roads, shallow pits and abandoned lands with plants sparsely distributed (three to five plants m^{-2}). We refer to plants in these conditions as 'Stray good', (ii) unfavourable growth conditions characteristic of abandoned lands subjected to repeated drought with gravelly and sandy soils. Here also, the plants were sparsely distributed (three to five plants m^{-2}). We refer to these plants as 'Stray poor' and (iii) dense growth associated with high competition between plants of *Croton* themselves and/or with other species. These areas occurred in and around permanent water channels and other moist areas. Plants in this condition are referred to as 'Competitive' (30 to 40 plants m^{-2}).

We selected two sites for each of the above three habitats in and around Bangalore (12° 58′ N, 77° 35′ E), India, spanning a diameter of about 30 km. These sites were undisturbed during this study.

Table 2. *Number of male and female flowers and sex ratio per inflorescence at the five 'Stages' for 'Stray good', 'Stray poor' and 'Competitive' habitats of* Croton bonplandianum

'Stages'	Characters	*N*	'Stray good'	*N*	'Stray poor'	*N*	'Competitive'	*N*	Average over habitats
I	Males	14	61·9±3·1^{a}	18	55·3±2·7^{a}	18	61·5±6·2^{a}	50	58·8±2·00
	Females		2·1±0·1^{a}		2·4±0·2^{a}		2·6±0·2^{a}		2·3±0·06
	Sex ratio		31·0±3·2^{a}		23·5±2·1^{a}		24·0±2·6^{a}		25·0±2·05
II	Males	35	72·3±2·1^{a}	79	67·5±1·6^{a}	32	74·5±4·5^{a}	146	70·2±1·43
	Females		3·6±0·2^{a}		4·8±0·1^{b}		5·4±0·2^{b}		4·6±0·11
	Sex ratio		20·5±0·8^{a}		14·9±0·5^{b}		14·4±0·8^{ab}		15·0±0·63
III	Males	27	77·4±2·4^{a}	75	61·2±20·^{b}	25	70·3±5·9^{ab}	127	65·8±1·99
	Females		5·4±0·2^{a}		7·0±0·2^{b}		7·0±0·3^{b}		6·6±0·18
	Sex ratio		14·7±0·5^{a}		9·0±0·3^{b}		9·7±0·9^{b}		9·9±0·42
IV	Males	50	85·9±2·1^{a}	77	58·0±2·0^{b}	43	64·1±2·2^{a}	170	68·2±1·43
	Females		7·5±0·2^{ab}		7·3±0·2^{a}		7·8±0·3^{b}		7·5±0·34
	Sex ratio		11·5±0·3^{a}		8·1±0·2^{b}		8·7±0·4^{b}		9·0±0·26
V	Males	28	74·5±1·8^{a}	23	62·1±4·8^{b}	21	49·0±1·9^{c}	72	63·1±2·18
	Females		9·7±0·5^{a}		7·8±0·6^{b}		7·2±0·3^{b}		8·4±0·32
	Sex ratio		7·9±0·2^{a}		8·6±0·2^{a}		6·7±0·2^{b}		7·5±0·29

± Values refer to standard error of means.
Numbers followed by the same letter are not significant at $P = 0{\cdot}05$; comparison is between habitats.

Collection of data

For 2 years, 1979 to 1980 and 1980 to 1981, the number of male and female flowers for an inflorescence was counted and the sex ratio computed as a ratio of the number of male to female flowers for plants selected at random each year at their respective sites. Simultaneously, data, collected on fruit set, were expressed as percentage of flowers setting fruits, and seed set as percentage ovules setting seeds. Plant height was measured to the tip of the terminal inflorescence. As a measure of the success of pollen grains in reaching the stigma, the number of pollen grains deposited on the stigma was counted for each 'Stage'. This was done by collecting female flowers that were about to close but before the male flowers on the same inflorescence opened. From these flowers, the stigmas were excised and the pollen grains on each stigma counted under the microscope. The number of pollen grains per flower was counted following Uma Shaanker & Ganeshaiah (1980, 1982).

Analyses

The sample means were compared among habitats using Student's *t*-test (Cochran & Cox, 1957). Simple correlation co-efficients were derived following Goulden (1959). Path coefficient analysis was conducted to arrive at the direct and indirect contribution of the several variables to sex ratio following the abbreviated Doo-little method (Goulden, 1959).

RESULTS

Table 2 records the number of male and female flowers per inflorescence and their ratios for the three habitats. The number of male flowers per inflorescence

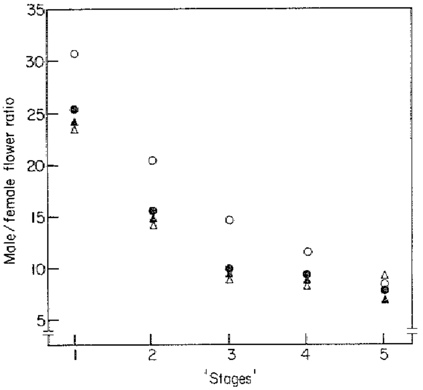

Fig. 1. Male to female flower ratio (sex ratio) for the three habitats and their average at the five 'stages'. ○, 'stray good'; ▲, 'Competitive'; △, 'stray poor'; ●, average over habitats.

Table 3. *Fruit set (percentage) at the five 'Stages' of* Croton bonplandianum *for 'Stray good', 'Stray poor' and 'Competitive' habitats*

	'Stray good'			'Stray poor'			'Competitive'		
'Stages'	*N*	Mean	Variance	*N*	Mean	Variance	*N*	Mean	Variance
I	22	56·8±5·9	761·7	10	43·5±8·8	771·5	18	14·6±6·1	666·65
II	44	62·7±4·4	836·4	31	47·5±3·5	387·0	20	37·2±4·5	408·41
III	55	70·0±3·1	538·7	42	56·2±3·4	500·5	21	58·8±4·7	459·6
IV	36	72·2±3·2	377·9	34	54·0±3·5	418·4	23	62·0±4·2	410·5
V	45	86·0±2·5	294·3	37	77·9±3·3	495·8	42	76·3±2·6	281·82

± Values refer to standard error of means.

increases slightly between the first and second 'Stages' in all the habitats but the differences are not significant. In the succeeding 'Stages', however, while no particular pattern of change in the number of male flowers can be discerned, differences between habitats become apparent. 'Stray good' plants have more male flowers than either 'Stray poor' or 'Competitive' plants.

Unlike the male flowers, there is a steady increase in the number of female flowers per inflorescence to a plateau between the last two 'Stages'. Differences between 'Stray good' plants on one hand and 'Stray poor' and 'Competitive' on the other become apparent from the second 'Stage' onwards. 'Stray poor' and 'Competitive' plants by themselves, however, do not differ significantly in number of female flowers per inflorescence.

The sex ratio declines in successive 'Stages' in a similar fashion in all habitats (Fig. 1). The degree of fruit set (Table 3) increases with successive 'Stages' (Fig. 2) and differs significantly between habitats. This increase could be a response to increased gain of resources by the plant and/or increased success of fertilization. The latter possibility is supported by the number of pollen grains per stigma (P/st) (Table 4). There is an almost linear increase in the number of pollen grains

Table 4. *Pollen grain number per stigma, pollen number per anther and plant height of* Croton bonplandianum *at the five 'Stages' for a 'Stray good' habitat*

	Pollen grains/stigma			Plant height (cm)		Pollen grains/anther	
'Stages'	*N*	Mean	Variance	*N*	Mean	*N*	Mean
I	8	3·0±0·7	4·0	15	16·4±0·8	10	307·1±11·3
II	21	7·7±1·0	21·1	15	25·5±0·8	7	257·0±23·5
III	22	11·5±1·3	40·0	22	33·7±0·2	7	263·5±51·0
IV	11	17·0±2·0	46·5	11	38·6±0·6	7	211·2±45·0
V	11	23·4±5·0	273·5	11	44·7±2·9	8	272·4±19·5

±Values refer to standard error of means.

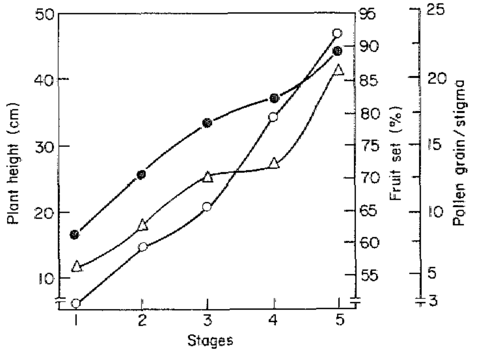

Fig. 2. Plant height, fruit set percentage and pollen grain number per stigma for the five stages in a 'stray good' habitat. ●, Plant height; ○, pollen grain number per stigma; △, fruit set percentage.

deposited on the stigmatic surface through the 'Stages' (Fig. 2). The increase in P/st seems to be influenced by the height to which the female flower is elevated and not by any increase in the number of pollen grains per female flower. Indeed, a highly significant positive correlation between plant height and P/st is observed (Table 5). Hence this increased P/st may be due to the better exposure of the female flower at the later 'Stages' to the pollen-carrying wind at greater heights.

Sex ratio is negatively correlated with P/st, plant height, fruit set and number of female and male flowers (Table 5). The number of male flowers per inflorescence was not correlated to any of the other variables. Plant height, fruit set and number of females showed positive association with each other.

Table 6 records the path co-efficient values indicating the direct and indirect effects of different variables. Plant height appears to have the greatest effect on the sex ratio followed by female flower number, fruit set and the male flower number. Though male flower number is expected to contribute to sex ratio, its direct effect as indicated by this analysis is low, while that of the female number is high. Thus, plant height appears to have a pivotal role in shaping the sex ratio, probably because it is an indicator of both gain of resources and also success of fertilization (through increasing P/st).

Table 5. *Correlation matrix*

Character	Pollen/ stigma	Plant height	Number of females	Number of males	Fruit set (%)	Sex ratio
Pollen/stigma	1·00	0·66**	0·48**	−0·06	0·41**	−0·53**
Plant height	—	1·00	0·71**	0·15	0·55**	−0·80**
Number of females	—	—	1·00	0·14	0·55**	−0·72**
Number of males	—	—	—	1·00	0·15	−0·25*
Fruit set (%)	—	—	—	—	1·00	−0·67**

* Significant at $P = 0{\cdot}05$; ** significant at $P = 0{\cdot}01$ level.

Table 6. *Matrix of path-coefficient values of the five variables studied on sex ratio*

Character	Pollen/ stigma	Plant height	Number of females	Number of males	Fruit set (%)	Correlation with sex ratio
Pollen/stigma	**−0·03**	−0·31	−0·11	0·00	−0·08	−0·53**
Plant height	−0·01	**−0·47**	−0·17	−0·01	−0·10	−0·80**
Number of females	−0·01	−0·34	**−0·24**	−0·01	−0·10	−0·72**
Number of males	0·00	−0·07	−0·03	**−0·11**	−0·31	−0·25*
Fruit set (%)	−0·01	−0·26	−0·13	−0·01	**−0·19**	−0·67**

The figures in bold type indicate the direct effect, while those above and below it refer to the indirect effect.

DISCUSSION

The observed decrease in ratio of male to female flowers with age in *Croton* will be discussed under the four following headings: (A) maximization of reproductive success through re-allocation of resources between the sexes, (B) sexual selection in shaping the sex ratio, (C) other plant factors influencing the sex ratio and (D) differences in sex ratio between the habitats.

(*A*) *Maximization of reproductive success, re-allocation of resources and sex ratio*

Male success (measured by the number of pollen grains on the stigma) and female success (measured by the fruit set), which increase with age in *Croton*, might result in two competitive events. Natural selection may favour either plants in which fitness is increased by allocation of more of resources to production of female flowers or plants in which fitness is increased by re-allocation of reproductive resource to the male flowers, thereby increasing the possibility of exploiting additional ovules.

Though both events are equally likely, it is probable that selection would favour an enhanced allocation of resource to females for the following four reasons. (a) While the female success in plants is generally constrained by the availability of resource, that of the male is limited by number of ovules (Lloyd & Webb, 1977). In *C. bonpandianum*, where there is an accumulation of resource with age, increase in number of female flowers may be expected. (b) Increase in number of female flowers maximizes the net reproductive gains through increasing fecundity whereas decrease in number of male flowers does not confer any additional advantage. (c) The variance for female success (fruit set) decreases with age while that for male success (P/st) increases (Tables 3 and 4). In other words, female rather than male units contribute more consistently to reproductive fitness in older 'Stages'. Investment in a reproductive unit which gives a consistent return in terms of increased fitness clearly pays in *Croton* (cf. Wade, 1979). (d) Owing to the increased success of pollen grains in reaching the stigma, competition results among those on the stigma for mates (ovules). Hence, there will be a decreasing reward for every additional pollen grain on the stigma (Lloyd & Webb, 1977) (i.e. the probability that any given pollen will fertilize an ovule decreases with increase in their numbers on the stigma). This force limits increase in number of male flowers, so restricting competition with the females for resource. Thus, females would be favoured from that 'Stage' when competition among pollen grains sets in. This explanation implies that sex ratio and number of pollen grains on the stigma will be negatively associated after the 'Stage' at which the competition among pollen grains for ovules begins (i.e. when P/st exceeds ovule number). Till this 'Stage', an increase in the male to female flower ratio will occur. In favourable growth conditions ('Stray good'), where the number of pollen grains on the stigma equals ovule number per flower at 'Stage I', such a negative association does occur.

(*B*) *Sexual selection and sex ratio*

Although selection favours an increase in number of females at later 'Stages', there is an increase with age in the number of pollen grains per stigma. To explain this, the theory of sexual selection, where selection would favour males as females are constrained by limitation of resources, must be invoked (Charnov, 1979, 1980; Lloyd, 1979; Willson, 1979; Bawa & Beach, 1981). Thus, in a population where competition already exists among males for mates (females), the fitness of individuals is increased by their contributing a greater proportion of the population of pollen grains. This explanation is justified in the present context for, as more competition for mates is generated at later 'Stages', additional male reproductive success follows from increased female success (fruit set). However, contrary to the argument by Willson (1979), increased competition for mates need not necessarily cause an increased allocation of resource to males because competition for mates can be enhanced merely by altering the efficiency of pollen donation and capture. This point is well exemplified in *Croton*, where, owing to better display of the female flowers at increasing height as plants age, stigmas are better exposed to winds carrying pollen.

(*C*) *Other plant factors influencing sex ratio*

Though the foregoing discussion amply demonstrates the impact of P/st in shaping the sex ratio of successive 'Stages', the number of pollen grains currently deposited on the stigma may be expected to have little, if any, effect on the sex ratio of the following 'Stage'. This is because changes in sex ratio occur as a response to changes in the P/st over a number of generations. However, plant height, number of female and male flowers and fruit set directly influence the current sex ratio as shown below.

Plant height which shows the highest correlation with sex ratio ($r = -0{\cdot}80$) has the highest direct effect also ($-0{\cdot}47$) (Tables 5 and 6). Plant height is an indicator of 'resource status' of a given 'Stage' (Suryanarayana, 1975). Hence its direct relation to sex ratio may not be unexpected as 'resource status' of a plant influences the sex ratio through its effect on the female. Plant height affects sex through P/st also. Increase in P/st increases the fruit set ($r = +0{\cdot}40$), resulting in a greater demand for the resource for the developing fruits. As this puts a limit on the available resources for subsequent 'Stages', the allocation of resources between males and females may alter in the ensuing 'Stages'. Such re-allocation also explains the negative correlation ($r = -0{\cdot}67$) and the negative direct effect ($-0{\cdot}19$) of fruit set on sex ratio. Of the direct determinants of sex ratio, number of male flowers has a greater direct effect ($-0{\cdot}24$) than that of females ($-0{\cdot}13$) during the development of the plant.

(*D*) *Habitat differences in sex ratio*

Differences in sex ratio between 'Stray good' plants on the one hand and 'Stray poor' and 'Competitive' plants on the other are noticeable only *after* 'Stage I'. That the plants of the different habitats do not differ at 'Stage I' may indicate the failure of the germinating seeds to 'sense' conditions in the habitat and/or the failure of the seeds to carry over information about the quality of the habitat of the parent generation. As a parent cannot evaluate the habitat into which its offsprings will enter, lack of carry over of information about habitat quality might be generally advantageous, especially so, when the fitness of each sex is strongly determined by the habitat in which it finds itself (Charnov & Bull, 1977).

Plants of 'Stray poor' and 'Competitive' habitats have an increased number of female flowers per inflorescence over those of 'Stray good' (Table 2). If the proportion of female flowers at an early 'Stage' is calculated as a percentage of the number of female flowers at 'Stage V', the value for 'Stray poor' and 'Competitive' plants are 90 and 97% compared to only 55% in 'Stray good' plants. In fact, there are more females at 'Stage I'.

'Stray poor' plants suffer owing to density-independent factors such as poor soil and drought, while 'Competitive' plants suffer mostly owing to density-dependent factors such as severe competition for space and nutrients and disturbed pollen flow. As plants in both habitats face imminent death at every 'Stage', adoption of pessimistic reproductive strategy (i.e. rapid achievement of maximum reproductive growth) pays better (Zeide, 1978). Thus by 'Stage III', these plants have numbers of female flowers equal to 90% ('Stray poor') and 97% ('Competitive') of what they would have produced at the final 'Stage' if they survived till then. In this way, at the cost of future reproduction, 'Stray poor' and 'Competitive' plants maximize their current reproductive effort. However, the nature of the adaptive value of such 'female-biased resource allocation' under conditions limited by resources then arises. Unlike 'Stray good' plants, 'Stray poor' plants are stunted and 'Competitive' plants are crowded. As these conditions restrict movement of pollen, pollination in these two habitats may be at a low rate compared to that for 'Stray good' plants. Hence, natural selection will favour plants that reproduce through increased production of females. Increased production of pollen will result in dismally low probability of success under these situations. The argument is similar to that of Trivers (1972) and Williams (1975). Willson (1979) also cites two examples wherein, under dense conspecific canopies where pollen movement is hindered, females are favoured.

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