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Reproductive effort and sex allocation strategy in *Commelina benghalensis* L., a common monsoon weed

VEENU KAUL*, NAMRATA SHARMA and A. K. KOUL

Department of Botany, University of Jammu, Jammu-180 006 (J & K), India

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Commelina benghalensis L. exhibits variability in both foliar and floral features; every plant bears three types of branches and four types of flowers. The branches are negatively geotropic, positively geotropic and diageotropic. The flowers are uni- or bisexual, chasmogamous and cleistogamous. This variability influences the breeding system as well as resource allocation to male and female functions. The plants allocate c. 15% of their total resources to reproduction, the major part of which (68.9%) is devoted to production of aerial branches. The proportion of reproductive effort (RE) allocated to various branch systems is correlated with the availability of resources at the time of their differentiation. The pollen/ovule (P/O) ratio, female : male biomass ratio and reproductive output vary between different flower and branch types; variation is more pronounced in the latter. These variations notwithstanding, the results are in line with Charnov's sex allocation theory. The cleistogamous flowers of aerial branches are, however, an exception, being male- rather than female-biased. The reason behind the deviation is, in all probability, their recent evolution from chasmogamous flowers. © 2002 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2002, **140**, 403–413.

ADDITIONAL KEYWORDS: breeding system – chasmogamous – cleistogamous – female : male biomass ratio – P/O ratio – output – sex allocation – underground.

INTRODUCTION

Commelina benghalensis L., a prolific rainy season annual/perennial weed which grows throughout tropical India is complex in its foliar and floral morphology. All plants of the species have three types of branches/shoots: negatively geotropic cauline (NG), positively geotropic subterranean (PG) and diageotropic (DG) which run parallel to the soil surface. All three systems are flower-bearing, but only two (NG and DG) bear leaves. Flowers are mainly of three types: male chasmogamous (M), hermaphrodite chasmogamous (CH) and hermaphrodite cleistogamous (CL) (Maheshwari & Maheshwari, 1955).While NG branches bear all three types of flowers (NG-M, NG-CH, NG-CL), DG and PG branches carry only hermaphrodite flowers which are chasmogamous in the former (DG-CH) and cleistogamous in the latter (PG-CL) (Table 1). A few plants within a population also bear female flowers on NG branches which have either no or non-functional stamens (V. Kaul, unpubl.). Male sterility in these flowers is caused either by the failure of anther dehiscence or differentiation of non-viable pollen grains. As such, the plants of *C. benghalensis* are andro- as well as gynomonoecious; the former is a regular feature and the latter an occasional event.

This polymorphy in foliar and floral parts of the plant prompted us to investigate the following: (1) whether different types of flowers and the branch systems bearing them vary in sex allocation strategies; (2) the reproductive output of different branch systems and the extent to which it is related to flower structure, and (3) the proportion of the total energy budget invested in reproduction.

MATERIAL AND METHODS

Plants of *C. benghalensis* grow in dense populations between May and December, when diurnal temperatures fluctuate between 31 and 40°C, and relative

*Corresponding author. Fax: +91 435256

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Table 1. Distribution of different flower types on the three branch systems. See text for abbreviations

No.	Character	Branch system		
		NG	DG	PG
1	No. of flowers per spathe	3 (1–4)	1	1
2	Sex expression of the flowers	Male CH CL	– CH –	– – CL
3	No. of shoots per plant	3 ± 0.2[a] (2–5)[b]	5 ± 0.7 (1–11)	7 ± 0.02 (2–15)
4	No. of spathes per plant	80 ± 8.9 (15–401)	16 ± 1.3 (4–38)	19 ± 1.7 (6–112)
5	No. of flowers per plant[c]	240	16	19

[a] Mean ± SE
[b] Range
[c] Product of nos. 1 & 4.

humidity ranges between 55 and 100%. Total rainfall during the period of growth ranges from 249 mm in the month of July to 7.0 mm in October. The flowering period extends from the last week of June to the end of October. The observations reported in this paper were conducted on 35 plants transplanted from the wild to experimental beds (3.8 × 1.4 m) in the University Botanic Garden, Jammu. Data were recorded over a period of 3 years (1995–97).

Flowers are encased in mucilage-filled axillary spathes. The number of spathes present in an axil varies; in DG and PG branches there is a single spathe per axil, while NG branches have 1–4. The total spathe count per branch varies among the three systems (Table 1).

Seeds germinate during May and the first leaf emerges 3–5 days after sowing. When the seedlings are small, with 8–10 leaves, a small subterranean shoot develops on which floral buds differentiate. When the seedlings become older and the number of leaves increases to 17–19, flowers start differentiating on aerial shoots.

Except in the few stray female flowers, which have either no or non-functional stamens, the androecium comprises three fertile and three vestigial stamens. One of the three fertile stamens has a long, curved, yellow, versatile anther; the other two, which are smaller, have dithecous, light grey and basifixed anthers. The gynoecium is tricarpellary, syncarpous and trilocular, with a long style and a trifid, papillate, violet stigma. All NG and DG-CH flowers have five ovules per ovary, two in each anticous and one in the posticous chamber. The single ovule of the posticous locule is much larger than the four present in the two anticous locules. The PG flowers have only three ovules per ovary; one per locule. Ovules of the PG pistils vary only slightly in size, the posticous ovule being slightly larger than the other two.

Ovule count was estimated by excising ovules from the ovaries and counting under a dissection microscope. Ovule size was measured using a calibrated ocular micrometer (Tandon, Shivanna & Mohan Ram, 2001).

The number of pollen grains was estimated for each flower type, separately for yellow and grey anthers. Pollen count per anther was estimated with the help of a haemocytometer. Pollen output per flower was calculated by multiplying pollen count per grey anther by 2 and adding the figure thus obtained to the pollen count of the yellow anther.

The vestigial anthers are yellow, vary in shape, and have short, slender filaments. Most of these are six-lobed; only two lobes contain pollen grains (Maheshwari & Maheshwari, 1955) which stain readily with 1% acetocarmine, aniline blue and Lewis's (1979) stain. They resemble the pollen contained in the fertile stamens in size, shape and stainability. These anthers are indehiscent and therefore functionally sterile. Since their pollen does not participate in gene flow, it has not been included in pollen count estimates (Olson & Antonovics, 2000).

The pollen/ovule (P/O) ratio was estimated by dividing the average pollen count per flower by the ovule count/flower, as proposed by Cruden (1977).

Reproductive effort (RE) was estimated by the dry biomass method (Sharma & Koul, 1995; Sadras, Bange & Milroy, 1997; Sharma, Koul & Kaul, 1999). For this purpose, 30 randomly selected plants were uprooted at the flower–fruit development stage. The uprooted plants were washed under running water and dried on blotting paper. They were then separated into leaves, stem, roots, spathes, etc. All parts of the plant were oven-dried at 60°C for 24–48 h and weighed separately on a K-12 single-pan electric analytical balance. RE was calculated separately for each branch system; the figures thus obtained were pooled for estimating RE per plant. Following Dunn & Sharitz (1991) the formula used was:

$$RE = (\text{Floral dry biomass}/\text{Total dry biomass}) \times 100$$

Male and female biomass was calculated from the dry weight of stamens and pistils, respectively (Cumaraswamy & Bawa, 1989; Niklas, 1993). For this purpose floral buds were collected at random from the plants raised in pots. Reproductive organs were excised from ten mature, still closed, unpollinated NG

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and DG-CH flowers of the same age (12 h prior to anthesis). The reproductive organs of the NG-CL flowers were excised at the time of anthesis of the NG-CH flowers, since they are mostly pollinated afterwards. Excision was carried out in the lab under a dissection microscope using a pair of sterilized fine forceps and sharp needles.

A few pots were flooded with water to facilitate easy uprooting and the plants washed under running water; the PG-CL flower buds were excised and the plants replanted, after which they were not disturbed. All the flowers were excised, along with their pedicels. The average length of the pedicel varies from 0.2 mm in PG-CL to 5.5 mm in male flowers. They were included in the estimates of dry weight. All flowers were oven-dried at 60°C for 24 h to a constant weight. The dry mass was weighed on the K-12 single pan electric analytical balance.

Lots of ten, randomly collected, flowers of each type from the three branch systems of the same plant comprised individual samples.

The flowers differentiate within spathes which are green in the NG and DG branches and pale white in the PG. Green spathes are capable of photosynthesis; little energy is expended on their differentiation and they have not been included in the estimation of resource allocation. The PG spathes are white and therefore incapable of manufacturing their own resources. To ensure fair comparison, these spathes also have been excluded from biomass estimation.

Ontogenetically, the vestigial stamens/staminodes are male, but functionally they are ancillary. They have been treated as a part of the male reproductive apparatus. They constitute a part, although small, of the floral display to enhance pollinator visitation and ensure efficient pollen flow.

For estimation of seed output, seeds set on different branch systems of the plant were harvested and counted separately. The seed output per plant was estimated by adding the number of seeds set on the three branch systems. The seed set per flower was calculated separately on a percentage basis, by applying the following formula:

$$\% \text{ age seed set per flower} = (\text{No. of seeds set per fruit} / \text{No. of ovules per flower}) \times 100$$

All NG and DG flowers have five ovules and all PG flowers have three; the number of seeds set per fruit varies between 0 and 5 in the former and 0–3 in the latter. The harvested fruits were classified into six groups (four of them subterranean) on the basis of the number of seeds they contained.

The RE of the female flowers comprises an interesting part of the study which is being published separately.

A one-way ANOVA (Sokal & Rohlf, 1973) was conducted to determine the effect of branch and flower type on P/O ratio and on female : male allocation. Seed number and seed weight per plant were correlated by regression analysis and compared for branch and flower types.

RESULTS

Reproductive effort (RE)

Plants of *C. benghalensis* invest an average of 14.8% (5.6–18.6%) of their total resources in reproduction. The major part of this investment is appropriated by the NG branch system (Fig. 1; Table 2). The proportion allocated to the differentiation of shoots and spathes is equal in DG branches, while in PG branches the allocation to spathes is greater (Fig. 2).

Pollen production

Pollen output varies between the anthers of a flower and between flowers of the same and different branch systems (Fig. 3; Table 3). In general, the output of the yellow anther of the male flower is the largest and that of the light grey anther of the PG flower the smallest. Pollen production varies between 24 274 per male to 6915 per PG flower.

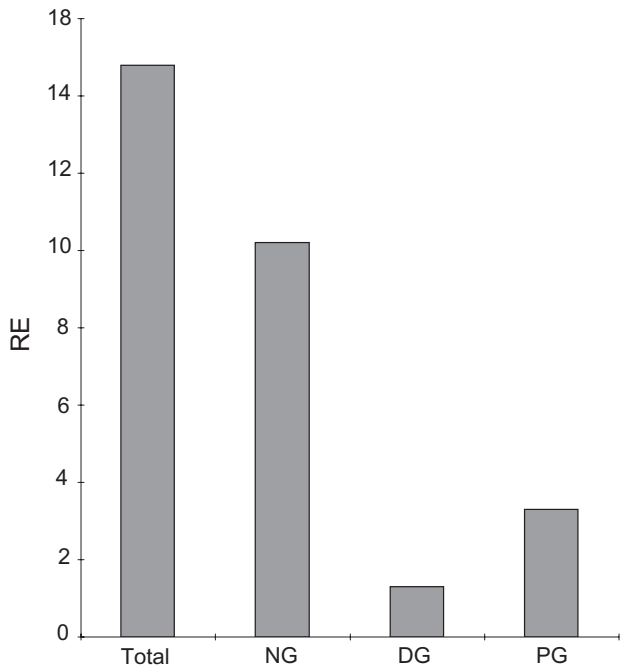

Figure 1. Relationship between reproductive effort (RE) of the plants of *Commelina benghalensis* and the share of different branch systems.

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Table 2. Estimates of reproductive effort (RE) calculated from dry biomass allocation

Biomass (g) of different plant parts	Whole plant	Branch System		
		NG	DG	PG
Roots	0.25 ± 0.04[a] (0.01–1.14)[b]	–	–	–
Leaves	1.35 ± 0.2 (0.19–7.70)	–	–	–
Stem	–	0.91 ± 0.2 (0.04–6.65)	0.04 ± 0.01 (0.001–0.11)	0.04 ± 0.01 (0.01–0.16)
Spathes	–	0.31 ± 0.07 (0.01–3.13)	0.04 ± 0.01 (0.001–0.16)	0.10 ± 0.01 (0.004–0.30)
Total dry biomass per plant	3.04 (0.27–19.35)	–	–	–
Total floral dry biomass per plant	0.45 (0.015–3.59)	–	–	–
RE/branch system (%)	–	10.2	1.3	3.3
RE/plant	14.8 (5.6–18.6)	–	–	–
% relative allocation	–	68.9	8.9	22.2

[a] Mean ± SE
[b] Range
Sample size, $N = 30$.

POLLEN/OVULE RATIO

The P/O ratio also varies a great deal between flowers of different branch systems. Irrespective of whether they are cleisto- or chasmogamous, NG flowers, in general, have a higher P/O ratio than those of the other two systems (Table 3); the ratio is also higher in DG-CH than PG-CL flowers. Results of one-way ANOVA carried out separately for flower and branch types exhibit significant variation among branch as well as among the flower types (Table 4). The intraplant ratio is more variable than the interplant ratio. About 97.6% variation occurs among and only 2.4% within branch types. By contrast, almost equal variation occurs among (48%) and within (52%) flower types.

FLORAL BIOMASS

The dry weight of accessory (pedicels, sepals and petals) and reproductive (stamens and pistil) parts of flowers of different branch systems varies (Fig. 4; Table 5). The total weight of the NG-CH flowers is greatest and that of the PG flowers is least. However, the ratio between weight of accessory and essential floral parts is highest in male, equal in DG and least in the PG flowers.

BIOMASS OF MALE AND FEMALE REPRODUCTIVE ORGANS

The dry weights of androecium and gynoecium vary in flowers of different types; they are highest in NG-CH and lowest in PG (Table 6). The ratio between the dry weights of pistil and stamens is highest in PG and lowest in flowers of DG spathes. Reproductive allocation reveals a parallel trend in branch and flower type comparisons. Results of one-way ANOVA exhibit significant variation at the 0.01 level in branch and 0.05 level in flower types. Relatively more variation occurs within than between a particular branch or flower type (Table 7).

REPRODUCTIVE OUTPUT

Seed set

In *C. benghalensis* seed production is very high. The NG-CL flowers set most seed (81.8 ± 0.5%), while the

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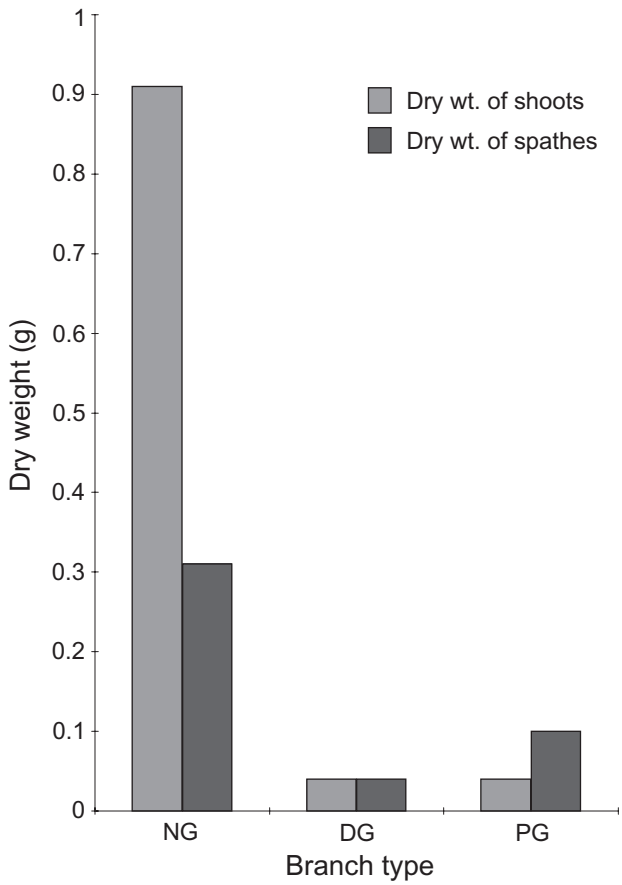

Figure 2. Dry weight estimates of the allocation of energy to the shoots and spathes of different branch systems.

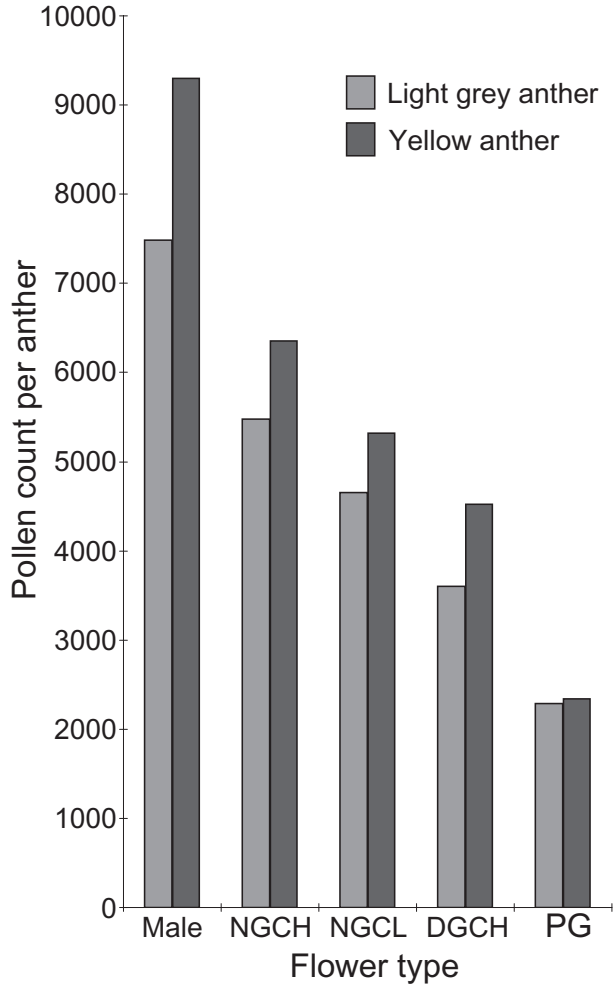

Figure 3. Per anther pollen counts of different flower types of *Commelina benghalensis*. Note that the yellow anther differentiates a larger number of pollen grains.

PG-CL flowers are almost equally efficient; the DG flowers are the least productive (Table 6).

The number of seeds set was estimated separately for comparison between branch systems. The greatest number is set on the NG branches, the least on the DG branches (Table 8) while the PG branches fall in between.

Seed weight

Seeds set by the two types of hermaphrodite flowers of the NG spathes vary in their weight. The posticous seed of the NG-CL flower on average weighs 7.4 mg and the corresponding seed of its NG-CH neighbour weighs 6.8 mg. The anticous seeds of the two do not vary much in weight, it is 3.7 mg in the former and 3.6 mg in the latter.

Seeds produced by the PG flowers are the heaviest; the average weight of an individual seed is 9.6 mg (Table 8). Seeds differentiating in the DG flowers are smaller and lighter. Seed number and seed weight are not related. This is borne out by the linear regression analysis between the two features for branch and flower types. No significant difference was observed at 0.01 level ($t = 3.24$ and 3.00 at df 3 and 2, respectively). This led to the acceptance of null hypothesis.

DISCUSSION

Plants of *C. benghalensis* invest 14.8% of their total resources in reproduction, which is carried out by flowers distributed on the three branch/shoot systems of the plant. Flowers borne by the aerial (NG) branches corner a major part of the RE, followed by those on the subterranean (PG) and diageotropic (DG) branches (Table 2). This difference in resource outlay is caused by the variation in the total number of flowers differentiating on the three systems. Against an average of 240 flowers on an NG branch, the DG

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Table 3. Pollen and ovule count, and pollen–ovule ratio in flowers of different types

Type of flower	Pollen count: Light grey anther	Pollen count: Yellow anther	Pollen count per flower	Ovule count per flower	P/O ratio
Male	7488 ± 105.6[a] 4318–9871)[b] *N* = 16	9298 ± 383.4 (6822–11332) *N* = 15	24274	–	–
NG CH	5475 ± 182.9 (3379–8149) *N* = 30	6352 ± 287.8 (4724–9864) *N* = 26	17302	5	3460 : 1
NG CL	4652 ± 172.5 (3161–5890) *N* = 28	5319 ± 256.2 (3878–7721) *N* = 24	14623	5	2925 : 1
DG CH	3602 ± 261.3 (2557–4349) *N* = 7	4519 ± 323.3 (3409–5568) *N* = 7	11723	5	2345 : 1
PG CL	2288 ± 111.6 (1053–3714) *N* = 29	2339 ± 181.9 (1308–4277) *N* = 24	6915	3	2305 : 1

[a] Mean ± SE
[b] Range
N = sample size.

Table 4. Analysis of variance of the effects of branch type (A) and flower type (B) on pollen/ovule ratio

Source of variation	df	*F*
A. Branch type		
Among branches	2	566.5*
Within branches	43	
Total	45	
$F_{0.05[2,43]} = 3.2132$	$F_{0.01[2,43]} = 5.1382$	
B. Flower type		
Between flowers	3	18.6*
Within flowers	77	
Total	80	
$F_{0.05[3,77]} = 2.7246$	$F_{0.01[3,77]} = 4.0504$	

*Significant at 0.05 and 0.01.

and PG branches have as few as 16 and 19 flowers, respectively (Table 1).

Accordingly, the reproductive output (in terms of number of seeds), of NG branches is maximum. Nevertheless, seeds produced on PG branches are the heaviest. The difference in seed weight can be correlated with the interesting pattern of resource partitioning in plants of *C. benghalensis*.

Resource partitioning starts very early in the life cycle of *C. benghalensis*. When the seedlings are still young with 7–10 leaves, floral buds start differentiating on the subterranean shoots. Under laboratory con-

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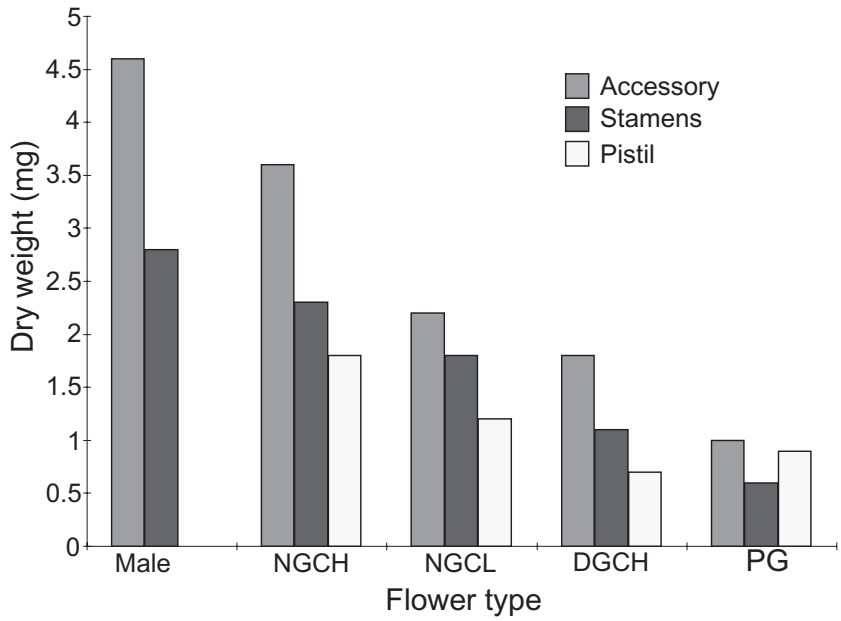

Figure 4. Dry weight estimates of allocation of energy to the various parts of the flowers of different types.

Table 5. Dry weight of accessory and reproductive (stamens and pistil) parts of flowers of different types and the ratios thereof

	Dry weight (mg) of:				
		Essential floral parts:			Ratio
Type of flower	Accessory floral parts (1)	Stamens (2)	Pistil (3)	1/(2 + 3)	Female : Male Biomass 3/2
Male	4.6 ± 0.6[a] (2.4–10.2)[b] *N* = 14	2.8 ± 0.3 (1.2–5.4) *N* = 14	–	1.64 : 1	–
NG-CH	3.6 ± 0.5 (1.9–6.3) *N* = 11	2.3 ± 0.3 (1.0–3.9) *N* = 13	1.8 ± 0.2 (0.5–2.8) *N* = 15	0.88 : 1	0.78 : 1
NG-CL	2.2 ± 0.3 (1.2–4.4) *N* = 13	1.8 ± 0.1 (1.0–2.1) *N* = 13	1.2 ± 0.2 (0.8–2.2) *N* = 15	0.73 : 1	0.67 : 1
DG-CH	1.8 ± 0.2 (0.6–1.8) *N* = 6	1.1 ± 0.5 (0.4–3.6) *N* = 7	0.7 ± 0.3 (0.3–2.0) *N* = 6	1 : 1	0.64 : 1
PG-CL	1.0 ± 0.1 (0.8–2.0) *N* = 17	0.6 ± 0.05 (0.3–1.0) *N* = 14	0.9 ± 0.09 (0.3–1.80) *N* = 16	0.71 : 1	1.50 : 1

[a] Mean ± SE
[b] Range
N = sample size.

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Table 6. Seed set and resource allocation (in percent) to male and female reproductive organs of different flowers of *Commelina benghalensis*

	Dry weight (mg) of:		% relative allocation:		
Type of flower	Stamens (1)	Pistil (2)	Female parts[†]	Male parts[‡]	% seed set
Male	2.8 ± 0.3 (1.2–5.4) *N* = 14	–	0.0	100.0	–
NG-CH	2.3 ± 0.3 (1.0–3.9) *N* = 13	1.8 ± 0.1 (0.5–2.8) *N* = 15	43.9	56.1	74.8 ± 0.02[a] (60.9–90.5)[b] *N* = 2131
NG-CL	1.8 ± 0.1 (1.0–2.1) *N* = 13	1.2 ± 0.1 (0.8–2.1) *N* = 15	40.0	60.0	81.8 ± 0.05 (67.2–95.4) *N* = 579
DG-CH	1.1 ± 0.4 (0.4–2.6) *N* = 7	0.7 ± 0.3 (0.3–2.0) *N* = 6	38.9	61.1	65.2 ± 3.6 (20.0–100.0) *N* = 62
PG-CL	0.6 ± 0.06 (0.3–1.0) *N* = 14	0.9 ± 0.1 (0.3–1.8) *N* = 16	60.0	40.0	73.2 ± 0.02 (53.6–99.9) *N* = 3423

[†] Calculated by the formula: $[2/(1 + 2)] \times 100$
[‡] Calculated by the formula: $[1/(1 + 2)] \times 100$
[a] Mean ± SE
[b] Range
N = sample size.

Table 7. Analysis of variance of the effects of branch type (A) and flower type (B) on female : male allocation ratio

Source of variation	df	*F*
A. Branch type		
Between branches	2	8.0189**
Within branches	35	
Total	37	
$F_{0.05[2,35]} = 3.2685$	$F_{0.01[2,35]} = 5.270$	
B. Flower type		
Between flowers	3	4.0127*
Within flowers	48	
Total	51	
$F_{0.05[3,48]} = 2.8$	$F_{0.01[3,48]} = 4.22$	

** Significant at 0.05 and 0.01
* Significant at 0.05 only.

ditions, the buds differentiate even earlier, at the five-leaf stage (pers. observ.). This pattern of resource allocation is comparable to eight other amphicarpic plants belonging to five phylogenetically unrelated families (Cheplick & Quinn, 1982; Cheplick, 1994). Such early allocation for reproduction when vegetative growth is just beginning has been called 'pessimistic strategy' by Zeide (1978) and Cheplick & Quinn (1982).

The first flower on the NG branch differentiates when the leaf number of the seedlings has increased to 17–19. By this time flowers on the PG branches have already set fruits and seeds. The same pattern has also been observed in other amphicarpic annuals, e.g. *Amphicarpum purshii* (McNamara & Quinn, 1977; Cheplick & Quinn, 1982; Cheplick, 1987, 1994), *Gymnarrhena micrantha* (Koller & Roth, 1964; Zeide, 1978) and *Emex spinosa* (Weiss, 1980). In *C. benghalensis* CL flowers produce seeds before as well as at the same time as CH flowers. This pattern of seed development covers all risks that may arise from seedling to adult stage.

Selection in annuals favours plants that respond appropriately to cues indicative of the end of the

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Table 8. Seed weight and share (in percent) of different branch systems in total seed output

Branch system	Seed set per branch system $N = 20$	% age share in the total seed set	Weight (mg) of:	
			Large seed	Small seed
NG-CH	664 ± 78.5	50.08	6.8 ± 0.09[a] (2.8–9.8)[b] $N = 204$	3.6 ± 0.03 (1.1–5.6) $N = 733$
NG-CL	401 ± 81.3	30.24	7.4 ± 0.1 (3.6–11.7) $N = 129$	3.7 ± 0.04 (1.2–6.7) $N = 431$
DG-CH.	99 ± 21.9	7.47	4.6 ± 0.2 (2.4–5.9) $N = 35$	2.4 ± 0.05 (1.4–3.7) $N = 114$
PG-CL	162 ± 11.7	12.22	9.6 ± 0.1 (2.9–21.1) $N = 769$	–

[a] Mean ± SE
[b] Range
N = sample size.

season. In the event that this proves to be unpredictable, natural selection favours individuals that reproduce early enough to ensure that at least some seed is produced, even in years when the season ends early and abruptly (Waller, 1979). *C. benghalensis* is a rainy season weed. It roots in soil that is saturated with water at least during the early part of its life. Thereafter, the plants thrive even after the soil dries (Wilson, 1981; Kaul, 1998). Obviously the plants require well-watered soils initially to establish themselves. Failure of monsoon and the resultant dry spell exposes the plants to risk which *C. benghalensis* partly averts by early flowering and fruiting underground.

The NG flowers and PG fruits thus differentiate and develop in a resource-rich environment, and corner a major part of the reproductive effort and reproductive output of the plant, respectively.

RE AND SEX ALLOCATION

An important aspect of the RE of any plant is its sex allocation strategy (Schoen, 1982; Charnov, 1982; Charlesworth & Charlesworth, 1987; Mckone, 1987; Sharma & Koul, 1995; Sharma *et al*., 1999) i.e. the proportion in which it produces male and female gametes. Higher pollen output compared with ovule count is mostly characteristic of plants in which pollen transfer from anthers to stigma is not foolproof. The more efficient the mechanism of pollen transfer, the lower the pollen output of the plant (Cruden, 1977, 2000; Wyatt, 1984; Cruden & Lyon, 1989). In *C. benghalensis* flowers of the three branch systems display diversity in sex allocation strategy. The P/O ratio is highest in NG-CH and lowest in PG flowers. This pattern is in accord with their mode of pollination. However, the P/O ratio in NG-CL flowers is closer to that of the NG-CH flowers (Table 3) than that of the PG-CL flowers. The difference in P/O ratio of the CL flowers differentiating at two different sites on the same plant is rather intriguing as both types practise a similar mechanism of pollination. In all probability, the difference is an outcome of difference in their position on the plant, size of the flowers before pollination and time of differentiation. Variation in P/O ratio among flowers of the same plant of *Lamium amplexicaule* has been explained on similar grounds (Lord, 1980).

Lord's (1980) findings suggest that resource availability at the time of flower differentiation holds the key to difference in P/O ratios among flowers of a plant. Lord (1980) considers pollen count/flower to be a function of the position the flower holds in the inflorescence, the environmental conditions under which the plant grows and the plant's genetic make-up.Lord (1979) observed ontogenic shift from cleisto- to chasmogamy (through intermediate forms) with the progressive maturation of inflorescence. This shift affects the P/O ratio as well as other traits. In *C. benghalensis,* PG flowers differentiate very early in the life-cycle,

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when the accumulated resources within the plant are meagre. The flowers are CL and therefore obligately autogamous. Provided pollination and seed set are assured, low resource availability would appear to select for the small PG-CL flowers having low pollen and ovule counts.

Following increase in leaf number, a greater quantity of photosynthate becomes available to the plant. The aerial spathes differentiate in a resource-rich environment. As a result, they are larger and contain a higher number of large flowers. As the plant ages, the resources decline. The DG spathes differentiate around this time of the life-cycle and are therefore small, containing a single flower with smaller floral parts and a low P/O ratio.

The NG-M flower of each spathe functions as an additional pollen source. The number of ovules available for fertilization within each spathe is five. On average 41 580 pollen grains released by NG-M and NG-CH flowers are available for their fertilization. Therefore, the P/O ratio for NG-CH flowers works out at 8315 : 1, which fits Cruden's (1977) estimates for flowers of the xenogamous category. Against this, the P/O ratios for NG-CL and PG-CL flowers work out at 2925 : 1 and 2305 : 1, respectively. More intra- than interplant variation in P/O ratio (Tables 4,5) may be due to such modifying influences as differences in organogenesis, physiology, environment and ecology.

Inferences drawn on the basis of the P/O ratio are in conformity with those drawn on the basis of the dry biomass of the sex organs. The general belief is that the resource outlay to male function reduces with increase in selfing rate (Charnov, 1982; Schoen, 1982; Cruden & Lyon, 1985; Mckone, 1987). In other words, reduction in resource consumption for male function is accompanied by a proportionate increase in allocation for female function (Cumaraswamy & Bawa, 1989; Kohn, 1989; Dunn & Sharitz, 1991; Delesalle & Mooreside, 1995); this manifests in higher pistil size (Cumaraswamy & Bawa, 1989), pistil weight and ovule and seed count (Lloyd, 1965; Solbrig & Rollins, 1977; Schoen, 1982).

In PG-CL flowers of *C. benghalensis,* which are structurally as well as functionally cleistogamous, resource investment in pistil differentiation exceeds that in stamen differentiation by 20% (Table 6), indicating that the ratio between pistil and stamen biomass is unambiguously female-biased (Tables 5, 6). In contrast, in all CH flowers, irrespective of location, 56–61% of the total reproductive investment is diverted to male function (Kaul, Koul & Sharma, 2000, Koul, Kaul & Sharma, 2001) (Table 6). It is unusual that in NG-CL flowers the ratio between pistil and stamen biomass is male-biased (Table 6) unlike that of their PG-CL counterparts. This investment pattern defies the generalization that higher selfing rate leads to a female-biased ratio. In all other flowers the investment pattern fits the generalized models of sex allocation theory. The male-biased sex allocation ratio of the NG-CL flowers suggests that in the not too distant past these flowers have been chasmogamous. Over the years, failure of anthesis in these flowers has been selected to ensure fertilization and seed set. Regression in size of individual floral parts and P/O ratio are subsequent changes that have followed the shift from chasmo- to cleistogamy. The reduction is not yet complete. That is why although they are cleistogamous, these flowers display a male-biased ratio like that of their CH counterparts.

In reproductive output NG-CL flowers overtake their NG-CH counterparts. Seed set in these flowers is highest; in seed weight they are second only to the PG-CL flowers.

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