

Figure 2. *Pseudolimea rajnathi* n. sp. Holotype (sp. no. M 86/1537) from bed no. 1 (Oxfordian). *a*, Left valve exterior. *b*, Dorsal view.

Description: Shell inequilateral, subtrapezoidal in outline, produced anteriorly and strongly inflated. Umbo pointed and prominent. Anterior margin long and straight; posterior one gently convex; ventral margin asymmetrical. Shell surface ornamented with 21 broad, angular radial ribs; anterior region rather narrow and posterior almost smooth. There are traces of faint threads which cross the radial ribs and provide a distinctive appearance. Tiny but distinct wings present, of which the posterior one is bigger.

The lone specimen has lost its test partially and also undergone some degree of erosion and that is why the finer ornamentation is somewhat subdued. Its nearest ally seems to be the Upper Oxfordian species *Pseudolimea mandawaensis* Cox¹ from Tanganyika (Tanzania) from which, however, it can be differentiated by its anteriorly more produced outline, lesser number of ribs which are less conspicuous. This new species also differs from the common Kachchh species *P. duplicata* J. de C. Sowerby, recorded by Cox², in its more transversely elongated outline, stronger inflation and greater number of radials separated by moderately deep interspaces.

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Floral sex ratios in monoecious species — Why are trees more male-biased than herbs?

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Bulmer and Taylor¹ suggested that in geographically structured populations, differential sibling competition generated through sexes is an important factor in determining the equilibrium sex ratios. They showed that reproductive resource allocation would be biased in favour of that sex which is dispersed to farther distances, and thus reduces sibling competition for local resources. This suggestion has important implications for explaining the evolution of resource allocation to the sexes across habits in plants. In this paper, we argue that the effective dispersal of pollen grains compared to that of seeds is relatively more in trees than in herbs; pollen grains hence generate less competition for maternal resources in trees compared to that in herbs. We suggest that such differential dispersal of sexes should bias the resource allocation relatively to males in trees than in herbs. We provide a test of this argument using a set of 53 monoecious species.

Most herbs, in contrast to trees, are annuals and have short flowering periods. Further, because of the limited resources available, herbs have less elaborate flower display features. Hence, pollen dispersal ability in herbs is relatively limited both in space and time, leading to an intense inbreeding within the colonies. This results in an increased genetic similarity among siblings developing within a fruit or on the plant, and generates an intense intra- or inter-brood sibling competition for maternal resources. On the other hand, because seeds remain viable for longer periods, and can be dispersed to farther distances, their dispersal efficiency is not as much affected by the short flowering periods and limited reproductive resources in herbs. Consequently, in herbs, the sibling competition generated through seeds is less intense compared to that through pollen grains. Hence, resource allocation may be expected to be biased to seeds (females) than to the pollen grains (males) in herbs¹.

In contrast, shrubs and trees are generally outbreeders². Their prolonged periods of flowering and high investments on elaborate display features to attract pollinators increase their effective pollen dispersal

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Table 1. Sex ratio in 53 monoecious species.

Species	Habit	N Trees	Inflo- rescences	Sex ratio [male] [female]	Source
Alistamaceae					
<i>Sagittaria brevirostra</i>	Shrub			3.3	
Anacardiaceae*					
<i>Anacardium occidentale</i>	Tree			4.00	21
<i>Mangifera indica</i>	Tree			2.62	22
Apiaceae					
<i>Smyrrium olusarum</i>	Herb			4.00	14
Asteraceae					
<i>Cotula albida</i>	Herb			2.03	13
<i>C. alpina</i>	Herb			0.49	13
<i>C. atrata</i>	Herb			1.56	13
<i>C. dispersa</i>	Herb			1.00	13
<i>C. featherstonii</i>	Herb			0.64	13
<i>C. intermedia</i>	Herb			4.00	13
<i>C. lanata</i>	Herb			0.85	13
<i>C. manitota</i>	Herb			1.04	13
<i>C. membranacea</i>	Herb			0.40	13
<i>C. mexicana</i>	Herb			0.29	13
<i>C. minor</i>	Herb			1.08	13
<i>C. nana</i>	Herb			0.22	13
<i>C. pectinata</i>	Herb			1.77	13
<i>C. piliformis</i>	Herb			1.00	13
<i>C. plumosa</i>	Herb			0.85	13
<i>C. potentillina</i>	Herb			1.77	13
<i>C. pyrethrifolia</i>	Herb			2.33	13
Euphorbiaceae					
<i>Acalypha ciliata</i>	Herb	10	25	1.00	
<i>A. indica</i>	Herb	10	50	12.04	
<i>A. lanceolata</i>	Herb	10	15	1.00	
<i>Cnidocolus urens</i>	Herb			7.63	19
<i>Croton bonplandianum</i>	Herb	50	100	16.00	
<i>Phyllanthus asperculatus</i>	Herb	30	100	1.00	
<i>P. gardenaria</i>	Herb	40	80	3.05	
<i>P. madraspatensis</i>	Herb	35	120	4.00	
<i>P. niruri</i>	Herb	50	75	1.00	
<i>P. rheedi</i>	Herb	15	60	3.00	
<i>P. urinaria</i>	Herb	20	70	4.30	
<i>P. virgatus</i>	Herb	25	50	3.00	
<i>Phyllanthus</i> sp. 1	Herb	10	45	1.50	
<i>Phyllanthus</i> sp. 2	Herb	15	50	1.50	
<i>Ricinus communis</i>	Herb/ shrub	8	30	3.00	
<i>Acalypha fruticosa</i>	Shrub	25	100	107.00	20
<i>Breynia patens</i>	Shrub	14	50	4.00	
<i>B. rhamnoides</i>	Shrub	10	20	0.80	
<i>Cnidocolus caudatus</i>	Shrub	5	20	10.50	
<i>C. klotzschianus</i>	Shrub	5	10	20.00	
<i>Jatropha curcas</i>	Shrub	20	70	10.70	
<i>J. gossipifolia</i>	Shrub	3	30	22.00	
<i>J. multifida</i>	Shrub	2	25	34.60	
<i>Kirganelia reticulata</i>	Shrub	8	30	5.00	
<i>Manihot</i> sp.	Shrub	3	20	6.70	
<i>Phyllanthus nivosus</i>	Shrub	3	15	29.00	
<i>P. polyphyllus</i>	Shrub	20	50	13.84	
<i>Aleurites montana</i>	Tree	5	20	13.85	
<i>Glochidion zeylanicum</i>	Tree	4	12	96.00	
<i>Hura crepitans</i>	Tree	5	18	227.00	
<i>Manihot glaziovii</i>	Tree	3	40	12.30	
<i>Phyllanthus acidus</i>	Tree	10	50	16.11	

*Andromonoecious.

Mean sex ratios of the three habits.

Habit	N	Min	Max	Median	Mean	SE
Euphorbiaceae						
Herbs	15	1.00	16.00	4.00	4.20	1.14
Shrubs	12	0.80	107.00	10.60	20.50	7.75
Trees	5	12.30	227.00	16.11	88.24	50.04
All species						
Herbs	33	0.22	16.00	1.56	2.67	0.58
Shrubs	13	0.80	107.00	10.50	20.42	7.78
Trees	7	2.62	227.00	13.85	53.12	31.47

ability. Though these features may also facilitate the dispersal of seeds, relatively, differences between the effective dispersal of pollen grains and of seeds are less in shrubs and trees. Accordingly, shrubs and trees could be expected to be more male-biased in resource allocation compared to herbs.

We tested this using floral sex ratios in 53 monoecious species from five families (Table 1). The floral sex ratios (ratio of male to female flowers) were recorded and their means were computed for herbs, shrubs and trees (see Table 1 for sample sizes). We have used floral sex ratios as a measure of the relative resource allocation to sexes among habits for two reasons: (a) Our aim in the paper is not to compare the absolute allocation of resources to sexes within habits, rather to compare the relative allocation to sexes among habits, and (b) The resource allocation to female flowers generally outweighs that to the males³⁻⁵, especially because, the production (and development) of ovules is more costly compared to that of pollen grains⁴⁻⁶. However, the relative proportion of resources allocated to individual male and female flowers does not change drastically. Hence the differences in floral sex ratios among habits do indicate the relative biasness in resource allocation to sexes.

The sex ratio increased from herbs to shrubs to trees (Kruskal Wallis test; $P < 0.0001$ for 53 species; $P < 0.0001$ for 32 species within Euphorbiaceae; Figures 1 and 2). Thus, shrubs and trees are relatively more male-biased than herbs as predicted.

Though our results support the prediction emerging from Bulmer and Taylor¹ that the resource allocation will be biased in favour of the sex that reduces the

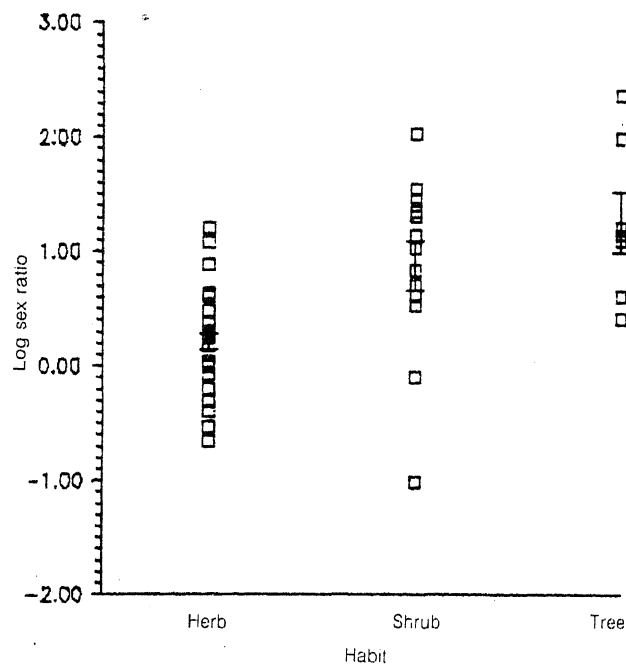


Figure 1. Sex ratios of herbs, shrubs and trees of 53 monoecious species. The vertical bars indicate standard error of mean.

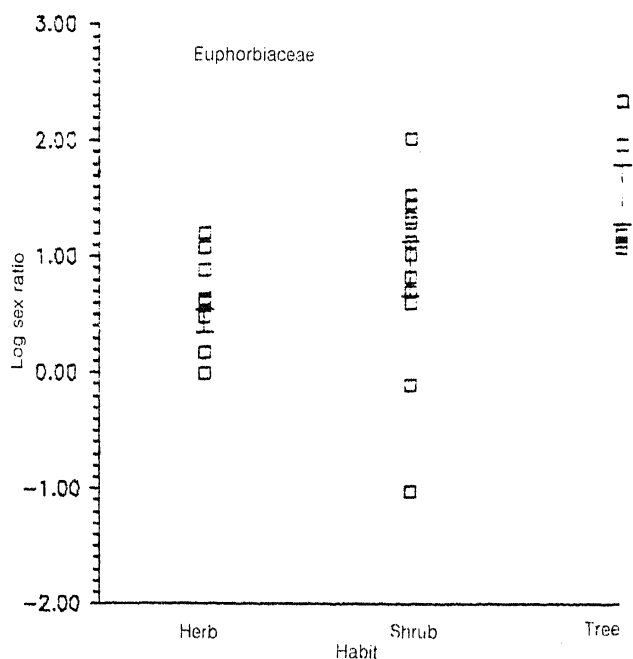


Figure 2. Sex ratios of herbs, shrubs and trees of 32 monoecious species belonging to Euphorbiaceae. The vertical bars indicate standard error of mean.

extent of sibling competition, other factors such as local mate competition⁷ cannot be precluded. Because herbs constitute small inbreeding populations⁸⁻¹⁰, a severe local mate competition is generated among the pollen grains for ovules reducing the average fitness value of each pollen grain. Hamilton⁷ showed that when mating occurs within such small local groups, sex allocation and hence sex ratios will be biased towards females. In plants, such relation was shown to exist by Schoen¹¹ and Charnov³ (and theoretically by Charlesworth and Charlesworth¹²). We have not been able to test this prediction for lack of data on resource allocated to male and female flowers. However, based on floral sex ratios, herbs showed relatively less male-biased allocation compared to trees.

In contrast, shrubs and trees are widely dispersed in space and are predominantly outbreeders². Consequently, there is a reduced local mate competition among pollen grains increasing their average contribution to fitness. This favours a biased resource allocation to male aspects in shrubs and trees compared to herbs.

Several explanations have been offered for the observed variations in the floral sex ratios in monoecious species^{3,4,13-20} and most of these confine to identifying the specific factors, such as nutrient status, resource levels, age of the plants, etc. For instance, Doust¹⁴ and Vasudev *et al.*²⁰ demonstrated an increase in male to female flower ratio with height of plants. These results can be explained assuming that with increase in height, dispersal ability of male gametes increases relative to that of seeds, favouring a male-biased resource allocation in such species. Our study suggests that there could in fact be a common over-

riding denominator, namely the habit of the plant, influencing the wide variations observed in floral sex ratios.

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Occurrence of sweet potato feathery mottle virus in germplasm of *Ipomoea batatas* (L) in India

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Infected sweet potato germplasm exhibited faint and distinct chlorotic spot, ring spot and mild mottle

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