The ages obtained for the carbonized wood samples from Karwar shelf are comparable to the ages of onshore occurrences of peat from Wellington island, Cochin (8080 yr BP)[2], Tellicherry (7230 ± 120 yr BP)[3] and Changanacherry (7050 yr BP)[4]. Pollen analysis of core samples from the Arabian Sea indicated a humid climate with maximum mangrove vegetation in the west coast around 10,000 yr BP[5]. Relicts of mangrove vegetation exist even today along the west coast[6]. The transgression of the sea might have resulted in the destruction of coastal vegetation, giving rise to carbonized wood and peat beds. The age data indicate that this transgression was around 9000–10,000 yr BP in the Karwar area. The age of the shell zone correlates with the ages reported for limeshells of Vembanad lake, Kerala (3710 ± 90, 3130 ± 100 yr BP). The deposition of limeshells has been related to an event of retrogression between 3000 and 5000 yr BP[3].

The rate of accumulation of sediments was computed from the age data, assuming a uniform rate in the sites subsequent to the deposition of dated material. The accumulation rate is 0.89 mm y^{-1} at PC-1459, which is 5 km away from the coast. The lowest rate of sedimentation (0.44 mm y^{-1}) occurs at PC-1464, located at a distance of 18 km from the present coast. At PC-1490, the rate of accumulation is 0.67 mm y^{-1}. This relatively higher rate may be due to the presence of intermittent laminations of fine sand in clayey sediments, which accumulates at a rate faster than that of clay. This indicates that sedimentation rates are highly variable within short distances in the inner-shelf region and the deposition is faster nearer the coast. These sedimentation rates, however, are marginally higher than those reported for sediments off Mulki (0.35 mm y^{-1})[7] and Mangalore (0.33 mm y^{-1})[8] based on ^{210}Pb activity.

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Received 8 December 1990; accepted 2 March 1991

On the reproductive phenology and sex ratio of *Mallotus philippensis* Muell. Arg.

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In dioecious plants, i.e. plants in which male and female flowers are borne on different individuals, environmental factors, especially sunlight, may affect male and female individuals differently. We report here that *Mallotus philippensis*, a dioecious undertree species, shows variation in reproductive phenology and sex ratio in two adjacent forest communities with different light-intensity regimes. Sex ratio was always male-biased and more so under the lower-light regime. Number and density of male flowers per inflorescence were much higher under the lower-light regime. Peaks of anthesis and receptive female flowers did not synchronize. In addition to these, early flowering in males and longer span of male flowering suggest that, in this anemophilous species, selection favours males to ensure availability of sufficient pollen to every female flower irrespective of light regime.

Mallotus philippensis (Euphorbiaceae), well known for its Kamala dye, is a dioecious undertree species that grows abundantly in sal (*Shorea robusta*)-dominated communities. The male and female individuals are difficult to distinguish in the vegetative phase. Resources, especially sunlight, may have differential value to sex functions[1], and in several cases male and female plants have been found to occupy different habitats, suggesting environmental sex determination[2]. Secondary sex characters and sex ratio[3–5] as well as the adaptive significance of dimorphic flowers and inflorescence[6,7] have been discussed for a number of annual and perennial species. These aspects are little understood in Indian forest communities except for a few general phenological accounts[8,9]. Here we discuss reproductive phenology and sex ratio in *Mallotus philippensis* growing in two adjacent forest communities under different light regimes.

The study was carried out in two adjacent commun-

Table 1. Reproductive phenology and sex ratio data for *Mallotus Philippensis* in two forest communities.

		Sal stand (≥800 lux)	Mixed forest (≤300 lux)	χ^2
Flowering individuals (f)	Male	192	188	0.04 (NS)
	Female	160	124	3.0[c]
	χ^2 =	2.9[a]	13.1[b]	
Sex ratio (female/male)		0.84	0.66	0.2 (NS)
Non-flowering individuals (nf)		60	84	4.0[d]
Flowering ratio (f/nf)		5.87	3.71	0.48 (NS)

The χ^2 values are significant at 10% (*a*, *c*), 0.1% (*b*) and 5% (*d*) level; NS, not significant.

Table 2. Flowering in male and female *Mallotus philippensis* in two forest communities.

	Sal stand (≥800 lux)		Mixed forest (≤300 lux)	
	Male	Female	Male	Female
Inflorescences per twig	4.5 ± 1.5^a	1.7 ± 0.6	3.4 ± 1.7^a	2.3 ± 1.4
Inflorescence length (cm)	11.9 ± 4.0^b	3.5 ± 1.3	8.4 ± 2.7^b	3.2 ± 0.98
Flowers/inflorescence	34.3 ± 15.1^b	9.3 ± 3.1	53.4 ± 14.4^b	9.5 ± 3.8
Flowers per cm of peduncle	3.1 ± 0.6^b	3.2 ± 1.2	6.5 ± 1.6^b	3.3 ± 1.2

Differences between values for males under the two light regimes are significant at 1% (*a*) and at 0.1% (*b*) level by Student's *t*-test; differences for females are not significant.

ities, a sal stand and a mixed forest dominated by sal of similar age (40 ± 5 yr) in Lachhmipur Range of Gorakhpur Forest Division, North India. The two communities are quite similar in their general edaphic characteristics but density and species diversity of trees in the mixed forest were significantly higher ($P < 0.01$) than in the sal stand (Shukla and Pandey, unpublished data). The sal stand allowed more than 800 lux of light and the denser mixed community diminished the light to 300 lux at ground level. The illumination was measured by an illuminometer (Kyoritsu, 5200) at 10 random and nearly equidistant points on the floor of each of the two communities during sunny days of November 1989 at midday. Age of the trees was derived on the basis of their growth features[10] and girth tally.

Individuals of five years and above, present in a hectare area, were counted in each community. The number of inflorescences per twig, the length of inflorescence axis or peduncle, and the number of flowers per inflorescence and per unit length of peduncle were recorded on 20 samples from similar positions of five mature trees in each community. Phenological data were based on weekly observations on 20 ± 3 tagged trees in each of the two adjacent communities.

Though the total number of male plants in flowering was greater than females, the latter occurred more frequently under higher-light regime, unlike the observation reported for a few herbaceous species[2,3]. The absolute number of male individuals showed no effect of light-intensity regimes, and sex ratio in this species was always male-biased (Table 1), as reported also for several herbaceous species[11]. The sexes apparently had closely similar niches since they were found to occur together in many instances, and, therefore, a relationship between the distribution of the sexes and the nature of the environment with respect to light intensity within the given range was not noticeable. However, the suggestion[12] that 'the niche differences between the sexes may be due in part to the energy requirements for reproduction in male and female plants' and the observation that plants of several species grown in bright sunlight turn out to be female and those grown in shade turn out to be male[1,2] provide reasons for the occurrence of more females under higher-light regime in this species. The highly significant male-biased sex ratio in the mixed forest (low-light regime) compared to the sal stand (high-light regime) suggests that, in this species, selection favours male bias in poor habitat[2]. Further, males had more inflorescences and flowers than females (Table 2), like the majority of dioecious species, including Costa Rican trees[7]. The higher number of flowers produced by males may be regarded in terms of optimal distribution of pollen for each ovule[13] in a predominantly anemophilous species. Though number of male inflorescences per twig and peduncle length were significantly higher under high-light environment, the number of flowers per inflorescence was higher under the more shady condition of the mixed-forest community (Table 2). This suggests that, under a lower-light regime, the species allocates less resources to the reproductive accessories without reducing the number of male flowers, thus assuring availability of sufficient pollen even in the dim conditions of a denser community.

Male plants started flowering much earlier and continued for longer than females, as reported also for several herb and fruit-tree species[14]. The peaks of anthesis and receptive female flowers, expressed as per cent of number of individuals, were not synchronized temporally (Figure 1). Often each subphase of reproductive activity gradually merged in the next before reaching the peak.

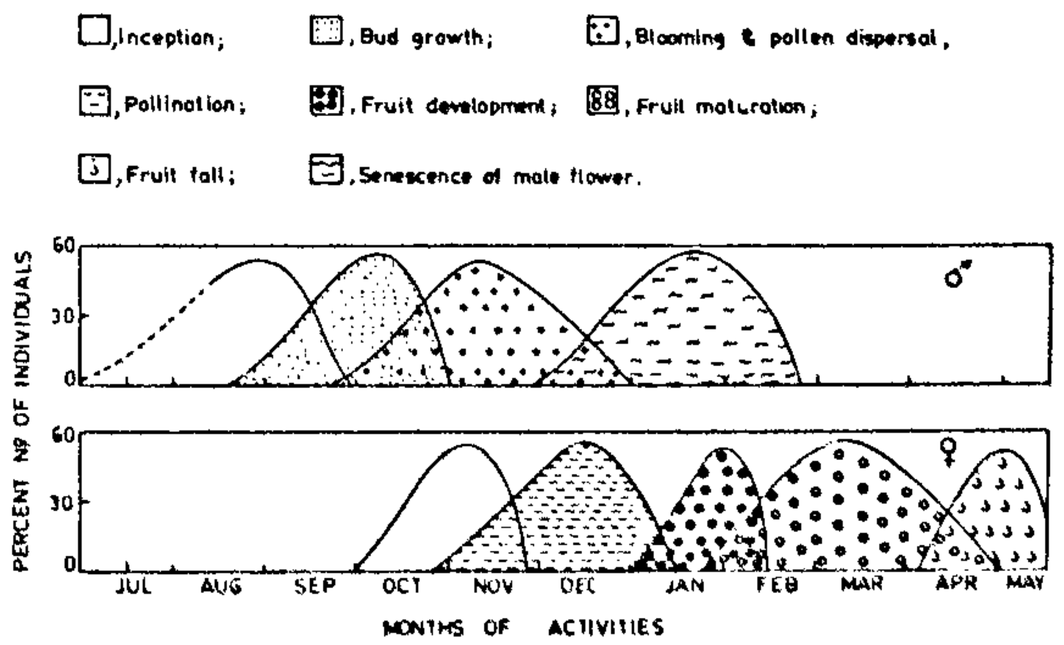

Figure 1. Reproductive phenology of male and female individuals of *Mallotus philippensis*, showing spread and overlapping of different reproductive phases.

The early flowering and longer span of male activity, highly male-biased sex ratio, and high male-flower density under poor light regime suggest that, in this species selection favours males to ensure availability of sufficient pollen to every female flower irrespective of the light conditions under which it grows. The greater number of females favoured under high light regime is probably to minimize resource constraint for developing seeds.

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ACKNOWLEDGEMENTS. This work was supported by the Department of Science and Technology, New Delhi. We thank O. P. Gupta for assistance in data collection.

Received 7 July 1990; revised accepted 8 January 1991

A novel cross-linking technique to study nuclear lamina–membrane interactions

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Protein cross-linking studies using various bifunctional reagents can provide information about the organization of complex proteinaceous structures. We have studied the association of the nuclear lamina with membrane proteins using bifunctional cross-linkers of the bis-(imidoester) class. Analysis of cross-linked products by two-dimensional diagonal gel electrophoresis demonstrates that the lamins are closely associated with three nuclear membrane proteins (54, 50 and 45 kDa) in intact nuclear envelopes. This interaction does not occur when the envelope organization is disrupted with detergent or urea.

THE inner surface of the nuclear envelope in a eukaryotic cell is closely associated with a filamentous network or lamina, composed of intermediate filament-like proteins called the lamins[1–4]. The lamins may be classified into two major types: the A-type, which get solubilized during mitosis[5,6], and represented by lamins A and C in most cells; and the relatively insoluble B-type lamin. Lamin B is strongly associated with the nuclear membrane[7] and remains bound to membrane vesicles during nuclear-envelope disassembly at mitosis and subsequent reformation of the envelope[5]. The biochemical basis of interaction of the lamina with the inner nuclear membrane is not clearly understood. Recent studies with purified lamin B and lamin-depleted nuclear membranes suggest that lamin B is anchored to the membrane via a 58-kDa receptor protein in avian and yeast cells[8–10].

In the present study, we have adopted a direct approach to look at the interactions of the lamina with nuclear membrane proteins in mammalian cells by chemical cross-linking studies with purified nuclear envelopes using bifunctional imidoesters and analysis of cross-linked products by two-dimensional diagonal gel electrophoresis.

Nuclear envelopes were isolated from purified mouse liver nuclei by Kaufmann's procedure[11], and characterized in detail by biochemical and morphological criteria as described earlier[12]. Nuclear envelopes were obtained as intact, double-membrane vesicles, similar in size to nuclei and devoid of intranuclear and cytoplasmic contaminants. Envelopes were fractionated with (i) 8 M urea, or (ii) 2% Triton X-100 and low or high concentrations of salt (20 mM or 300 mM KCl) or 4 M urea by published methods[8,13,14].

In a typical cross-linking reaction, intact or extracted nuclear envelopes (~100 μg protein) were incubated with 5 mM dimethyl suberimidate (DMS; Pierce Chemicals, USA) for 30 min at 30°C in 100 μl of 100 mM triethanolamine·HCl, pH 8.0 (refs. 15–17). The reaction was quenched with excess glycine and the samples separated by SDS–polyacrylamide gel electrophoresis (8% polyacrylamide gels)[18]. These conditions were found to be suitable after standardization with respect to concentration of cross-linking reagent (0.5–20 mM) and time (15 min–24 h). Under these conditions, up to 10% of cross-linked higher-molecular-mass species were detectable for a known tetrameric protein, alcohol dehydrogenase, the remainder being mostly products of addition of several molecules of cross-linker to monomers of the protein. Experiments were also carried out with dimethyl pimelimidate (DMP) and dimethyl adipimidate (DMA) (which form shorter bridges) under similar conditions. Samples of cross-linked proteins (in triplicate) were separated by SDS–polyacrylamide gel electrophoresis. One lane was stained with Coomassie blue and the second lane was treated with methylamine exactly as described[16]. The treated lane and the third, untreated lane were separated in the second dimension by SDS–polyacrylamide gel electrophoresis (8% polyacrylamide gels). The two-dimensional gels were stained by the more sensitive