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Coexistence of closely related *Eupatorium* species. I. *Eupatorium odoratum* L. versus *Eupatorium adenophorum* Spreng. and *Eupatorium adenophorum* Spreng. versus *Eupatorium riparium* Regel. at different altitudes

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Abstract. At their altitudinal limits at 950 m elevation, *Eupatorium adenophorum* was more susceptible to density-dependent mortality but plasticity of individual organs including reproductive growth was more adversely affected in *Eupatorium odoratum*. In mixtures, *Eupatorium adenophorum* had an edge over *Eupatorium odoratum* suggesting that the former checks the upper altitudinal limit of the latter. *Eupatorium adenophorum* and *Eupatorium riparium* coexist well in their mid-altitudinal range of 1500 m. In pure stands, *Eupatorium adenophorum* was more susceptible to density stress than *Eupatorium riparium*. *Eupatorium riparium* was more aggressive than *Eupatorium adenophorum* in the mixture of increased interspecific competition. In mixtures, these two sets of competing species are less affected than could be expected from the effect of crowding; they, perhaps, occupy different ecologic niches.

Keywords. Coexistence; competition; population dynamics; weed biology.

1. Introduction

The ecology of coexistence of closely related species has been the concern of many studies. These studies often dealt with the controlling influence of a species to its turn density and a comparison of this to the density of the associated species (Harper and Chancellor 1959; Harper and McNaughton 1962; Marshall and Jain 1969; Ramakrishnan and Jeet 1972). Since coexistence often implies that the species concerned possesses niche differentiations for mutual avoidance, some of the studies also dealt with differential requirements from the same site (Ramakrishnan and Gupta 1972; Bergh van den and Breakhekee 1978).

The present series of studies on the competitive relationships of closely related species of *Eupatorium*, viz *E. odoratum* L., *E. adenophorum* Spreng. and *E. riparium* Regel were taken up as these taxa have distinct altitudinal ranges of distribution which overlap, and since competitive mechanisms of their restriction would determine population behaviour. These weeds form an important component of the early successional stages following slash and burn agriculture (jhum) in north-eastern India (Toky and Ramakrishnan 1983; Mishra and Ramakrishnan 1983). With the jhum cycle (the intervening fallow period between two successive croppings in the same site) now being more common for 4–5 years, the secondary succession gets arrested at the weed stage resulting in the rapid spread of these species over vast tracts of land (Kushwaha *et al* 1981; Ramakrishnan and Mishra 1981). This study,

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*To whom all correspondence should be addressed therefore is also significant from an applied angle for designing biological weed control measures (Saxena and Ramakrishnan 1984).

2. Altitudinal distribution and climate

The study area located in the Khasi Hills of Meghalaya (26° N 91° E) has a range of altitudinal situations from 100 m at Burnihat, 950 m at Barapani, 1500 m at Shillong and 1700 m at Upper Shillong with the highest point at 1950 m. Climate at these sites is similar except for temperature differences related to altitude, it is typically monsoonal with an annual average rainfall of 1800 to 2200 mm, about 90% of which occurring between May and October (Kushwaha *et al* 1981; Ramakrishnan and Mishra 1981). During summer months (March–April) the mean maximum temperature ranges between 21°C on the other extreme at Burnihat. Similarly during winter (November–February) the seasonal minimum varies between 4°C at upper Shillong and 15°C at Burnihat. About 10% of the total annual rainfall comes as occassional showers during the winter months.

Altitudinal distribution of the 3 species of *Eupatorium* is shown in figure 1. *E. odoratum* grows upto an elevation of 950 m, *E. adenophorum* between 550 and 1960 m, and *E. riparium* between 950 and 1700 m.

3. Methods of study

Competition experiments between *E. odoratum* and *E. adenophorum* were done at Barapani (950 m elevation), at their overlapping marginal zone using seeds collected in February–March. The experiments between *E. adenophorum* and *E. riparium* were done at Shillong (1500 m elevation), in the mid-range of their altitudinal spread. To avoid soil heterogeneity, experiments were done in plastic pots (20·8 cm dia.) filled with a 3 : 1 soil mixture of garden soil and cow dung (dry wt. basis). Excess seeds were sown and the seedlings were subsequently thinned down to the desired numbers. Pure stands of the species had densities of 30, 90, 150, 300, 750, 1500 or 3000 individuals per m^2 with 3 replicates. Mixed stand studies were based on de Wit's replacement series where the proportion of the two species varied, but the overall density per m^2 remained constant (de Wit 1960) as follows:

E. adenophorum	0	150	300	450	600
E. odoratum	600	450	300	150	0
E. riparium					

Harvests were done after 24 weeks and 48 weeks coinciding with the peak vegetative and reproductive phases; each harvest had 3 replicates for all the treatments.

Apart from measuring mortal and plastic responses in pure and mixed stands, relative yield (RY), RY quotient (RYQ) and RY totals (RYT) were calculated following Bergh van den (1968). Thus RY was calculated as the ratio between the yield of a particular species in the mixture and its yield in mono-culture at the same total density, RYT the sum of relative yields of the two competing species in the mixture and RYQ calculated using the formula:

$$\text{RYQ of species (a)} = \frac{\text{RY of species (a) in } n\text{th harvest}}{\text{RY of species (b) in } n\text{th harvest}}$$

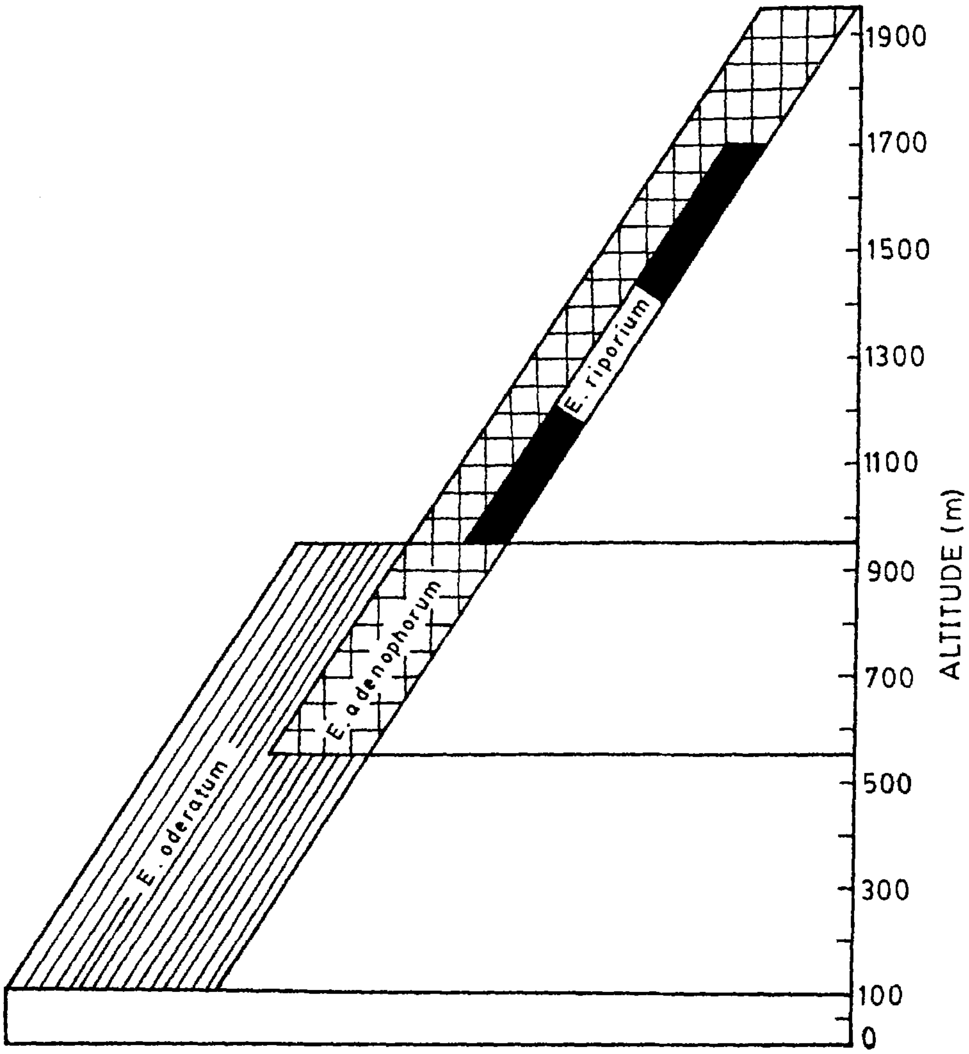

Figure 1. Altitudinal distribution of *Eupatorium* species in the Khasi hills of Meghalaya, north-eastern India.

4. Results

4.1 *E. odoratum and E. adenophorum in pure stands*

E. odoratum and *E. adenophorum* showed varied degrees of mortal and plastic responses to increasing density (figure 2; table 1). No mortality occurred up to a density of 300 plants per m^2. Beyond this, mortality increased with increase in density, and at 1500 plants per m^2 62% only of *E. odoratum* and 52% of *E. adenophorum* survived. Plant height and leaf area per plant of both species (table 1) decreased significantly with increase in density. *E. odoratum* had significantly higher values at lower

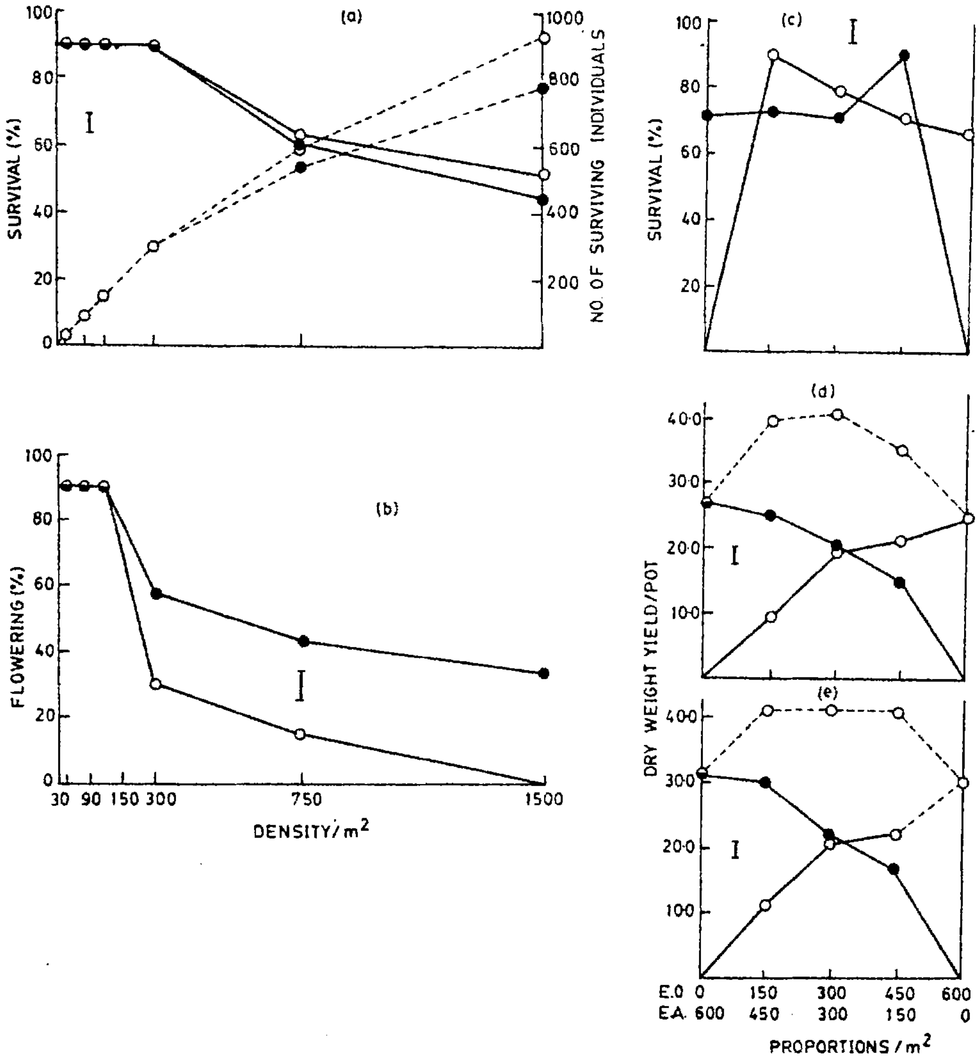

Figure 2. Effect of pure population density on percentage survival and survival number (**a**). and percentage flowering (**b**); effect of mixed population stress on percentage survival (**c**) and dry weight yield per pot (**d**). (○), *E. odoratum*; (●), *E. adenophorum*. Vertical lines represent LSD at $P = 0{\cdot}05$.

densities; at higher densities, the two species did not differ significantly. Dry weight yield per plant of both species (table 1) declined with increase in density and this decline was more pronounced for *E. adenophorum*. The yield per m^2 of both increased with increase in density (table 1) but more markedly in the case of *E. odoratum*. Upto a density of 150 plants per m^2, all individuals of both species flowered (figure 2). Beyond this, flowering declined drastically. The decline in *E. odoratum* was more pronounced than in *E. adenophorum*; *E. odoratum* did not flower at all at 1500 plants per m^2 while about 1/3 of the individuals of *E. adenophorum* flowered at this density. The number of capitula per plant (table 1) at a given density

Table 1. Effect of increasing density on pure stands of *E. adenophorum* (Ea) and *E. odoratum* (Eo).

	Density per m^2												
	30		90		150		300		750		1500		LSD
	Ea	Eo	Ea	Eo	Ea	Eo	Ea	Eo	Ea	Eo	Ea	Eo	(P = 0·05)
Plant height (cm)	37·0	55·8	27·8	45·0	25·0	33·7	24·3	28·2	22·3	24·3	17·0	19·0	6·84
Leaf area (cm^2)	416·0	797·3	210·7	402·0	136·3	258·6	119·1	99·4	100·0	63·4	58·6	40·4	56·1
Dry wt. yield/plant (g)	6·3	6·7	2·9	2·7	2·1	2·5	1·2	2·0	0·7	0·9	0·4	0·7	0·76
Dry wt. yield/m^2 (g)	190·3	171·0	258·0	239·0	321·0	369·0	357·9	600·0	507·0	700·0	615·0	975·0	19·5
Capitula/plant	1520·0	517·3	812·2	250·0	307·5	104·2	71·6	39·8	22·5	5·1	11·0	0·0	42·5
Capitula/m^2	45600	15519	73098	22500	46125	15630	21480	11940	16725	3825	16500	0	2691·3

Table 2. Effect of different proportions of *E. adenophorum* (Ea) and *E. odoratum* (Eo) in mixed stands.

	Proportion per m^2, Ea – Eo										LSD (P = 0·05)
	600 + 0		450 + 150		300 + 300		150 + 450		0 + 600		
	Ea	Eo	Ea	Eo	Ea	Eo	Ea	Eo	Ea	Eo	
Capitula/plant	36·0	—	51·3	30·1	83·6	21·2	117·7	20·7	—	10·6	6·03
Dry wt. yield/plant at 24 weeks	1·4	—	1·7	2·1	2·1	2·1	3·2	1·6	—	1·3	0·17
Dry wt. yield/plant at 48 weeks	1·7	—	2·0	2·5	2·3	2·0	3·5	1·8	—	1·5	0·20
RYT at 24 weeks			1·36		1·57		1·50				
RYT at 48 weeks			1·29		1·32		1·33				

was lower in *E. odoratum* compared to *E. adenophorum*. The decline in capitula per plant with increase in density was more pronounced in the former. Fruit production in both species increased up to 90 plants per m^2 beyond which it declined. *E. odoratum* did not produce any capitula at the highest density.

4.2 *E. odoratum and E. adenophorum in mixed stands*

Mortality % observed in both species increased with increase in intraspecific competition and was highest in pure stands (figure 2). Increased intraspecific competition in the mixture resulted in marked decline in capitula per plant in both species (table 2). In pure stands, *E. odoratum* had less than 1/3 yield of capitula as compared to *E. adenophorum*. In all comparable mixtures too, capitula production by *E. odoratum* was significantly lower than that of *E. adenophorum*. With increase in intraspecific competition in the mixture, the yield per plant (table 2) of both species declined with minimal yield in pure stands. In comparable mixtures, in general, *E. odoratum* was more adversely affected compared to *E. adenophorum*. In a given mixture, the minority species did better than the majority species.

The pattern of dry weight yield per pot (figure 2) was similar at first and second harvests. The total yield of the two species in mixtures was higher than in pure stands. In comparable mixtures where intraspecific or interspecific competition was more, *E. adenophorum* was the higher yielder. In mixtures where both intra- and interspecific competition was equal, the two species did not differ. RYT of the mixtures (table 2) was always greater than one. In all mixtures, a decline in RYT occurred in the second harvest. Except in mixtures of equal proportions RYQ of *E. adenophorum/E. odoratum* (table 3) was greater than one. Where the species concerned was in a minority in the mixture, RYQ was the highest. In this mixture, RYQ declined markedly during the second harvest. In mixtures of equal proportion, RYQ during the second harvest increased to a value of about one.

4.3 *E. adenophorum and E. riparium in pure stands*

E. adenophorum and *E. riparium* showed mortality and plasticity. Mortality (figure 3) did not set in the former upto a density of 300 plants per m^2 and in the latter upto 750 plants per m^2. Both species had 40% mortality at 3000 plants per m^2. Increase in intraspecific competition adversely affected the proportion of flowering individuals (figure 3) in both species. At 300 plants per m^2 *E. adenophorum* had 100% flowering whereas *E. riparium* had only 90%. However, at 3000 plants per m^2 12% of *E. adenophorum* and 30% of *E. riparium* flowered.

Table 3. Relative yield quotient of *E. adenophorum* and *E. odoratum* in mixed cultures at two harvest periods.

Proportion/m^2 (%)	RYQ (*E. adenophorum/E. odoratum*)	
	1st Harvest	2nd Harvest
25	1·36	1·19
50	0·80	0·97
75	1·08	1·05

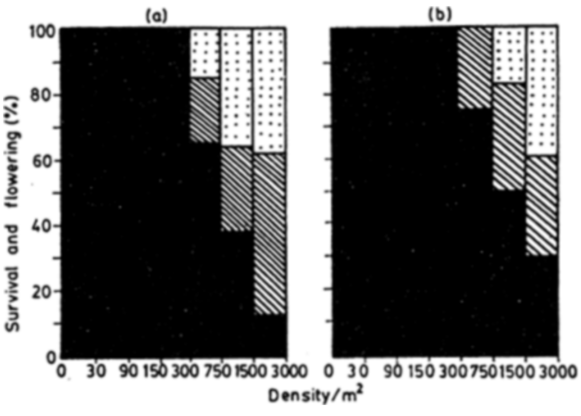

Figure 3. Density-dependent percentage mortality (stippled column), percentage of planta remaining vegetative (hatched column), and percentage of flowering individuals (closed column) of *E. adenophorum* (**a**) and *E. riparium* (**b**).

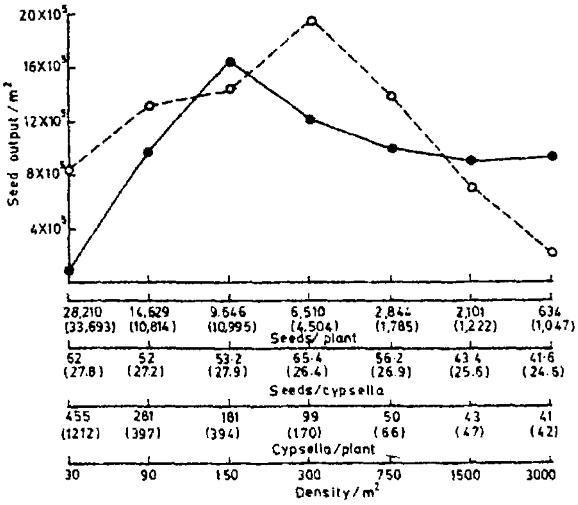

Figure 4. Density-dependent reproductive plasticity of *E. adenophorum* (○) and *E. riparium* (values in parenthesis; ●).

Under density stress, fruit production (figure 3) of both species declined drastically, but the seeds per fruit was affected to a lesser degree. *E. adenophorum* was more adversely affected than *E. riparium* with respect to fruit and seed outputs. Seed number per fruit (figure 3) was consistently higher in *E. adenophorum* than in *E. riparium*. Seed productions per m^2 (figure 4) increased with increase in density, upto 300 plants per m^2 in *E. adenophorum* and 150 plants per m^2 in *E. riparium*; it declined at higher densities, more markedly in *E. adenophorum*.

Though *E. adenophorum* was taller than *E. riparium*, the decline at higher densities was greater in the former (table 4). The decline in dry weight yield due to density stress was also more pronounced in *E. adenophorum* than in *E. riparium*. The diffe-

Table 4. Effect of increasing density on pure stands of *E. adenophorum* (Ea) and *E. riparium* (Er).

	Density per m^2														
	30		90		150		300		750		1500		3000		LSD
	Ea	Er	Ea	Er	Ea	Er	Ea	Er	Ea	Er	Ea	Er	Ea	Er	(P=0·05)
Plant ht. (cm)	100·3	55·7	105·7	47·8	98·1	56·01	87·8	57·1	78·2	45·7	64·6	41·7	54·0	43·5	10·2
Dry wt. yield/plant (g)	33·3	12·0	20·6	5·7	8·9	4·3	5·5	3·8	3·3	1·8	2·4	1·5	1·2	0·6	2·0
Dry wt. yield/m^2 (g)	999·9	360·6	1850·4	543·4	1344·0	637·5	1647·0	1145·0	2099·2	1320·0	2901·0	1823·5	2017·8	1068·7	548·2

Table 5. Effect of different proportions of *E. adenophorum* (Ea) and *E. riparium* (Er) in mixed stands.

	Proportion per m^2, Ea + Er										
	600 + 0		450 + 150		300 + 300		150 + 450		0 + 600		LSD
	Ea	Er	Ea	Er	Er	Ea	Er	Ea	Er	Ea	(P=0·05)
Percentage Survival	76·0	—	80·0	100·0	91·7	96·7	100·0	91·1	—	90·0	(8·1)
	(61·8)		(63·4)	(90·0)	(73·6)	(79·4)	(90·0)	(72·6)		(71·6)	
Percentage flowering	73·9	—	48·9	100·0	56·7	96·7	73·3	91·1	—	90·0	(7·6)
	(59·2)		(44·3)	(90·0)	(48·8)	(79·4)	(58·9)	(72·6)		(71·6)	
Capitula per plant	26·0	—	28·0	77·5	39·6	69·1	52·4	100·4	—	171·4	20·5
Dry wt. yield/plant (g) in 1st Harvest	2·17	—	2·57	3·04	2·57	2·35	2·50	2·17	—	2·20	0·50
Dry wt. yield/plant (g) in 2nd harvest	2·81	—	2·85	3·79	2·75	2·63	3·40	2·18	—	2·28	0·80
RYT	—	—	1·23	1·18	1·12	1·07	1·02	1·02	—	—	

Figures in parenthesis are angular transformed values.

rence in yield between the two species was significant at lower densities only. The dry weight yield per m^2 in both species increased upto 1500 plants and declined subsequently; *E. riparium* had consistently lower yield per m^2 compared to *E. adenophorum*.

4.4 *E. adenophorum and E. riparium in mixtures*

E. adenophorum had higher mortality than *E. riparium* in pure stands alone but not in mixtures (table 5). Mortality increased with increase in their own density in the mixture and this was more pronounced in *E. adenophorum*. The proportion of flowering individuals and fruit production (table 5) were higher in *E. riparium* than in *E. adenophorum*. *E. adenophorum* was more susceptible to intraspecific competition whereas *E. riparium* suffered more from interspecific effect. *E. riparium* had significantly higher yield per plant (table 5) in mixtures of higher interspecific competition in the first harvest alone; the yield in both declined with increase in intraspecific competition. In mixtures where intraspecific competition was higher, yield per pot (figure 5) was higher for *E. adenophorum* than for *E. riparium*. In the first harvest the total yield in mixtures generally exceeded the yield in pure stands of the two species; this difference was confined only to that mixture with 450 individuals of *E. adenophorum* during the second harvest. RYT was consistently more than one (table 5) in the mixtures, with higher values for mixtures where *E. adenophorum* was in majority. RYQ *E. adenophorum* /*E. riparium* was less than one (table 6) in mixtures

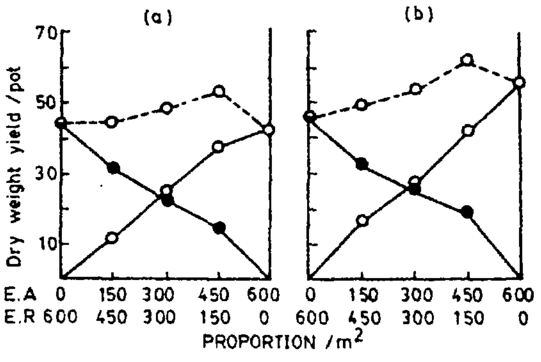

Figure 5. Dry weight yield (g) per pot of *E. adenophorum* (○) and yield of *E. riparium* (●) in mixtures of varied proportions at first harvest (**a**) and second harvest (**b**).

Table 6. RYQ of *E. adenophorum* and *E. riparium* in mixtures.

Proportion/m^2 (%)	RYQ *E. adenophorum* 1st Harvest	 *E. riparium* 2nd Harvest
25	0·80	0·71
50	1·11	0·84
75	1·19	1·06

of lower proportions but more than one in those of higher proportions. The quotient during second harvest was lesser than the first harvest.

5. Discussion

5.1 *Pure population studies*

While in pure populations, *E. odoratum* and *E. adenophorum* responded to increasing density through both mortality and plasticity, density-dependant mortality was higher in *E. adenophorum* compared to *E. odoratum*. Similarly, the dry weight yield per plant was more adversely affected in *E. adenophorum*. In contrast, *E. odoratum* was more susceptible to density-dependant plasticity of individual organs as reflected in plant height and individual leaf area. Plasticity of reproductive growth was also more adversely affected in *E. odoratum*, as expressed by the proportion of plants which flowered or by capitula production. Such differential behaviour related to dry weight yield versus reproductive growth is also reported by Deschenes (1974) and Raynal and Bazzaz (1975). This suggests that the total yield behaviour to density stress and the proportional allocation of photosynthates to different organs follow totally different patterns (Harper 1961; Ramakrishnan and Kumar 1971).

Between *E. adenophorum* and *E. riparium*, the former was more susceptible to density-dependant mortality and plasticity. However, a character such as fruit production was more plastic compared to another reproductive feature like seed number. This suggests that some reproductive characters are more conservative than others (Bradshaw 1965).

5.2 *Mixed population studies*

In mixtures, the two sets of species were susceptible to intraspecific mortality as reported in earlier studies (Harper 1961; Harper and McNaughton 1962; Marshall and Jain 1969). Greater susceptibility to intraspecific competition is also reflected in vegetative and reproductive growth of *E. odoratum* and *E. adenophorum* in mixtures, but the reproductive growth alone of *E. adenophorum* and *E. riparium*. The latter set of two species were, however, susceptible to intraspecific effect with respect to dry weight yield per plant. Such a differential between total yield versus reproductive yield suggests of a pattern that is different for reproductive allocation out of the total photosynthate produced.

In mixtures, *E. adenophorum* in general, had an edge over *E. odoratum* in terms of both vegetative and reproductive growth; the relative yield quotient (*E. adenophorum*/*E. odoratum*) confirms this, particularly in mixtures where the proportion of the two competing species are unequal. In mixtures of equal proportion, *E. odoratum* had initially an edge over *E. adenophorum* as seen from the first harvest, but the quotient was about one in the subsequent harvest suggesting that the latter species almost equalled the former in competition.

The RYT values obtained for both the sets of species suggest that both species in a given mixture are less affected than could be expected from the effect of crowding. The two species apparently occupy different ecologic niches. Such a coexistence and niche differentiation could be related to differential nutritional requirements as was shown for two closely related species of *Argemone* (Ramakrishnan and Gupta 1972) but, perhaps, not so for these two species as shown by our nutritional studies. In the present case, coexistence may be more related to differential shade tolerance, as *E. riparium* was more tolerant than *E. adenophorum* (Dev 1981).

However, the reduced vegetative and reproductive vigour of *E. odoratum* when competing with *E. adenophorum* suggests that the latter is able to effectively restrict the former at the altitudinal limit where they overlap. It seems reasonable to assume that values for temperature higher than the optimum for a given species seems to be competitively more advantageous compared to a value lesser than the optimum. Thus *E. adenophorum* at its lower altitudinal limits under temperatures higher than the optimum for its growth has a competitive advantage over *E. odoratum* which is under temperatures lower than the optimum and at its upper altitudinal limit of distribution.

E. riparium is more aggressive than *E. adenophorum* in mixtures of higher proportion, whereas the aggressiveness of the former declined in mixtures of lower proportions. The coexistence of these two species at this altitudinal zone (1500 m) at Shillong, where both are in their mid-range of ecological amplitude, is possible partly due to niche differentiation and partly depending upon the proportion of the two in the mixture, which would determine the relative dominance of one over the other.

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