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# Coexistence of closely related *Eupatorium* species. II. *Eupatorium adenophorum* Spreng. and *Eupatorium riparium* Regel. at different altitudes

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**Abstract.** The competitive relationships between *Eupatorium adenophorum* and *Eupatorium riparium* were studied at Barapani (950 m) and Upper Shillong (1700 m) using 3 altitudinal populations of the former and one population of the latter. *Eupatorium riparium* was generally more susceptible to competition from the native population of *Eupatorium adenophorum* compared to the introduced population. The two species tended to avoid each other in mixtures to a certain degree, due to niche differentiation.

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

## 1. Introduction

In an earlier paper in this series, the competitive relationships between closely related species, *Eupatorium odoratum* L. and *E. adenophorum* Spreng. coexisting at their upper and lower limits of altitudinal range at 950 m (Dev and Ramakrishnan 1987) and that between *E. adenophorum* and *E. riparium* Regel. coexisting at their mid-altitudinal range at 1500 m (Dev and Ramakrishnan 1987) were considered.

*E. adenophorum* with an altitudinal range of 550 to 1900 m is close to its lower and upper limits of ecological amplitude at the two sites at Barapani (950 m) and upper Shillong (1700 m). *E. riparium* is abundant at an altitude of 1500 m. The present study deals with the competitive relationships between *E. adenophorum* and *E. riparium* at 950 and 1700 m altitude, considering *E. riparium* population from Shillong and 3 populations of *E. adenophorum* from Barapani (950 m), Shillong (1500 m) and upper Shillong (1700 m).

## 2. Methods of study

Seeds of *E. adenophorum* collected from Barapani (950 m), Shillong (1500 m) and upper Shillong (1700 m) were used for experiments at Barapani and upper Shillong. Since *E. riparium* is rare at these two sites, the seeds of this species collected from Shillong were used at both sites. Mixed culture experiments with 3 replicates for each treatment followed de Wit's replacement series (de Wit 1960) and had the following proportion in the mixtures:

| | | | | | |
|---|---|---|---|---|---|
| *E. adenophorum* | 600 | 450 | 300 | 150 | 0 |
| *E. riparium* | 0 | 150 | 300 | 450 | 600. |

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Excess seedlings were raised in plastic pots (20·8 cm diam.) and were thinned down to the desired density after emergence. Garden soil mixed with organic manure in the proportion of 3:1 to remove soil heterogeneity was used. One set of competition experiments done (expt. 1) was carried out at Barapani using seeds of *E. adenophorum* from Barapani or Shillong and seeds of *E. riparium* from Shillong. Another set was carried out at upper Shillong (expt. 2) using seeds of *E. adenophorum* from Shillong or upper Shillong and of *E. riparium* from Shillong.

## 3. Results

### 3.1 *Experiment* 1

Since competition interaction between the two species is very much dependent upon the location of the species within their ecological amplitude, the two experiments were done at their extreme altitudinal sites. This is in contrast to the studies on the two species at their mid-altitudinal range where their growth performance was optimal (Dev and Ramakrishnan 1987). *E. riparium* has an altitudinal range of 950 to 1700 m, but is vigorous only at 1500 m. This along with the fact that this species has a single homogenous population covering the whole altitudinal range (P Dev and P S Ramakrishnan, unpublished results) permitted use of seeds from Shillong site (1500 m). On the other hand, because of altitudinal differences in *E. adenophorum* 3 populations from 950, 1500 and 1700 m elevations were used. Mortality in both the species increased with increase in intraspecific competition (table 1). Mortality in both populations was generally higher where *E. adenophorum* from Shillong was involved compared to that where Barapani population of *E. adenophorum* was used. *E. adenophorum* in general, was more susceptible compared to *E. riparium*. Capitula production declined with increase in intraspecific competition in *E. adenophorum* (table 1), but with increase in inter-specific competition in *E. riparium*. In pure stands, *E. riparium* had 10 times or more reproductive output compared to *E. adenophorum*. This difference between the two species was seen also in mixtures, but less pronounced in comparable mixtures where interspecific competition was more. Capitula production was generally lower in the set up involving *E. adenophorum* from Shillong compared to that from Barapani. Dry weight yield of both species declined with increase in intraspecific competition in the mixture (table 1). Yield of the Shillong population of *E. adenophorum* was in general lower compared to Barapani population. *E. riparium* from Shillong tended to be superior to *E. adenophorum* when competing with Shillong population of the latter than when competing with Barapani population.

*E. riparium* had an advantage over *E. adenophorum* in both sets of experiments (figure 1). The former, however, was more competitive where Shillong population of *E. adenophorum* was involved than when competing with the Barapani population. The total yield in mixtures was about the same where Shillong population of *E. adenophorum* was involved, but was significantly higher than in pure stand yield of *E. riparium* though lower than that of *E. adenophorum*, where the Barapani population of the latter was competing. The relative yield total was consistently greater than one in both sets of experiments; where the Shillong population of *E. adenophorum* was involved, RYT was higher (table 1). In mixtures of higher proportion, the relative

**Table 1.** Competition between population of *E. adenophorum* (Ea) and *E. riparium* (Er) at Barapani.

| | Proportion/m² | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Population | 600 Ea | + | 0 Er | 450 Ea | + | 150 Er | 300 Ea | + | 300 Er | 150 Ea | + | 450 Er | 0 Ea | + | 600 Er |
| Ea (Barapani population) + Er (Shillong population) | | | | | | | | | | | | | | | |
| Survival (%) | 65·00 | | — | 80·00 | | 100·00 | 80·00 | | 100·00 | 100·00 | | 93·00 | — | | 80·00 |
| | (54·80) | | | (62·61) | | (90·00) | (67·86) | | (90·00) | (90·00) | | (77·84) | | | (58·00) |
| Capitula production/plant | 10·67 | | — | 12·67 | | 49·50 | 18·00 | | 92·17 | 20·00 | | 80·34 | — | | 98·67 |
| Dry wt yield of shoot (g) | 0·49 | | — | 0·72 | | 0·89 | 0·73 | | 0·56 | 0·92 | | 0·50 | — | | 0·40 |
| Relative yield total (*RYT*) | | | | | 1·13 | | | 1·38 | | | 1·33 | | | | |
| Ea (Shillong population) + Er (Shillong population) | | | | | | | | | | | | | | | |
| Survival (%) | 65·00 | | — | 60·00 | | 100·00 | 70·00 | | 90·00 | 80·00 | | 80·00 | — | | 75·00 |
| | (54·81) | | | (51·14) | | (90·00) | (57·79) | | (75·00) | (68·07) | | (58·00) | — | | (60·00) |
| Capitula production/plant | 6·66 | | — | 8·00 | | 34·33 | 11·33 | | 58·67 | 13·67 | | 73·33 | — | | 92·00 |
| Dry wt yield of shoot (g) | 0·37 | | — | 0·50 | | 0·69 | 0·53 | | 0·60 | 0·52 | | 0·57 | — | | 0·50 |
| Relative yield total (RYT) | | | | | 1·42 | | | 1·49 | | | 1·55 | | | | |

**Table 2.** Relative yield quotient (*E. adenophorum/E. riparium*) in mixtures of two altitudinal populations of *E. adenophorum* and *E. riparium* at Barapani.

| Proportion/m$^2$ (%) | *E. riparium* with Barapani population of *E. adenophorum* | *E. riparium* with Shillong population of *E. adenophorum* |
|---|---|---|
| 25 | 0·85 | 0·80 |
| 50 | 0·94 | 0·80 |
| 75 | 1·18 | 0·93 |

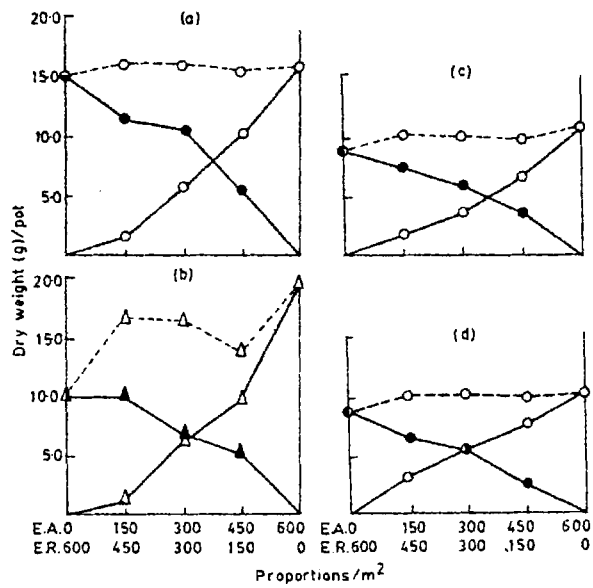


**Figure 1.** Dry weight field (g) per pot of *E. adenophorum* and *E. riparium* in mixtures at Barapani. (**a**) With Shillong population of *E. adenophorum*; (**b**) with Barapani population of *E. adenophorum*; dry weight yield (g) per pot of *E. adenophorum* and *E. riparium* in mixtures at upper Shillong; (**c**) with upper Shillong population of *E. adenophorum*; (**d**) with Shillong population of *E. adenophorum*.

yield quotient (*E. adenophorum/E. riparium*) increased. However, RYQ was generally lower in the mixture where *E. adenophorum* from Shillong was competing (table 2).

### 3.2 *Experiment* 2

Mortality in all cases increased with increase in intraspecific competition. In pure stands, *E. adenophorum* suffered greater mortality compared to *E. riparium* (table 3). In mixtures of equal proportion, both the species suffered greater mortality in mixtures where the upper Shillong population of *E. adenophorum* was involved. Capitula production declined with increase in intraspecific competition in *E. adenophorum*, but with increase in intraspecific competition in *E. riparium* (table 3). In pure stands, capitula per plant was significantly higher in *E. riparium* while reverse was true in comparable mixtures where interspecific competition was higher or where they equalled with only upper Shillong population of *E. adenophorum*. Where

**Table 3.** Competition between population of *E. adenophorum* (Ea) and *E. riparium* (Er) at upper Shillong.

| | Proportion/m² | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 600 Ea | + | 0 Er | 450 Ea | + | 150 Er | 300 Ea | + | 300 Er | 150 Ea | + | 450 Er | 0 Ea | + | 600 Er |
| Ea (Upper Shillong population) + Er (Shillong population) | | | | | | | | | | | | | | | |
| Survival (%) | 76·65 | | — | 62·20 | | 100·00 | 66·66 | | 70·00 | 100·00 | | 80·00 | — | | 90·00 |
| | (61·46) | | | (52·10) | | (90·00) | (54·78) | | (57·79) | (90·00) | | (64·38) | — | | (71·95) |
| Capitula production per plant | 8·00 | | — | 10·00 | | 5·67 | 13·67 | | 4·33 | 15·67 | | 9·00 | — | | 11·00 |
| Dry wt yield per shoot (g) | 0·23 | | — | 0·22 | | 0·47 | 0·23 | | 0·44 | 0·26 | | 0·39 | — | | 0·35 |
| Relative yield total | | | | | 1·79 | | | 1·80 | | | 1·78 | | | | |
| Ea (Shillong population) + Er (Shillong population) | | | | | | | | | | | | | | | |
| Survival (%) | 71·50 | | — | 77·73 | | 100·00 | 90·00 | | 90·00 | 100·00 | | 86·67 | — | | 86·66 |
| | (57·98) | | | (62·86) | | (90·00) | (75·00) | | (75·00) | (90·00) | | (68·99) | | | (69·24) |
| Capitula production per plant | 5·00 | | — | 6·00 | | 5·67 | 8·33 | | 8·33 | 9·00 | | 11·00 | — | | 16·67 |
| Dry wt yield per shoot (g) | 0·32 | | — | 0·32 | | 0·33 | 0·34 | | 0·37 | 0·34 | | 0·33 | — | | 0·34 |
| Relative yield total | | | | | 2·01 | | | 1·86 | | | 1·97 | | | | |

Shillong population of *E. adenophorum* was involved, *E. riparium* had higher capitula production only in mixture of higher interspecific competition.

Dry weight yield per plant of both the species decreased with increase in intraspecific competition and was the lowest in pure stands (table 3). Shillong population of *E. adenophorum* had higher yield compared to upper Shillong population. In mixtures where Shillong population of *E. adenophorum* was involved, the yield of *E. riparium* was consistently lower. In the mixtures with *E. riparium*, *E. adenophorum* populations had a distinct advantage (figure 1). The total yield in mixtures was not significantly different from the yield of either of the two species in pure stands. The relative yield total was consistently higher than one in both sets of experiments, but was higher where the Shillong population of *E. adenophorum* was involved (table 3). Relative yield quotient (*E. adenophorum*/*E. riparium*) was more than one where the upper Shillong population of *E. adenophorum* was involved, whereas it was one or less where the Shillong population of *E. adenophorum* was competing (table 4).

## 4. Discussion

### 4.1 *Experiment* 1

At Barapani, mortality was higher and the dry weight yield and reproductive effort were generally lower for the Shillong population of *E. adenophorum* when compared with Barapani population, suggesting thereby that the native population is superior to the introduced population. In mixtures, *E. riparium* was more susceptible to competition from the Barapani population of *E. adenophorum* than that from Shillong, as seen from the relative yield based on dry weight yield values. However, in terms of mortality or reproductive effort, *E. riparium* seems to be more susceptible to competition from the Shillong population of *E. adenophorum*. A higher mortality for *E. riparium* when competing with the Shillong population of *E. adenophorum* is intriguing since the mortality of the latter was also higher in this experimental set up.

The differential behavioural pattern of *E. riparium* with respect to dry weight yield and reproductive effort in mixtures with the two populations of *E. adenophorum* suggests that though the total photosynthetic effort may follow a given pattern, the proportional allocation of photosynthates to different organs may follow a different pattern. This is in agreement with similar conclusions of earlier studies (Harper 1961; Ramakrishnan and Kumar 1971) and our earlier results in this series (Dev and Ramakrishnan 1987).

### 4.2 *Experiment* 2

*E. adenophorum* population of Shillong and from its mid-range of ecological ampli-

**Table 4.** Relative yield quotient (RYQ) (*E. adenophorum*/*E. riparium*) of two altitudinal populations of *E. adenophorum* and *E. riparium* in mixtures at upper Shillong.

| Proportion/$m^2$ (%) | *E. riparium* with Upper Shillong population of *E. adenophorum* | *E. riparium* with Shillong population of *E. adenophorum* |
|---|---|---|
| 25 | 1·17 | 0·95 |
| 50 | 1·25 | 1·02 |
| 75 | 1·19 | 0·91 |

tude seems to be generally more vigorous in its growth at the extreme limit of distribution of the species at upper Shillong compared to the native upper Shillong population both in pure and mixed stands. However, *E. riparium* was more susceptible to competition in mixtures where upper Shillong population of *E. adenophorum* was involved than when the Shillong population was involved as seen from relative yield quotient values. This suggests the competitive superiority of the native population of *E. adenophorum* in its native habitat. This is also reflected in the values for reproductive effort in mixtures of equal proportion where the two populations of *E. adenophorum* was involved. Confirming the earlier observation, both the species were in general more susceptible to intraspecific competition, the exception being the reproductive effort of *E. riparium* with more susceptibility to increased interspecific effect. This supports the earlier conclusion that while the dry weight yield follows a given pattern, the proportional allocation of biomass, such as for reproductive effort, may follow a different pattern, as a consequence to competition.

The two species tend to occupy different ecologic niches as seen from relative yield total values of more than one, in the mixtures. Thus, they tend to avoid each other, to a certain extent, and the differential behaviour of the two species in mixtures cannot be explained as solely a competitive response.

The altitudinal distribution of the 3 related species of *Eupatorium* is dependent to a large measure on their ecological amplitude. The competitive interaction between the species in overlapping situations also contributes to the restriction of the species and more importantly in determining the vigour of the species. Where two species are competing in their marginal habitats as *E. odoratum* and *E. adenophorum* at Barapani (950 m), the latter from a higher altitudinal range has an advantage over the former from a lower altitudinal zone. Between *E. adenophorum* and *E. riparium*, the former always has a competitive superiority over the latter, at Barapani and Shillong conditions. However, the native population of *E. adenophorum* from Barapani, Shillong and upper Shillong had better competitive advantage even in their native environment compared with an introduced population and this was reflected in the relative adverse effect on *E. riparium* when competing in mixtures. In mixtures, the two competing species tended to avoid each other, to a certain degree, due to niche differences.

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