



Nordic Society Oikos

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Source: *Oikos*, Vol. 36, No. 3 (Mar., 1981), pp. 355-361

Published by: Blackwell Publishing on behalf of Nordic Society Oikos

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Population dynamics of the ruderal weed *Eupatorium odoratum* and its natural regulation

A. S. Yadav and R. S. Tripathi

Yadav, A. S. and Tripathi, R. S. 1981. Population dynamics of the ruderal weed *Eupatorium odoratum* and its natural regulation. – Oikos 36: 355–361.

The paper deals with the dynamics and regulation of a population of *Eupatorium odoratum* L., which is a dominant ruderal weed in abandoned cultivated fields, and on wastelands and roadsides in many parts of the world.

The recruitment and mortality of the individuals has been studied in a five year old fallow following their fate at short intervals over a one year period. The population flux, age structure of the weed population and survivorship of the plants of different age groups have been presented in the paper. The seedling population experienced very heavy mortality with only 1.4% survivors left at the end of the one year study period, while the older population showed greater survivorship. An attempt has also been made to identify the factors regulating the population size. The presence of associated vegetation greatly suppressed the production of fertile shoots and seeds. The poor growth exhibited by the *E. odoratum* seedlings transplanted near its adult plants indicates the role played by the adults in regulating the population growth of *E. odoratum*.

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Статья касается изучения динамики и регуляции численности *Eupatorium odoratum* L., доминирующего рудерального сорняка на заброшенных полях, пустошах и обочинах дорог во многих районах земного шара. Пополнение и отпад растений в популяциях исследовали на 5-летнем паху через короткие интервалы времени в течение периода более года. В статье представлены данные по потоку энергии через популяцию, возрастной структуре, выживаемости растений разных возрастных групп. В популяции всходов наблюдается высокая смертность, выживало лишь 1,42% растений в конце годичного периода исследований, а у растений более старшего возраста выживаемость выше. Была сделана также попытка идентификации факторов, регулирующих размеры популяции. Наличие других растений в этих ассоциациях снижает продукцию плодоносящих побегов и проростков. Слабый рост проростков *E. odoratum* трансплантированных вблизи взрослых растений, показал роль зрелых растений в регуляции плотности популяции *E. odoratum*.

Accepted 20 June 1980

© OIKOS 0030-1299/81/030355-07 \$ 02.50/0

Introduction

Eupatorium odoratum L. is a serious weed in many parts of the world. Although a recent introduction to the flora of India, it has become a dominant weed due to its rapid spread during the last few decades. It is an early colonizer in abandoned cultivated fields. It also grows profusely on the wasteland and roadsides in the north eastern region of India and elsewhere at lower altitudes. This weed produces a large number of cypselae that are carried by wind. The seed germination starts with the onset of rains. Any attempt to control the species can be effective only when its biology and population behaviour are thoroughly known. Thus, the population growth, and the mechanism of population regulation in nature should be carefully studied. A thorough knowledge of mortality, recruitment and longevity of individuals is a pre-requisite for any study of population dynamics. These aspects have engaged the attention of many workers (e.g. Sagar 1959, Foster 1964, Antonovics 1972, Sarukhán and Harper 1973, Hawthorn and Cavers 1976). Harper and White (1971) have described schematic models for the successive stages involved in the regulation of number and mass in plant populations. However, the natural regulation of the numbers of individuals has not been intensively studied.

The population regulation may be attributed to the death and suppression of growth of individuals caused by the competition from the associated vegetation, besides interactions between seedlings and adult plants of the same species. In perennials, the adult plants regulate the growth and survivorship of new recruits to a great extent. This is clear from the work of Friedman (1971) who found that the growth of both naturally growing and transplanted seedlings was greatly suppressed when they were grown close to the adults.

The aim of the experiments reported in the present paper is to gather information on the population dynamics of *E. odoratum* and to identify some of the important factors that regulate the population growth. An attempt has also been made to study the effect of associated vegetation on the reproductive behaviour of the weed and of the adult population of *E. odoratum* on the survivorship and growth of its new recruits.

Materials and methods

E. odoratum is a perennial. The plants may grow very high, sometimes attaining 3 m. The seeds of *E. odoratum* start germinating with the onset of rains in the province of Meghalaya in May and June. The plants grow vegetatively until October after which sporadic flowering starts and reaches a peak in December, followed by fruiting. The fruits mature in February and are dispersed mostly by wind after maturation. Seeds start germinating in May.

Area of study

The site of the present study is situated at Burnihat (26°02'N, 91°52'E) in Meghalaya at an altitude of 100 m. The climate is humid (annual rainfall 2219 mm) and hot during most part of the year. During the winter months of December and January, the temperature goes down to 7°C while in summers it may rise to 37°C.

The study site was a five year old fallow on the top of a steep slope where *E. odoratum* was growing abundantly along with other species. The trees and shrubs of this area had been slashed and burned 5 yr ago and the study site has been left abandoned since then with no major disturbance to vegetation.

Vegetation of the site

The vegetation was mostly herbaceous dominated by *Imperata cylindrica*, a grass and *E. odoratum* (Tab. 1). However, certain tree species viz. *Dillenia indica*, *Bauhinia purpurea* and *Cassia fistula* were also present here and there. Some of the other less abundant species that also grow as associates on the study site are: *Setaria palmifolia*, *Paspalum conjugatum*, *Costus speciosus*, *Mimosa pudica*, *Sida rhombifolia*, *Wrightia tomentosa*, *Urena lobata* and *Dendrocalamus hamiltonii* but these species were not represented in the permanent quadrats.

Demographic studies

Demographic studies were made in three 1-m² permanent quadrats. Individuals of *E. odoratum* were labelled and mapped and their fate was followed at short and regular time intervals from June 1977 to June 1978. For the first six months (June to November 1977) when there was heavy mortality, mapping was done at 20 d intervals and during the latter half of the study period (December 1977 to June 1978) when the population was relatively stable the observations were made at monthly intervals. In the last week of June during the period of maximum recruitment, a cohort of seedlings was selected for survivorship study in a 50 cm² area on each of the three permanent quadrats. Each seedling was marked with a dot of black paint on the tip of its cotyledon and the fate of the cohort was followed until

Tab. 1. List of the major associates of *Eupatorium odoratum* and their density (Data based on observations in three permanent quadrats fixed for demographic studies).

Plant species	*No. per m ² (± S.E.)
<i>Imperata cylindrica</i>	203±21.9
<i>Rungia</i> sp.	24± 2.3
<i>Eupatorium odoratum</i>	27± 4.5
<i>Ottochloa nodosa</i>	8± 3.6
<i>Carex cubensis</i>	3± 0.8

* Density refers to the number of shoots in case of *Imperata cylindrica* and to whole plants in case of other species.

June 1978. The soil moisture content was also estimated to see if this was correlated with the survivorship of the plants. Soil moisture content was determined following the method outlined by Piper (1944) on the basis of 5 samples taken from 0–10 cm soil depth.

Dynamics of seed population

An attempt was made to study the seed population of *E. odoratum* in soil before and after the addition of fresh crop of seeds to the soil through dispersal. Thus, the seed population in the soil was estimated by taking 5 soil cores of 10 × 10 × 10 cm size from an area adjacent to the permanent quadrats in the month of February immediately before the seed dispersal and after the seed rain in the month of April. The soil cores were brought to the laboratory and sliced depthwise into five equal parts. The soil was air dried and seeds of *E. odoratum* that were large enough to be easily separated out of the soil, were counted. The seed production by *E. odoratum* growing in the permanent quadrats was also estimated in February to assess the seed population that might be available for seed dispersal.

Effects of adult on young transplants

In order to study the effect of adult plants of *E. odoratum* on the survivorship and growth of young transplants, three adult plants of *E. odoratum* were selected and all other plants growing within a 2 m radius were removed. Six *E. odoratum* seedlings at the four leaf stage were transplanted at 10 cm distance from the adults and 10 cm apart from each other. A control set without adult plants was maintained for comparison. In the control set, the seedlings were transplanted 10 cm apart in a circle around a central point instead of an adult plant. Both treatments had three replications. After eight months of growth, the transplants from both the treatments were harvested and various growth variables were measured.

Effect of associated vegetation on the reproductive behaviour of *E. odoratum*

For this experiment, a small area was chosen on the study site and the following two types of plots of 1 m² size were maintained, each type having 3 replicates:

(1) Two plants of *E. odoratum* were allowed to grow without competition from other species by constantly removing the latter from the plots.

(2) Two plants of *E. odoratum* were allowed to grow in competition with all other species.

Results

Population flux

The average population density of *E. odoratum* on the study site was 27 adult plants per m² in June 1977 (Tab. 2). These adults occasionally grew more than one shoot. Of these plants, only about 63% survived during the

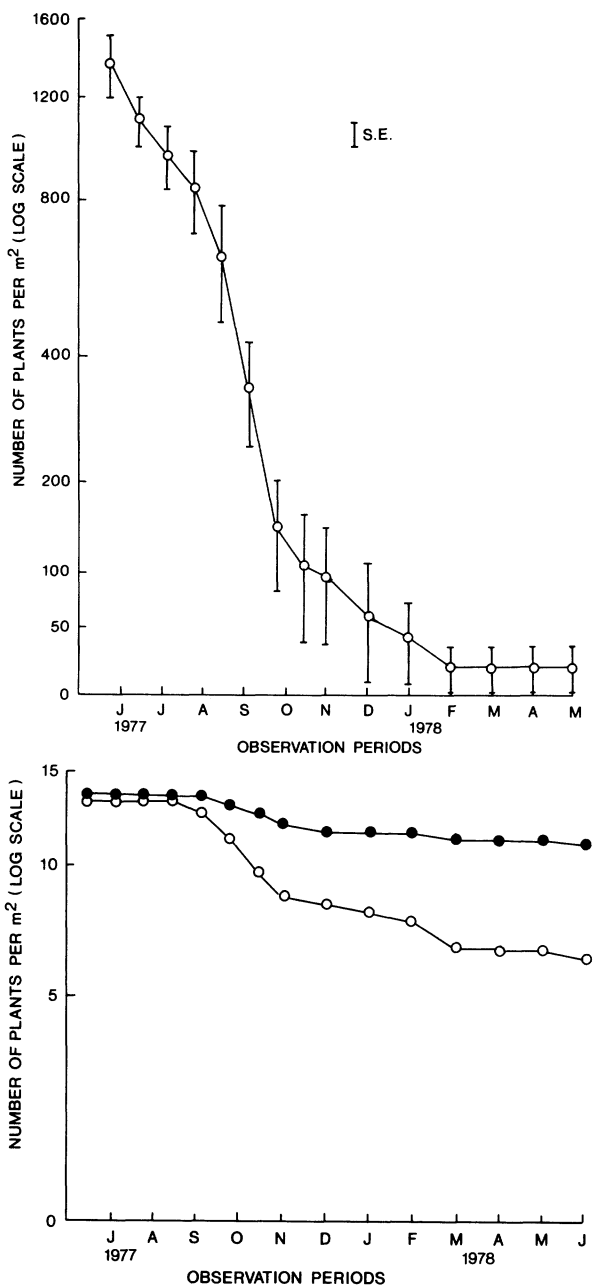


Fig. 1. Survivorship of *E. odoratum* in relation to age of its individuals in a five year old jhum fallow. Fig. 1 above: Seedling population (○—○); Fig. 1 below: one year old population (○—○) and more than one year old population (●—●); differences significant at 5% ($t = 3.26$).

study period. However, 19 new plants were added over a one year period increasing the population density to 36 plants per m² in June 1978. Thus there was a net gain of 9 plants per m² and the rate of population increase was 1.33. The annual mortality of the weed population was very high. Out of 1358 plants recruited (seedlings) over a one year period only 19 survived.

Tab. 2. Population flux of *E. odoratum* over a one year period (June 24 1977 to June 30 1978).

Variable	
a) No. of plants on 24 June 1977	27
b) No. of plants on 30 June 1978	36
c) Net change (b-a)	9
d) Rate of increase ($\frac{c}{a}$)	1.33
e) No. of plants recruited between 24 June 1977 and 30 June 1978	1358
f) Total no. of plants lost between 24 June 1977 and 30 June 1978	1349
g) Plants present on 24 June 1977 alive by 30 June 1978	17
h) Percentage survival of plants in (a) ($\frac{g}{a} \times 100$)	62.96
i) Total no. of plants recorded during the study period	1385
j) Percentage annual mortality of all individuals	97.4

The size of the population was largest in June, the period of maximum recruitment of seedlings and the population was lowest during winter months. Thus, the population of *E. odoratum* in the summer season although exhibiting considerable mortality, is characterised by net gain whilst during winter there is a net loss of individuals from the population.

Survivorship of seedling population

Seedlings experienced heavy mortality (Fig. 1 above). Two distinct periods of heavy mortality were observed, the first, during the active growing season (August to October) and second, in the winter months (December to February). Only 1.4% of the seedlings survived over the one year study period. The half-life of the seedling population was found to be 94 d which was quite low compared to the other two age groups.

Survivorship of mature plants

The survivorship of adults was very high in comparison to the seedling population. Two age groups could be recognised among the adults: one year old plants that were small and had 6 nodes, and more than one year old plants that were large and had more than 6 nodes. The survivorship of large plants was 80.5% while the sur-

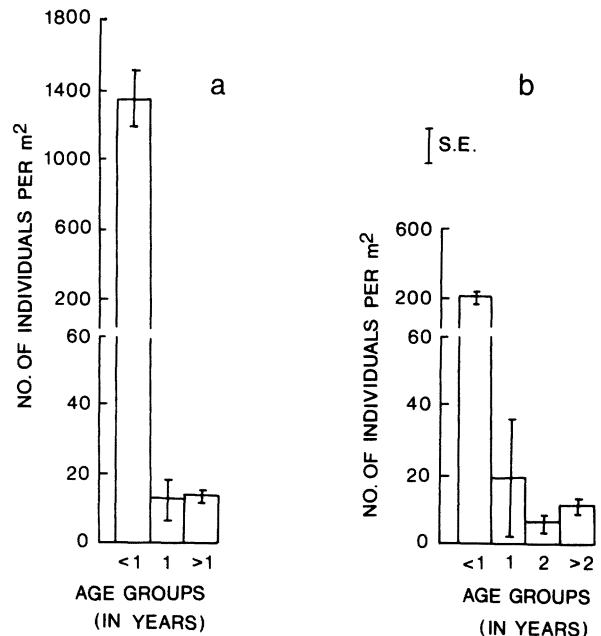


Fig. 2. Change in age structure of an *E. odoratum* population in a five year old fallow. Fig. 2 (a) and (b) refer to the age structure of *E. odoratum* populations in June 1977 and June 1978 respectively.

vivorship of one year old plants was only 47.5%. As shown by the survivorship curves (Fig. 1 below) the mortality among the young individuals started earlier. However, in both the age groups the maximum mortality was observed in the later part of the active growing season (October–November), presumably due to intense competition, and became constant for the rest of the study period (December 1977 to June 1978). The half-life of the one year old population was 306 d and that of the older population was presumably much greater though it was not possible to calculate.

Change in age structure of the population

The change in age structure of the population over one year (Fig. 2) shows that the recruitment of new seedlings was only 219 plants per m² in June 1978 while it was 1358 plants per m² in June 1977. The cause of this

Tab. 3. Effect of adult plants of *E. odoratum* on the survivorship and growth of its young transplants (data based on 15 survivors).

Variable	Transplants grown with adults	Transplants grown without adults	Calculated value of 't'
Survivorship (%)	93.51	91.33	0.563
Height of plants (cm)	13.26	28.94	4.798*
No. of leaves per plant	8	29	2.390
Leaf area per plant (cm ²)	74	481.15	1.975
Dry weight of root per plant (g)	0.079	0.507	1.000
Dry weight of shoot per plant (g)	0.482	3.198	4.005*

* Difference significant at 5% level.

Tab. 4. Effect of associated vegetation on the reproductive behaviour of *Eupatorium odoratum* (values represent the average of 6 plants).

Variable	<i>E. odoratum</i> grown with associates	<i>E. odoratum</i> grown without associates	Calculated value of 't'
Percentage of fertile shoots per plant	28.2	63.8	8.761*
No. of capitula per plant	975.3	4958.4	4.774*
No. of seeds per capitulum	28.4	31.0	2.025
Seed output per plant	27699	153710	4.248*

* Difference significant at 5% level.

great difference in recruitment between years is obscure. However, it could be argued that the difference in recruitment of seedlings could be on account of differences in climate between years that might have differential effect on flowering and germination although we have no data to substantiate this point.

Seed bank in soil

No seeds were found to be present in soil below 2 cm depth. The seed population of *E. odoratum* in the soil was zero in the month of February while after seed fall in April, values of 11240 seeds per m² were estimated.

Effect of adult plants of *E. odoratum* on the survivorship and growth of transplants

The growth of young transplants of *E. odoratum* was greatly suppressed close to the adult plants (Tab. 3). However, the survivorship of transplants in control and treatment plots was not much different. For variables like leaf area and dry matter yield of shoot and root of the transplants, there was a 6–7 fold decrease due to the proximity of adult plants of *E. odoratum*.

Effect of associates on the reproductive behaviour of *E. odoratum*

The reproductive potential of the *E. odoratum* plants was profoundly reduced by the presence of associated vegetation (Tab. 4). The seed production of *E. odoratum* was 27699 seeds per plant in the presence of associated vegetation while in devegetated plots it was as high as 153710 seeds per plant. Presence of the associated vegetation also caused a considerable decrease in the percentage of fertile shoots per plant and the number of capitula per plant (Tab. 4).

Discussion

The growth of a population is mainly dependent on recruitment, mortality and the longevity of individuals. According to Sarukhan and Harper (1973), a balance resulting from the complex interaction between the three, must be obtained if a population of a species is to maintain stability. The recruitment of new individuals of *E. odoratum* is greater than the numbers that are lost

from the established population over a one year period (Tab. 2). It shows that the weed has tremendous potential to increase its numbers. It produces a large amount of seed every year but only a fraction is able to establish as mature plants on account of a series of environmental constraints imposed on them at various stages of the life cycle. As shown in Fig. 5, a large number of seeds (about 87.2%) were lost to wind, water and other agencies. About 66% of the seeds falling in the plots were non-viable and the viable fraction does not all germinate due to non-availability of sufficient suitable microsites. Thus, only 12% of the total weed seeds present in soil could germinate. Further, not all the germinated seeds developed into mature plants.

The seedlings of *E. odoratum* show two peaks of mortality, one during the active growing season and the other during the winter months. As the plants grow, they place more and more demand on the available supplies and the keen competition that ensues, results in suppressed growth and heavy mortality. Many plants of *E. odoratum* also died due to heavy infection by stem rot. The second peak of mortality that was observed in

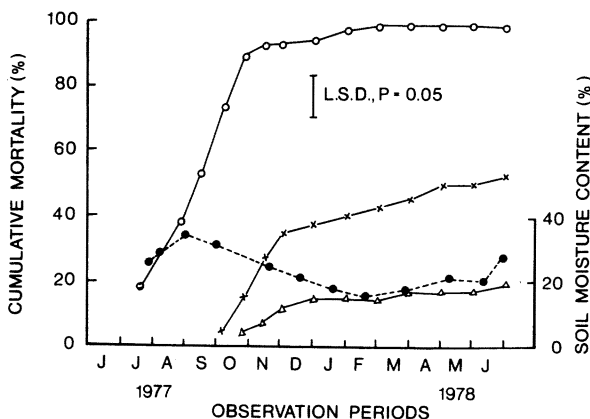


Fig. 3. Percentage cumulative mortality of different age groups of an *E. odoratum* population compared to the soil moisture content. The age groups considered are: less than one year old population (○—○), one year old population (×—×) and more than one year old population (△—△). The symbol (●-----●) indicates the soil moisture content.

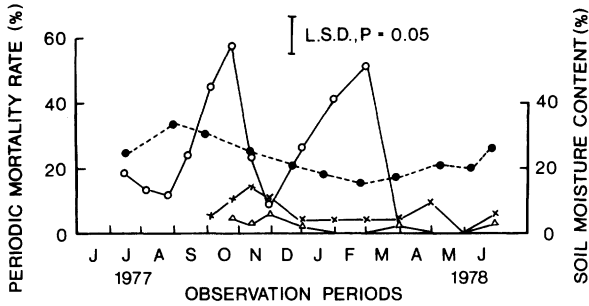


Fig. 4. Periodic mortality rate of different age groups of an *E. odoratum* population compared to the soil moisture content. The age groups considered are: less than one year old population (○—○), one year old population (×—×) and more than one year old population (△—△). The symbol (●—●), indicates the soil moisture content.

January–February may be attributed to low temperature and decreasing moisture content of the soil. Some mortality can be detected at all stages of the plant growth but the mortality risk was highest in seedling populations and decreased with the age of the plants (Fig. 3) so long as they were not senescent. The mortality increased with increasing soil moisture stress indicating that soil moisture content may play some role in the regulation of the population of this weed in nature.

However, the correlation between mortality and soil moisture content was statistically insignificant ($r = 0.2$).

The mortality pattern of the two age groups of adult plants was quite different from that of seedlings. The adults showed only one peak of mortality (Fig. 4) which appears to be independent of prevailing soil moisture stress and temperature conditions during winter months. Sarukhan and Harper (1973) suggested that the adult populations of *Ranunculus* spp. do not suffer from harsh climatic conditions, and the major risk for them comes during the active growing season. Similarly, Hawthorn and Cavers (1976) reported that the survivorship of mature plants was not affected by moisture stress. The adult population of *E. odoratum* also showed peak mortality in October–November which was the period of active vegetative growth and presumably most severe competition for resources. One year old adults suffered heavier mortality than 2 year old adult plants (Figs 3 and 4); they were smaller and appeared to be weaker competitors not only against the older plants of *E. odoratum* but also against the plants of other associated species. The half-life of the population increased with age of the cohorts indicating thereby an increase in longevity of the individuals that were established earlier.

The growth of associated vegetation seems to contribute considerably to the regulation of *E. odoratum* populations in nature. This is evident from the drastic

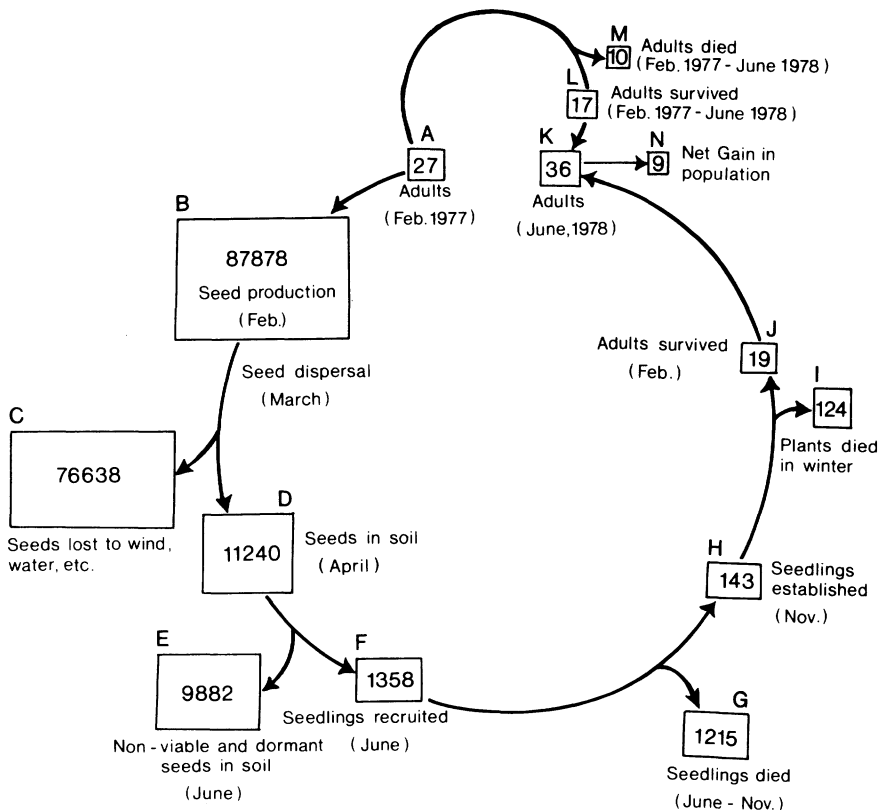


Fig. 5. Schematic summary of the population flux of *E. odoratum* in a five year old fallow. Data in boxes refer to the population of individuals (seeds or plants) per m². Box A: Adult population in February 1977 that remained unchanged until June 1977; Box J: Population of adults that survived in February 1978 remained unchanged until June 1978. Other boxes are explained in the figure.

reduction in the reproductive potential when grown in competition with the associates. Poor growth and survival of seedlings of *Chamaenerion angustifolium* has been attributed by Anandel and Rozema (1974) to a keen competition for water between seedling populations and associated vegetation where the latter is able to utilise the available resource more effectively. The role of associates in population regulation has also been emphasized by other workers (Sagar and Harper 1961, Putwain and Harper 1970, Tripathi and Dwivedi 1978). The adult plants of *E. odoratum* exercise a strong regulatory influence on the population growth of this weedy species. The growth of the young transplants introduced in the neighbourhood of the adults was found to be substantially reduced relative to transplants allowed to grow free from competition from adults (Tab. 3).

The schematic summary of the population dynamics of *E. odoratum* (Fig. 5) indicates that there resulted a net gain of only 9 individuals over a one year period to the population that existed in June 1977 despite a seed production of about 87900 per m². Obviously, there is a constant reduction in size of the population of seeds and plants with passage of time due to various environmental constraints operating at different stages of the life cycle. The possible factors that contribute to the regulation of the *E. odoratum* population are:

- (1) Wind, water, consumer organisms and other agencies responsible for the loss of seeds through their removal, predation and degeneration.
- (2) Non-availability of 'safe' microsites in sufficient numbers for the seeds to germinate and for seedlings to establish.
- (3) Competition for resources offered by the associated plant species and the established adult population of *E. odoratum*.
- (4) Soil moisture stress.
- (5) Low temperature conditions prevailing in winter.
- (6) Certain pathogens causing stem rot disease.
- (7) "Natural senescence" as the individuals die of old age.

In spite of all these hazards and regulatory forces, the adult population of 27 plants in June, 1977 increased to 36 after a period of one year which is a high rate of population growth. Population growth can be particularly rapid if the existing vegetation is disturbed as is clear from the high reproductive potential of the plants in the absence of competition from associated vegetation. If the *E. odoratum* population continues to grow at this speed, within a few years it may suppress and eliminate many useful elements of the original flora of the north-eastern region of India unless some other effective

regulatory forces become operative. It may be mentioned that the seedling population was far less in June 1978 as compared to that in the preceding year (Fig. 2) which indicates that some other regulatory factors are also involved, but whether these unidentified factors have been responsible for population regulation during the period of the present study only or exercise their influence on the population regularly in successive generations, is not yet known. In older fallows where the canopy of the vegetation was closed, the population of *E. odoratum* was observed to be low while in cleared areas of the present study site, the recruitment was very high presumably due to better availability of light indicating the role of light as well in population regulation of *E. odoratum* in nature.

Acknowledgements – We are grateful to Prof. J. L. Harper, Bangor, U.K. for his valuable comments on the manuscript. We also acknowledge the financial support from the University Grants Commission in form of a Junior Research Fellowship to A. S. Yadav.

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