

Growth Strategy and Allocation Pattern of *Eupatorium odoratum* and *Imperata cylindrica* at Different Fertility Levels of the Soil

K G SAXENA and P S RAMAKRISHNAN
Department of Botany, School of Life Sciences,
North Eastern Hill University, Shillong 793014

(Received 10 April 1981; after revision 22 October 1981)

Growth and allocation pattern of *Eupatorium odoratum* and *Imperata cylindrica* with contrasting photosynthetic and reproductive strategies were studied at varied fertility levels of the soil. Sexual reproductive allocation in *E. odoratum* was maintained irrespective of the imposed nutrient stress. However, plasticity in vegetative reproductive allocation was noted in the case of *I. cylindrica*. More nitrogen and phosphorus were allocated for reproductive growth in both the species as compared to potassium and this was achieved through greater translocation of these nutrients from other vegetative organs at the time of reproductive growth. *I. cylindrica*, a C₄ species, was more efficient from the point of nutrient uptake and its use as compared to *E. odoratum*, a C₃ species. However, the latter was found to be always more productive than the former. The significance of these results is discussed.

Key Words: Growth strategy, Allocation pattern, Soil fertility levels, Productivity

Introduction

Rapid growth and multiplication are two important features of the colonizing species (Gomez-Pompa & Vazquez-Yanes 1974, Grime 1979). A species may ensure its success either through heavy seed production combined with efficient dispersal mechanism or through effective vegetative multiplication or through both. A number of studies were made on the biomass/energy allocation pattern in relation to the reproductive strategy of different plant species in an attempt to explain the ecological success of a species

in a given environment (Harper & Ogden 1970, Ogden 1974, Abrahamson 1975a, b, Hawthorn & Cavers 1978, Pitelka 1977, Bell et al. 1979). However, only recently attention has been drawn to the allocation pattern of nutrients (Andel & Vera 1977, William & Bell 1981), which may be equally important particularly in situations with a limited supply (Harper & Ogden 1970).

Another important feature of the colonizing species is their ability to make efficient growth under high light and warmer

temperature regimes of an open environment. This high photosynthetic capacity of the early successional species has often been associated with C_4 photosynthetic pathway (Black 1971). However, the ecological implications of this photosynthetic strategy have been questioned by a number of workers (Bull 1971, Gifford 1974, Baskin & Baskin 1978).

Eupatorium odoratum L. and *Imperata cylindrica* Beauv. var. major are two important perennial weeds of early successional fallows of 4–5 years of age after slash and burn agriculture in north-eastern India (Ramakrishnan et al. 1981). The former species is a C_3 plant exclusively dependent upon sexual reproductive strategy, while the latter is a C_4 species with efficient vegetative reproduction through its underground rhizomatous system. The present study analyses the growth and allocation strategy of these two contrasting species under different nutrient regimes.

Study area and Climate

The study was carried out in Byrnihat in the Khasi Hills about 90 km north of Shillong and is located at 26°N and 91.5°E . The Precambrian rocks are represented by gneiss, schists and granites. The soil is red sandy loam and of laterite origin. The fertility status of the soil is very poor and has been discussed in detail elsewhere (Ramakrishnan and Toky 1981). The pH ranges from 5 to 7 and the angle of slopes from 20° to 40° .

The climate of the area can be divided into three distinct seasons. The dry summer runs from mid-February to May. The rainy season extends from May to September with an annual rainfall of 2200 mm. This is a warm period with high humidity. The mild winter which is practically rainless except for a few showers, extends from November to February. The annual maximum temperatures are 33°C and 70°C respectively.

Methods of Study

Soil from a depth of 0–10 cm of the soil profile from a site where *E. odoratum* and *I. cylindrica* were abundant, was used for culture experiments. Three nutrient levels were arranged in a series of pots (32 cm diam.): (i) soil-sand mixture (1 : 1 volume), (ii) soil-sand mixture (2 : 1 volume), and (iii) unaltered soil (referred subsequently as Fertility levels I, II and III respectively). *E. odoratum* was grown through seedling transplant at the cotyledonary stage, while *I. cylindrica* was grown through rhizome cuttings of uniform size (1.5 cm long) in June 1979. One seedling or rhizome cutting was raised per pot in all the cases. Plants were watered regularly. Four harvests were taken at an interval of 60 days. Harvested plants were separated into different components like root, rhizome, stem, leaf and seed. Different component organs were dried at $80 \pm 5^\circ\text{C}$ for 48 hr and weighed. Culm, in the case of *I. cylindrica* was considered as a supporting organ and, therefore, included in the stem component. The fallen leaves and seeds were also considered following Hickman (1975). Fire replicates were done for all the treatments.

Nutrient concentration in different components was determined following standard methods as described by Allen (1974). Nutrient uptake efficiency was calculated as mg nutrient absorbed per g root biomass following Blair and Cordero (1978) and nutrient use efficiency as mg dry matter production per mg nutrient uptake (Brown 1978).

Results

The data on mean dry matter production (figure 1) show that at all the three fertility levels, *E. odoratum* had better growth yield over *I. cylindrica* in all harvests ($P < 0.01$) and this became more pronounced during the later harvests. Further, while *E. odoratum*, showed marked increase in growth between 180 and 240 days the growth was insignificant

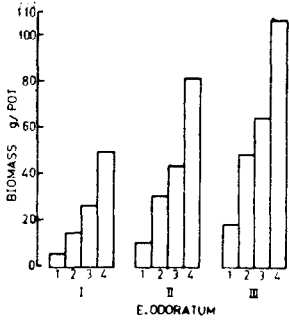
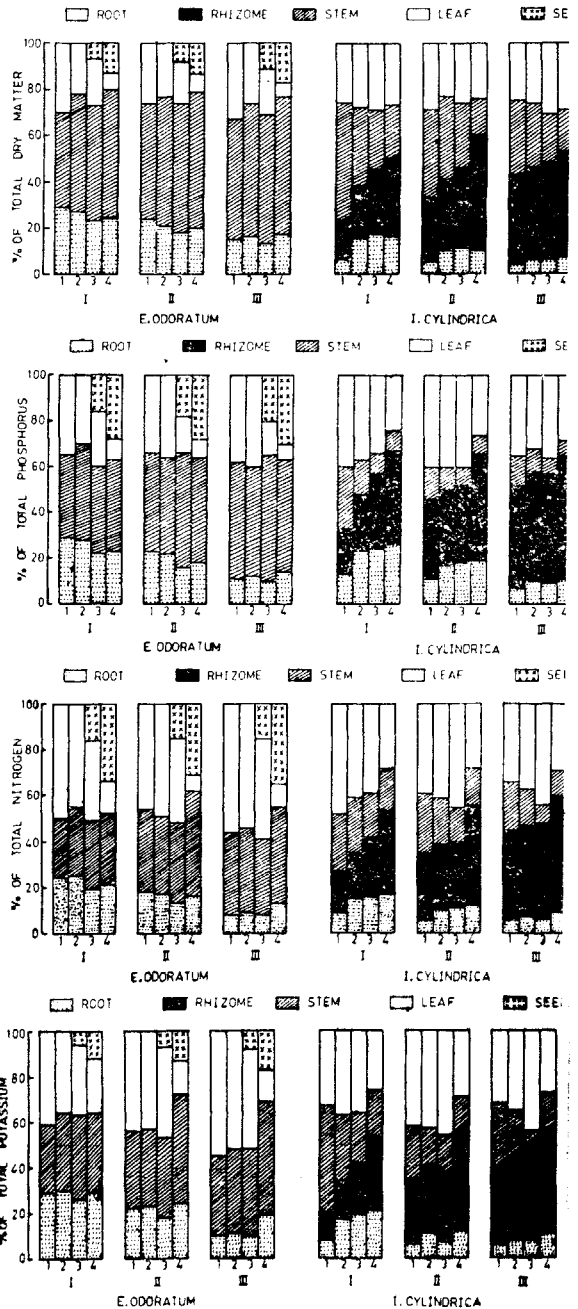


Figure 1 Mean dry weight per pot of *E. odoratum* *I. cylindrica* grown at fertility levels, I, soil-sand mixture (1 : 1); II, soil-sand mixture (2 : 1); III, unaltered soil, 1, 2, 3, 4 represent the harvests taken at 60, 120, 180 and 240 days of growth

in the case of *I. cylindrica*. Biomass increased significantly ($P < 0.01$) with the rise in fertility level of the soil being more pronounced in the case of *E. odoratum*.

A significant decline ($P < 0.05$) in the allocation to root was found in *E. odoratum* at the beginning of sexual reproductive growth, followed by an increase towards the end of growth period (figure 2 a-d). However, the decline was more pronounced at lower fertility levels. *I. cylindrica* showed a significant increase ($P < 0.01$) in allocation to the root during the early phase of growth and it was more marked at lower nutrient levels.

Allocation of biomass to the stem increased significantly ($P < 0.05$) in *E. odoratum* during the second and fourth harvests in all the treatments. However, allocation of all the nutrients to stem increased significantly ($P < 0.05$) for this species only in the initial stage at fertility level I. At fertility levels II and III, the proportion of nitrogen and potassium allocated to the stem increased significantly ($P < 0.05$) towards the end of growth while that of phosphorus declined after an initial increase ($P < 0.05$). For *I. cylindrica*, a gradual decline in allocation to the stem, both in terms of biomass and nutrients, was noted.



Figures 2 a-3 Allocation of biomass and nutrients to various compartments (expressed as percentage of the total capital) during growth of *E. odoratum* and *I. cylindrica* at different fertility levels (I, II, III). 1, 2, 3, 4 are the harvests at different times during growth as given in figure 1

Allocation to leaf decreased during growth in the case of *E. odoratum* and this was more marked during sexual reproductive growth. Such a clear cut pattern was not observed in *I. cylindrica* except for a significant decline ($P < 0.01$) in the allocation of nutrients after 180 days of growth.

Allocation to rhizome, at all fertility levels, in the case of *I. cylindrica* increased gradually during growth.

Proportional allocation to the root compartment decreased with the increasing fertility level ($P < 0.01$) in both the species. Allocation to stem increased with the increasing fertility level in *E. odoratum* while reverse was the case for *I. cylindrica*. Sexual reproductive allocation in *E. odoratum* did not differ significantly ($P > 0.05$) at different fertility levels. On the other hand, a significant increase ($P < 0.01$) with increase in fertility level in the vegetative reproductive allocation was noted for *I. cylindrica*. Reproductive allocation of nitrogen and phosphorus was much higher as compared to that of biomass and potassium.

Nutrient uptake efficiency for nitrogen, phosphorus and potassium all, increased with the increasing fertility status of the soil ($P < 0.01$). This efficiency was significantly higher ($P < 0.05$) for *I. cylindrica* compared to *E. odoratum* in all the treatments table 1.

Nutrient use efficiency only of nitrogen and phosphorus decreased with increasing soil fertility ($P < 0.05$) in both the species whereas that of potassium was unaffected, *I. cylindrica* showed significantly higher ($P < 0.01$) values for all the nutrients than that for *E. odoratum* in all treatments (table 2).

Discussion

It has been often shown that vegetative reproductive effort of the colonizing species is more plastic towards various environmental

Table 1 Nutrient-uptake efficiency (mg nutrient absorbed/g root biomass) of *E. odoratum* and *I. cylindrica* at different fertility levels

Nutrient uptake efficiency	Fertility levels		
	I	II	III
Nitrogen			
<i>E. odoratum</i>	41.40	57.02	74.88
<i>I. cylindrica</i>	54.23	71.61	115.77
Phosphorus			
<i>E. odoratum</i>	5.31	6.63	9.25
<i>I. cylindrica</i>	7.26	11.87	18.77
Potassium			
<i>E. odoratum</i>	32.60	44.49	51.77
<i>I. cylindrica</i>	39.60	56.12	89.27

Level of significance ($P < 0.05$)

Table 2 Nutrient-use efficiency (mg dry matter production per mg nutrient absorbed) of *E. odoratum* and *I. cylindrica* at different fertility levels

Nutrient-use efficiency	Fertility levels		
	I	II	III
Nitrogen			
<i>E. odoratum</i>	101.47	86.60	78.65
<i>I. cylindrica</i>	151.81	135.11	124.77
Phosphorus			
<i>E. odoratum</i>	790.80	744.76	636.91
<i>I. cylindrica</i>	858.57	815.15	769.49
Potassium			
<i>E. odoratum</i>	118.03	116.10	113.70
<i>I. cylindrica</i>	162.88	164.11	162.14

Level of significance ($P < 0.01$)

stresses while sexual reproductive allocation remains nearly fixed in terms of percentage allocation regardless of the stress (Harper & Ogden 1970, Ogden 1974, Thomas 1974, Abrahamson 1975a, b). This was reflected in plasticity in allocation to the rhizome in

I. cylindrica in contrast to the more stable sexual reproductive allocation pattern of *E. odoratum* even at the cost of lower allocation to stem component at poor fertility levels. Such results, however, should not be generalized too far in view of the plasticity in sexual reproductive effort shown in *Polygonum caseadense* and *Uvularia perfoliata* (Hickman 1975, Whigham 1974).

Comparatively higher reproductive allocation of nitrogen and phosphorus as compared to potassium in both the species may be due to greater transfer of the former two from other vegetative organs like leaf and stem/root during reproductive growth which is reflected in their sharp decrease in these compartments. Similar conclusions were also arrived at by other workers (Andel & Vera 1977, Austin et al. 1977, Williams & Bell 1981).

Based chiefly upon the physiological studies under manipulated environments, the speculation has often been advanced that plants with C_4 photosynthetic pathway should be more productive than those having C_3 pathway (Black et al. 1969, Black 1971). However, in the present case *E. odoratum* which is a C_3 plant accumulated significantly higher dry matter throughout its growth and at all fertility levels as compared to a C_4 plant like *I. cylindrica*, suggesting thereby that C_4 strategy may not be essentially superior to C_3 strategy (Wilson 1967, Slatyer 1970, 1971, Mooney et al. 1976, Baskin & Baskin 1978). In an earlier study (Saxena 1981), we have shown that the higher photosynthetic capacity of *E. odoratum* compared with *I. cylindrica* is associated with larger photosynthetic surface exposed by the former as also shown

by Slatyer (1970, 1971) and Caldwell (1977) in other species.

Though low nutrient uptake efficiency observed at low fertility levels may be related to decreased availability of nutrients (Blair & Corders 1978), both the species tended to compensate it through increased proportional allocation of biomass to the root system and more efficient use of nitrogen and phosphorus which are more critical. The higher nutrient uptake and use efficiency of *I. cylindrica* (C_4) as compared to *E. odoratum* may be associated with the evolution of C_4 strategy under stressful environments where efficient utilization of nutrients is the main objective (Brown 1978). This is also reflected from less pronounced decrease in dry matter production in *I. cylindrica* compared to *E. odoratum* at low fertility levels.

Heavy production of light and small seeds makes *E. odoratum* more successful in exploiting new sites and the disadvantage of minute size during the early phases of growth is compensated through higher photosynthetic capacity. On the other hand, *I. cylindrica* probably overcomes the disadvantage of its low photosynthetic capacity by rapid vegetative multiplication where low risk of mortality to the offspring is achieved through its attachment to the parent.

Acknowledgement

This research was supported by the Department of Science and Technology, Government of India under 'Man and Biosphere' programme.

References

- Abrahamson W G 1975a Reproductive strategies in dewberries; *Ecology* 56 721-726
 ——— 1975b Reproduction in *Rubus hispidus* L. in different habitats; *Am. Midl. Nat.* 93 471-478
 Allen S E 1974 *Chemical Analysis of Ecological Materials* (Oxford, London: Blackwell Scientific Publications)
 Andel Van J and Vera F 1977 Reproductive

- allocation in *Senecio sylvaticus* and *Chaemenerion angustifolium* in relation to mineral nutrition, *J. Ecol.* **65** 747-758
- Austin R B, Ford M A, Edrich J A and Blackwell R D 1977 The nitrogen economy of winter wheat; *J. Agric. Sci. Camb.* **88** 159-167
- Baskin J M and Baskin C C 1978 A discussion on the growth and competitive ability of C₃ and C₄ plants; *Castanea* **43** 75-76
- Bell K A, Hiatt H D and Niles W E 1979 Seasonal changes in biomass allocation in eight winter annuals of Mojave Desert; *J. Ecol.* **67** 781-787
- Black C C 1971 Ecological implications of dividing plants into groups with distinct photosynthetic production capacities; in *Advances in Ecological Research* Vol 7 pp. 87-114 ed. J B Cragg
- _____, Chen T M and Brown R H 1969 Biochemical basis for plant competition; *Weed Sci.* **17** 338-344
- Blair G J and Cordero S 1978 The phosphorus efficiency of three annual legumes; *Pl. Soil* **50** 387-398
- Brown R H 1978 A difference in N-use efficiency in C₃ and C₄ plants and its implication in adaptation and evolution; *Crop. Sci.* **18** 43-48
- Bull T A 1971 The C₄ pathway as related to growth rates in sugarcane; in *Photosynthesis and Photorespiration* 68-75 eds. M D Hatch, C B Osmond and R O Slatyer (New York: Wiley Interscience)
- Caldwell M M, White R S, Moore R T and Camp L B 1977 Carbon balance, productivity and water-use of cold winter desert shrub communities dominated by C₃ and C₄ species; *Oecologia* (Berlin) **29** 275-300
- Gifford R M 1974 A comparison of potential photosynthesis, productivity and yield of plant species with differing photosynthetic metabolisms; *Aust. J. Pl. Physiol.* **1** 107-117
- Gomez-Pompa A and Vazquez-Yanes Y 1974 Studies on secondary succession of lowland tropics: The life cycle of secondary species; *Proc. 1st int. Conf. Ecol.* 336-342
- Grime J P 1979 *Plant Strategies and Vegetation Processes* (New York: John Wiley & Sons)
- Harper J L and Ogden J 1970 The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris*. L.; *J. Ecol.* **58** 681-698
- Hawthorn W R and Cavers P B 1978 Resource allocation pattern of two perennial species of Plantago; *Can. J. Bot.* **56** 2533-2537
- Hickman J C 1975 Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadenae* (Polygonaceae); *J. Ecol.* **63** 689-701
- Mooney H A, Ehleringer and Berry J A 1976 High photosynthetic capacity of a winter annual in Death Valley; *Science* **194** 322-324
- Ogden J 1974 The reproductive strategy of higher plants. II. The reproductive strategy of *Tussilago farfara* L.; *J. Ecol.* **61** 291-324
- Pitelka L F 1977 Energy allocation in annual and perennial lupines (*Lupinus*: Leguminosae); *Ecology* **58** 1055-1065
- Ramakrishnan P S and Toky O P 1981 Soil nutrient status of hill agroecosystems and recovery pattern after slash and burn agriculture (Jhum) in north-eastern India; *Pl. Soil* **60** 41-64
- _____, Mishra B K and Saxena K G 1981 Slash and burn agriculture in Northeastern India; in *Fire Regimes and Ecosystem Properties* pp 570-586 eds H Mooney, N L Bonnicksen, J E Lotan Christensen and W A Reiners USDA For. Serv. Gen. Techn. Rep. (Washington: John Wiley & Sons)
- Saxena K G 1981 Studies on the Eco-Physiology of Early Successional Plant Populations of Jhum Fallows; Ph.D. Thesis, North Eastern Hill University, Shillong, India
- Slatyer R O 1970 Comparative photosynthesis, growth and transpiration of two species of *Atriplex*; *Planta* (Berlin) **93** 175-189
- _____, 1971 Relationship between plant growth and leaf photosynthesis in C₃ and C₄ species of *Atriplex*; in *Photosynthesis and Photorespiration* 76-81 eds M D Hatch, C B Osmond and R O Slatyer (New York: Wiley Interscience)
- Thomas A G 1974 Reproductive Strategies in *Hieracium*; *Plant Population Dynamics Symposium* AIBS meetings, Arizona Tempe
- Whigham D 1974 An ecological life study of *Uvularia perfoliata* L.; *Am. Midl. Nat.* **91** 343-359
- Williams R B and Bell K M 1981 Nitrogen allocation in Mojave Desert annuals; *Oecologia* (Berlin) **48** 145-150
- Wilson W J 1967 Effects of seasonal variation in radiation and temperature on net assimilation and growth rates in an arid climate; *Ann. Bot.* **31** 41-57