SECTION B

GROWTH AND ALLOCATION PATTERN OF SOME IMPORTANT WEEDS
CHAPTER VI

GROWTH AND ALLOCATION PATTERN OF SOME IMPORTANT ANNUAL WEEDS
INTRODUCTION

Optimization of reproductive output in plants is attained through a favourable partitioning of the available resources for various life-activities such as maintenance, growth and reproduction (Abrahamson and Gadgil 1973). MacArthur and Wilson (1967) predicted that organisms in an open environment are selected for high reproductive potential (r-selection), while those in a closed environment are selected for high competitive ability at the expense of lower reproductive potential (K-selection). However, this basic concept has been expanded from a number of other ecological and evolutionary viewpoints (Pianka 1970; 1972; Gadgil and Solbrig 1972; Grime 1974, 1977; Stearns 1975, 1977; Moore 1976).

Considerable attention has been given to the adaptive nature of biomass or energy distribution pattern in relation to various environmental conditions, growth habit and life-span of the plant and competitive interactions (e.g. Rodin and Bazilevich 1967; Gadgil and Solbrig 1972; Harper and Ogden 1970; Gaines et al 1973; Ogden 1974; Abrahamson 1975a, b; Hickman 1975; Pitelka 1977; Newell and Tramer 1978; Abrahamson 1979; Bell 1979; Clark and Burk 1980). However, only a few studies are available on the partitioning of nutrients (Van Andel and Vera 1977; Williams and Bell 1980) which may be equally important particularly in the situations with a limited supply (Harper and Ogden 1970).
Annual weedy species are of wide distribution particularly during the early stages of secondary succession following slash and burn in the north-eastern India. The present study deals with the growth and resource (biomass and nutrients) allocation pattern of four important annual weeds viz. *Borreria articulata* (L.f.) Will., *Cassia tora* L., *Ageratum conyzoides* L. and *Erigeron linifolius* Willd.

**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 gniess, schists and granites. The soil is red sandy loam and of laterite origin. The pH ranges from 5 to 7. The angle of slopes generally range 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 and minimum temperatures are 33°C and 7°C respectively.
METHODS OF STUDY

A 20 year old fallow which was slashed in December, 1977 and freshly burnt in March, 1978 was selected for the purpose of this study. Two leaved uniform seedlings of all the four species concerned, were transplanted to this site in April, 1978. A distance of 40 cm was maintained between two seedlings. Further, other weeds coming up in the site were regularly removed in order to avoid any competition. Seven randomly selected plants for each species were harvested at monthly intervals during the entire growing season. Belowground parts were carefully washed and the plants were separated into different components like-root, stem, leaf and reproductive structures. The pedicels of the inflorescence were included in the stem component. The fallen leaves and seeds were also considered following Hickman (1975). The different component organs were dried at 80 ± 5°C for 48 hours and weighed. Three lots of 100 seeds each were weighed for the determination of average seed weight. Seed output per plant was computed using average seed weight and total seed weight per plant. Leaf area estimations using a planimeter and leaf dry weight per unit area were based on three replicates and 50 leaves per replicate. Total leaf area per plant was obtained using leaf biomass and leaf dry weight per unit area.

Growth functions such as relative growth rate (RGR); net assimilation rate (NAR) and leaf area
ratio (LAR) (Hughes and Freeman 1967; Radford 1967) were calculated as:

\[
RGR = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \quad \text{(mg mg}^{-1} \text{d}^{-1})
\]

\[
NAR = \frac{(W_2 - W_1) (\ln A_2 - \ln A_1)}{(A_2 - A_1) (t_2 - t_1)} \quad \text{(mg cm}^{-2} \text{d}^{-1})
\]

\[
LAR = \frac{(A_2 - A_1) (\ln W_2 - \ln W_1)}{(\ln A_2 - \ln A_1) (t_2 - t_1)} \quad \text{(cm}^2 \text{mg}^{-1})
\]

where \(W_1\) and \(A_1\) are the biomass per plant and leaf area per plant respectively at time \(t_1\) and similarly \(W_2\) and \(A_2\) are the same at time \(t_2\).

The concentration of nutrients in different plant parts were determined following standard methods given by Allen (1974). Thus, nitrogen was analysed by micro-Kjeldahl method; phosphorus by molybdenum-blue method and potassium by flame photometry, after dry ashing.

Nutrient uptake efficiency was expressed as mg nutrient absorbed per g root biomass following Blair and Cordero (1978). Nutrient use efficiency was calculated as mg dry matter production per g nutrient absorbed (Brown 1978).
RESULTS

*Cassia* *tora* had maximum values for relative growth rate and net assimilation rate. Leaf area ratio was found to be maximum for *Borreria articularis*, though this species showed the least value for net assimilation rate. *Erigeron linifolius* had least value of leaf area ratio but its net assimilation rate was higher than that of *B. articularis* and *Ageratum conyzoides* (Table 6.1).

*C. tora* and *A. conyzoides* had significantly higher concentration of nitrogen in the leaf tissue as compared to the other two annuals, while *E. linifolius* gave the least value. On the other hand, potassium concentration was much higher in *E. linifolius* than in *C. tora* while *A. conyzoides* and *B. articularis* fell in between with no significant difference between themselves. Phosphorus concentration did not differ significantly between the different species (Table 6.2).

Nutrient uptake efficiency was significantly higher for *B. articularis* and *E. linifolius* than for the other two species. Significant differences were found between *B. articularis* and *E. linifolius* only with respect to phosphorus and potassium uptake efficiency. *C. tora* gave the minimum values for all the nutrients (Table 6.3).

*E. linifolius* and *B. articularis* had significantly higher nitrogen use efficiency as compared to *A. conyzoides*
Table 6.1. Mean values ± S.E.M. of growth functions during growth of different species.

<table>
<thead>
<tr>
<th>Species</th>
<th>RGR mg mg⁻¹ d⁻¹</th>
<th>HAR mg cm²⁻¹ d⁻¹</th>
<th>LAR cm² mg⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. articulavis</td>
<td>0.0206 ± 0.0093</td>
<td>0.0813 ± 0.0304</td>
<td>0.2460 ± 0.0398</td>
</tr>
<tr>
<td>C. tara</td>
<td>0.0330 ± 0.0114</td>
<td>0.2336 ± 0.0626</td>
<td>0.1242 ± 0.0141</td>
</tr>
<tr>
<td>A. conyzoides</td>
<td>0.0168 ± 0.0049</td>
<td>0.1145 ± 0.0306</td>
<td>0.1552 ± 0.0294</td>
</tr>
<tr>
<td>S. linifolius</td>
<td>0.0125 ± 0.0061</td>
<td>0.1770 ± 0.0727</td>
<td>0.0693 ± 0.0121</td>
</tr>
</tbody>
</table>
Table 6.2. Concentration of nutrients (Mean $\pm$ S.E.M.) in leaf tissue of different species during growth.

<table>
<thead>
<tr>
<th>Species</th>
<th>Nitrogen</th>
<th>Phosphorus</th>
<th>Potassium</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. articularis</td>
<td>2.23 ± 0.16</td>
<td>0.14 ± 0.01</td>
<td>0.72 ± 0.05</td>
</tr>
<tr>
<td>C. tora</td>
<td>2.88 ± 0.14</td>
<td>0.16 ± 0.01</td>
<td>0.46 ± 0.02</td>
</tr>
<tr>
<td>A. conyzoides</td>
<td>2.53 ± 0.19</td>
<td>0.16 ± 0.01</td>
<td>0.67 ± 0.05</td>
</tr>
<tr>
<td>E. linifolius</td>
<td>1.49 ± 0.24</td>
<td>0.16 ± 0.02</td>
<td>1.24 ± 0.08</td>
</tr>
</tbody>
</table>
Table 6.3. Nutrient uptake efficiency (mg nutrient absorbed per g root biomass) of the different species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Nitrogen</th>
<th>Phosphorus</th>
<th>Potassium</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. articulare</td>
<td>171.13</td>
<td>20.50</td>
<td>75.37</td>
</tr>
<tr>
<td>C. tora</td>
<td>85.83</td>
<td>7.03</td>
<td>19.94</td>
</tr>
<tr>
<td>A. conyzoides</td>
<td>135.03</td>
<td>10.89</td>
<td>47.09</td>
</tr>
<tr>
<td>E. linifolius</td>
<td>154.82</td>
<td>29.24</td>
<td>104.09</td>
</tr>
<tr>
<td>L.S.D. (P = 0.05)</td>
<td>20.40</td>
<td>5.40</td>
<td>25.70</td>
</tr>
</tbody>
</table>
Table 6.4. Nutrient use efficiency (Mean ± S.E.M.) expressed as mg dry matter production per mg nutrient uptake of different species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Nitrogen</th>
<th>Phosphorus</th>
<th>Potassium</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. articulatis</td>
<td>794.58 ± 86.23</td>
<td>8398.99 ± 240.50</td>
<td>1829.54 ± 176.27</td>
</tr>
<tr>
<td>C. tora</td>
<td>593.72 ± 53.14</td>
<td>8107.07 ± 547.33</td>
<td>2410.91 ± 259.22</td>
</tr>
<tr>
<td>A. conyzoides</td>
<td>609.59 ± 68.31</td>
<td>8563.66 ± 606.97</td>
<td>1892.51 ± 129.97</td>
</tr>
<tr>
<td>S. linifolius</td>
<td>1022.87 ± 53.51</td>
<td>6094.92 ± 399.98</td>
<td>1465.07 ± 98.09</td>
</tr>
</tbody>
</table>
and C. tora. Phosphorus use efficiency was found to be minimum in E. linifolius though there were no significant differences amongst the other species. Potassium use efficiency was maximum for C. tora (Table 6.4).

Fig. 6.1 illustrates the allocation pattern of biomass and nutrients to different compartments expressed as the percentage of the total capital. Certain marked differences were observed in the allocation pattern amongst different species. An initial and significant decline (P < 0.05) in allocation to root was noted in E. linifolius while in others, there was an initial increase followed by a gradual decline. Proportional allocation to stem both of biomass and all the nutrients increased continuously with the passage of time in A. conyzoides only. C. tora showed a significant decrease in allocation of nitrogen and phosphorus to stem at the time of reproductive growth. A similar pattern was also noted for the allocation of phosphorus in E. linifolius and E. articularis. Allocation to leaf declined during growth and this was more pronounced at the time of reproductive growth. Reproductive allocation of nitrogen and phosphorus was much higher than that of biomass and potassium in all the species. Comparing the % allocation to different compartments amongst the species, allocation to root was found to be significantly higher (P < 0.01) in C. tora and A. conyzoides compared to the two others. Stem received significantly higher proportion throughout the growth in
Fig. 6.1 (a-d) Allocation of biomass and nutrients to various compartments (expressed as percentage of the total capital) during the growth of different species.
Fig. 6.1

(a) Allocation of biomass
- Root
- Stem

(b) Allocation of nitrogen
- Leaf
- Seed

Species:
- Erigeron linifolius
- Aggeratum conyzoides
- Cassia tora
- Borreria articulans

Time period (Months)
Fig. 6.1

Allocation of phosphorus
- Root
- Stem

Erigeron linifolius

Allocation of potassium
- Leaf
- Seed

Aggeratum conyzoides

Cassia tora

Borrella articularis

Time period (Months)
Table 4.5. Reproductive efficiency (Mean ± S.E.M.) as number of seed per g plant biomass of the different species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Reproductive efficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. articularis</td>
<td>62.41 ± 12.96</td>
</tr>
<tr>
<td>C. tora</td>
<td>7.90 ± 0.57</td>
</tr>
<tr>
<td>A. conyzoides</td>
<td>274.83 ± 24.02</td>
</tr>
<tr>
<td>E. linifolius</td>
<td>6566.59 ± 327.46</td>
</tr>
</tbody>
</table>
E. linifolius than the others (P < 0.01). However, such differences were not found between E. linifolius and A. conyzoides towards the end of the growth. Allocation to leaf was always minimum in E. linifolius. Reproductive allocation was significantly (P < 0.001) lower in A. conyzoides than the others.

Reproductive efficiency, if considered as the number of seeds produced per g plant biomass, was found to be in the order of E. linifolius > A. conyzoides > B. articularris > Cassia tora (Table 6.5).

DISCUSSION

A striking feature of the pattern pertains to reproductive allocation of nitrogen and phosphorus which was much more expended as compared to biomass and potassium. High allocation of these two elements to the reproductive units has been reported for a variety of species (Spratt and Gaser 1970; Andel and Vera 1977; Austin and Blackwell 1977; Mooney and Rundel 1979; Benzing and Davidson 1979; Williams and Bell 1981), in such a way that these nutrients from the other organs like leaf and/or stem are transferred to the reproductive organs during this phase of growth.

Naturally occurring annuals are conceded to have the highest allocation of biomass ranging from 11% to 65% (Harper et al 1970; Hickman 1975; Pitelka 1977;
Abrahamson 1979; Bazzaz 1979; Bell 1979). In the present study, *A. conyzoides* showed an exceptionally low allocation (1.9%) of the total dry matter to fruits. This was also applicable for the allocation of nutrients, though such a comparison may not be relevant due to paucity of information available on allocation of nutrients except for a few studies (Andel and Vera 1977; Williams and Bell 1984). However, the number of seeds produced in relation to plant biomass, *A. conyzoides* showed substantially higher reproductive efficiency and it was much higher than that of *B. articulata* and *C. tora* in spite of the much higher reproductive allocation of dry matter in the latter two species. It seems that the strategy of *A. conyzoides* is to partition the limited reproductive biomass into a number of propagules instead of increasing the total cost of reproduction itself. It may be worth noting here that only recently has importance been given to seed production efficiency in terms of number (Harper et al. 1970; Moore 1976; Abrahamson 1979; Primack 1979) rather than the bulk biomass allocation.

A major proportion of the leaf nitrogen is usually associated with the photosynthetic components, specially chlorophyll and carboxylating enzymes and the concentration of this element is shown to be positively correlated with the photosynthetic rate, while phosphorus and potassium are less critical in this respect (Murata
1969; Brady 1973; Natr 1973; Terry and Ulrich 1973). Thus, higher net assimilation rate in *G. tora* followed by *A. conyzoides* and *B. articulare* may be associated with a similar pattern of nitrogen concentration in the leaf tissue. However, it was interesting to observe that *E. linifolius* which had minimum concentration of nitrogen in the leaf tissue and leaf area ratio also had markedly higher net assimilation rate than *A. conyzoides* and *B. articulare*. This is an aspect that needs to be looked into.

*E. linifolius* and *B. articulare* are two species which are more efficient in uptake efficiency of all the nutrients compared to the others. Yet the nitrogen utilization efficiency of these two species was also much higher compared to others. During slash and burn, nitrogen is partly volatalized (Ramakrishnan and Toky 1981). Though some recovery occurs subsequently (Ramakrishnan and Toky 1981), there is rapid depletion due to crop use (Toky and Ramakrishnan 1981) and also due to losses from the system through water (Toky and Ramakrishnan 1981). Thus, the high nutrient uptake efficiency, in spite of the low demand for nitrogen in the case of *E. linifolius* and *B. articulare* may enable them to colonize the nitrogen poor substratum and could be implicated for their wide distribution in seral communities.
SUMMARY

Four important annual weeds of the secondary successional environments following slash and burn agriculture, viz. *Rorera articulata*, *Cassia tora*, *Ageratum conyzoides* and *Brizas linifolius* were analysed for their growth and allocation pattern. *Cassia tora* had maximum value of relative growth rate and net assimilation rate. Nitrogen concentration in the leaf tissue was also maximum in this species. However, this species was found to be least efficient from the point of nutrient uptake and use.

Reproductive allocation of nitrogen and phosphorus was much more expended as compared to that of dry matter and potassium in all the species. *Ageratum conyzoides* showed the minimum allocation of biomass or nutrients to seeds but it had substantially higher seed production efficiency compared to *Rorera articulata* and *Cassia tora*. Results are discussed in relation to the ecological success of these species in the secondary successional environments.
CHAPTER VII

GROWTH AND ALLOCATION PATTERN OF SOME IMPORTANT PERENNIAL WEEDS WITH DIVERSE REPRODUCTIVE STRATEGY

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INTRODUCTION

Fire is a tool employed by the tribal populations of northeastern India for shifting agriculture, a practice locally referred to as 'Jhum'. After the burn, regeneration of vegetation may occur from insulated underground vegetative organs and through seeds present in the soil or brought in from elsewhere. These two contrasting regenerative strategies are considered to be significant both from ecological and evolutionary viewpoints (Jepson 1939; Horton and Kraebel 1955; Ahlgren 1960; Wells 1969; Hanes 1971; Kozlowski and Ahlgren 1974; Purdie 1977a,b; Muller-Dombois 1979).

Very few studies concern with comparative growth strategies of sprouting and non-sprouting weedy species coming up in seral communities. Keeley and Keeley (1977) made such an effort to study the dry matter allocation pattern in sprouting and non-sprouting species of Arctostaphylos in California Chaparral. However, these authors confined themselves to the absolute growth parameters only instead of also considering more appropriate proportionate analysis of resource distribution. Further, the importance of underground organs in the energy dynamics (Mooney and Ballings 1960; Jefford and Edelman 1961; Bradbury 1973; Chapin, Johnson and McKendrick 1980) was also ignored. The present study, therefore, concerns the growth and resource (biomass and nutrients) allocation pattern of four important perennials, with different regenerative strategies, establishing subsequent
to slash and burn in a site which was immediately fallowed without cropping.

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 gniess, schists and granites. The soil is red sandy loam and of laterite origin. The pH ranges from 5 to 7. The angle of slopes generally range 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 and minimum temperatures are 33°C and 7°C respectively.

METHODS OF STUDY

A 20 year old fallow, which was slashed in January, 1978 and freshly burnt in April, 1978 was selected for the purpose of the present study. Three nearly mono-specific patches, with respect to each of the perennial species studied were marked at the beginning of regrowth after the burn. Eupatorium
odoratum L. came through seedlings alone; Grewia elastica Royle., Thysanolaena maxima (Roxb.) O. Ketze. and Imperata cylindrica Beauv. var. major established exclusively through sprouts from the underground vegetative organs. Further, G. elastica was a root sprouter while I. maxima and I. cylindrica gave sprouts from rhizome. Three randomly placed quadrats (50 cm x 50 cm) were harvested throughout the growing period for each species. The sprouting species produced new shoots within a period of 10 days following the burn and therefore their sampling was started in May, 1978 whereas seedlings of G. odoratum came up in the month of May and therefore for this sampling was started in June, 1978. The harvested plants were seperated into belowground (root and rhizome), stem, leaf and seed components. Culm, in the case of I. cylindrica was a supporting organ and thereby was considered as stem. Different components were dried at 80 ± 5°C for 48 hours and weighed. The fallen leaves and seeds were also considered following Hickman (1975). Leaf area estimations using a planimeter and leaf dry weight per unit area were based on three replicates and 50 leaves per replicate. Total leaf area was computed from leaf dry weight per unit area and leaf biomass values. Growth functions such as relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) (Hughes and Freeman 1967; Radford 1967) were calculated as -
\[
\text{RGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}
\]

\[
\text{NAR} = \frac{(W_2 - W_1)(\ln A_2 - \ln A_1)}{(A_2 - A_1)(t_2 - t_1)}
\]

\[
\text{LAR} = \frac{(A_2 - A_1)(\ln W_2 - \ln W_1)}{(\ln A_2 - \ln A_1)(t_2 - t_1)}
\]

where \( W_1 \) and \( A_1 \) are biomass and leaf area values at time \( t_1 \) and similarly \( W_2 \) and \( A_2 \) at time \( t_2 \).

Concentrations of different nutrients in the component organs were determined following standard methods (Allen 1974). Thus, nitrogen was analysed by micro-Kjeldahl method; phosphorus by molybdenum-blue method and potassium by flame photometry, after dry ashing. Nutrient uptake efficiency was calculated as mg nutrient absorbed per g root biomass following Blair and Cordero (1978).

The leaf samples were hand sectioned within a few hours after collection and were examined under a microscope. The specimens were characterized for the presence of Kranz arrangement of leaf cells which is generally correlated with \( \text{C}_4 \) photosynthetic pathway (Laetsch 1971).
RESULTS

*Imperata cylindrica* and *Thysanolaena maxima* always showed the typical C leaf anatomy whereas *Eupatorium odoratum* and *Grewia elastica* did not exhibit such specialized anatomy.

*E. odoratum* had significantly higher relative growth rate and net assimilation rate compared to sprouting species, of which *G. elastica* had least values. However, *E. odoratum* and *G. elastica* had almost the same leaf area ratio. There were no marked differences between *I. cylindrica* and *T. maxima* for any of these growth functions (Table 7.1).

*E. odoratum* had significantly higher concentration of nitrogen, phosphorus and potassium in the leaf tissue than the others, the order being *E. odoratum* > *G. elastica* > *T. maxima* > *I. cylindrica* for nitrogen and phosphorus. The latter three species had almost the same concentration of potassium in leaf (Table 7.2).

Fig. 7.1 shows the relationship between dry matter yield and nutrient uptake during growth of different species. The slopes of the regression lines indicate that for a given dry matter yield, *E. odoratum* and *G. elastica* utilize higher quantity of nutrients than *T. maxima* and *I. cylindrica* ($P < 0.005$).

The allocation patterns of biomass and different nutrients, expressed as percentage of the total pool are shown in Fig. 7.2. There was a significant initial decline
Table 7.1. Mean values (± S.E.M.) of growth functions during growth for different species.

<table>
<thead>
<tr>
<th>Species</th>
<th>RGR</th>
<th>Growth Functions</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mg mg⁻¹ d⁻¹</td>
<td>NAR mg cm⁻² d⁻¹</td>
<td>LAR cm² g⁻¹</td>
<td></td>
</tr>
<tr>
<td>S. odoratum</td>
<td>0.0359±0.0154</td>
<td>0.3018±0.1152</td>
<td>0.1215±0.0309</td>
<td></td>
</tr>
<tr>
<td>G. elastica</td>
<td>0.0084±0.0026</td>
<td>0.0658±0.0140</td>
<td>0.1218±0.0400</td>
<td></td>
</tr>
<tr>
<td>I. cylindrica</td>
<td>0.0120±0.0040</td>
<td>0.1333±0.0430</td>
<td>0.0980±0.0160</td>
<td></td>
</tr>
<tr>
<td>T. maxima</td>
<td>0.0100±0.0036</td>
<td>0.1075±0.0201</td>
<td>0.0926±0.0180</td>
<td></td>
</tr>
</tbody>
</table>
Table 7.2. Mean concentration (± S.E.M.) of nutrients during the growing season in leaf tissue of different species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Nitrogen</th>
<th>Phosphorus</th>
<th>Potassium</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. odoratum</td>
<td>2.92 ± 0.12</td>
<td>0.28 ± 0.06</td>
<td>3.60 ± 0.32</td>
</tr>
<tr>
<td>G. elastica</td>
<td>1.70 ± 0.14</td>
<td>0.21 ± 0.04</td>
<td>1.32 ± 0.24</td>
</tr>
<tr>
<td>I. cylindrica</td>
<td>0.85 ± 0.05</td>
<td>0.11 ± 0.02</td>
<td>1.46 ± 0.24</td>
</tr>
<tr>
<td>T. maxima</td>
<td>1.40 ± 0.09</td>
<td>0.19 ± 0.04</td>
<td>1.54 ± 0.20</td>
</tr>
</tbody>
</table>
Fig. 7.4 (a-c) Relationship between dry matter yield and nutrient uptake (per m²) during the growth of different species.

- •, *S. odoratum*; 0, *G. elastica*;
Fig. 7.1
Fig. 7.1 C

Y = 3.80 + 0.04X
Y = 2.23 + 1.00X
Y = 2.51 + 0.91X
Y = 3.66 + 0.7X

Log potassium (mg)

Log biomass (g)
Fig. 7.2 (a-d). Allocation of biomass and nutrients to various compartments (expressed as percentage of the total capital) during the growth of different species.
Fig. 7.2

C: Allocation of phosphorus
- Poot.
- Rhizome.

d: Allocation of potassium
- Stem.
- Leaf.
- Seed.

% of total

Time period (Months)

M J J A S O N D J

M J J A S O N D J
(P < 0.01) in belowground allocation in *G. elastica* and *T. maxima*. The latter also showed another decline at the time of sexual reproductive growth also. On the other hand, *E. odoratum* and *I. cylindrica* showed a continuous increase (P < 0.01), but it was more pronounced in the latter towards the later part of the growth period. Proportional allocation to stem increased significantly with the passage of time in *E. odoratum* whereas no such clearcut pattern was observed for all the other three species. In all the species, allocation to leaf decreased gradually (P < 0.01) during growth, but this was more pronounced in *E. odoratum* as compared to those established through sprouts. Comparing the proportion allocated to various aboveground compartments, higher proportion was given to the stem in *E. odoratum* than in others, while the reverse was true for the leaf component (P < 0.005). However, such differences between *E. odoratum* and *G. elastica* were not found for the allocation pattern of potassium. Sexual reproductive allocation was much higher (P < 0.001) in *E. odoratum* than *T. maxima*, except for potassium. *G. elastica* and *I. cylindrica* did not flower during the period of study. Roots received significantly higher proportion in the nonrhizomatous species (*E. odoratum* and *G. elastica*) compared to the rhizomatous (*T. maxima* and *I. cylindrica*). However, belowground allocation (including rhizome) was much higher in the latter than the former in the later part of the growth only, the only exception being the allocation pattern for potassium.
Table 7.3. Nutrient uptake efficiency (mg nutrient absorbed per g root biomass) of different species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Nitrogen</th>
<th>Phosphorus</th>
<th>Potassium</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. odoratum</td>
<td>71.02</td>
<td>9.21</td>
<td>72.40</td>
</tr>
<tr>
<td>G. elastica</td>
<td>30.80</td>
<td>6.51</td>
<td>35.00</td>
</tr>
<tr>
<td>T. cylindrica</td>
<td>125.70</td>
<td>15.02</td>
<td>156.12</td>
</tr>
<tr>
<td>T. maxima</td>
<td>68.60</td>
<td>8.20</td>
<td>80.06</td>
</tr>
<tr>
<td>L.S.D. (P = 0.05)</td>
<td>8.90</td>
<td>2.02</td>
<td>12.10</td>
</tr>
</tbody>
</table>
Nutrient uptake efficiency of all the nutrients was maximum for *I. cylindrica* and least for *G. elastica* whereas *E. odoratum* and *T. maxima* fell in between with no significant differences between themselves (Table 7.3).

**DISCUSSION**

The adaptation of any weedy species coming after slash and burn of a forested ecosystem should be to capitalise upon the resources of an enriched substratum and make adequate growth as early as possible. The species under consideration here are of two types: (i) coming up exclusively through sprouts as in *G. elastica*, *T. maxima* and *I. cylindrica* and (ii) coming up through seeds at least in the initial stages of secondary succession immediately after slash and burn as in *E. odoratum*. It may be noted here that this species may also regenerate through root sprouts in old fallows or under very low intensity burn but not under the high intensity burn, as is the case in this study. The fast growing ability of *E. odoratum* seems to be an adaptive trait which has evolved in the absence of any stored reserve at the time of seedling regeneration. On the other hand, the disadvantage of comparatively slow growth rate in the others may be compensated for to some extent at least, by high initial reserves stored in their underground organs and transported for shoot growth (Schiar and Zasda 1973). The transfer of the underground reserves for the shoot growth was evident from
an initial decline in belowground allocation in *T. maxima* and *G. elastica*. However, such a prominent initial decline could not be observed in *I. cylindrica*. This may be due to rapid growth and multiplication of the underground rhizome, simultaneously with translocation for shoot growth.

Due to the preferential allocation of the available resources to the underground organs of regeneration, sprouting species are expected to have lower sexual reproductive effort as compared to non-sprouters (Keeley and Keeley 1977). Thus, *T. maxima* had much lower allocation of biomass and nutrients (except potassium which usually is of less importance compared to nitrogen and phosphorus) than *E. odoratum*. *I. cylindrica* and *G. elastica* could not even flower in the first post-fire year. Gill (1975) also reported a similar behaviour for a number of post-fire shrubs. Such a difference between the sprouting and non-sprouting strategy supports the prediction of Wilson (1971) that reproduction will seldom be attempted when on the average it fails.

Plants with *C*₄ photosynthetic pathway are assumed to have faster growth rates and therefore, more productive than those with *C*₃ photosynthetic pathway. The biochemical basis of this assumption is the comparatively more efficient fixation of carbon dioxide in *C*₄ species (Black, Chen and Brown 1969; Black 1971). In contrast to this, *E. odoratum* with *C*₃ leaf anatomy had much higher relative growth and net assimilation rates than *T. maxima* and *I. cylindrica*, with
C₄ leaf anatomy. Similar findings were reported by Warren Wilson (1967). High growth and assimilation rates in this C₃ species may be accounted as due to its high leaf area ratio which expresses the proportion of photosynthetic surface to respiratory mass. Buell (1971); Caldwell (1974) and Hofstra and Stienstra (1977) also emphasized the importance of light interception surface rather than the photosynthetic rate per unit area for comparing the productive potential of C₃ and C₄ plants. It may be worth mentioning here the conclusion drawn by Gifford (1974) that the large potential advantage of the C₄ species is progressively attenuated while moving from microscopic to macroscopic parameters and there remains even no apparent difference between the two photosynthetic pathways at the level of crop growth rate. Photosynthetic rate is often positively correlated with the leaf nitrogen concentration over a broad range because major portion of the leaf nitrogen is directly involved in photosynthesis as a component of photosynthetic enzymes and chlorophyll (Murata 1969; Brady 1973; Natr 1975). Higher efficiency of dry matter production in *E. odoratum* as compared to *G. elastica*, though both of these C₃ species have almost same leaf area ratio, may be associated with the much higher concentration of nutrients in the former.

Both the C₄ species *T. maxima* and *I. cylindrica* had significantly higher efficiency of nutrient utilization than the C₃ ones, *E. odoratum* and *G. elastica* as also reported
elsewhere (Brown 1978). Because of the high cost of nutrients for dry matter production (i.e. low nutrient use efficiency), *E. odoratum* and *G. elastica* would be expected to have higher nutrient absorption capacity than *T. maxima* and *I. cylindrica*. Interestingly enough, *I. cylindrica* with maximum nutrient use efficiency showed maximum uptake efficiency also. *T. maxima* showed the values nearly equal to that of *E. odoratum*, though the former was significantly more efficient in the utilization of nutrients. The higher nutrient uptake efficiency observed in these *C₄* species, in spite of their low nutrient demand, may be associated with the evolution of *C₄* strategy under stressful environments (Black 1971; Brown 1978) where efficient nutrient uptake is of prime importance.
SUMMARY

Growth and allocation pattern of four important perennial weeds viz. Eupatorium odoratum, Grewia elastica, Thysanolaena maxima and Imperata cylindrica were analysed. *E. odoratum* a C₃ species and dependent upon sexual mode of reproduction had maximum relative growth rate and net assimilation rate. This species also showed maximum concentration of nutrients in the leaf tissue. *E. odoratum* allocated a higher proportion of its total biomass as well as nutrients to the stem than in the other three. Sprouting species while the reverse was true for the leaf component. The two rhizomatous species *I. cylindrica* and *T. maxima* exhibited significantly higher allocation of resources to the belowground compartments compared to the non-rhizomatous species. The C₄ species *I. cylindrica* and *T. maxima* showed higher nutrient uptake efficiency in spite of their low nutrient demand for dry matter production compared to C₃ species *E. odoratum* and *G. elastica*.

Findings are discussed in relation to photosynthetic and regenerative strategies of these species.
CHAPTER VIII

GROWTH AND ALLOCATION PATTERN OF EUPATORIUM ODORATUM IN THE SECONDARY SUCCESSIONAL ENVIRONMENTS FOLLOWING SLASH AND BURN AGRICULTURE
INTRODUCTION

Partitioning of the available resources for various life activities such as maintenance, growth and reproduction is important from the ecological as well as evolutionary histories of plants (MacArthur and Wilson 1967; Harper and Ogden 1970; Gadgil and Solbrig 1972; Abrahamson and Gadgil 1973; Anderson and Loucks 1973; Abrahamson 1975a,b; Hickman 1975; Pitelka 1977; Bazzaz 1979). While the resource budget of plants may be limited by a number of limiting factors such as water, photosynthates and nutrients, most of the studies on allocation pattern are concerned with biomass or energy. Little attention has been given to the allocation of nutrients (Van-Andel and Vera 1977; Williams and Bell 1981), which may be equally important particularly in situations with a limited supply (Harper and Ogden 1970).

*Eupatorium odoratum* L. (Asteraceae) is an important early successional herbaceous perennial species with deciduous type of growth habit, in the abandoned fields subsequent to slash and burn agriculture in north-eastern India. The plants make their vegetative growth during rainy season (May to October), after which the flowering is initiated. Seed germination and its establishment through seedlings also occur at this time. While the population dynamics and flux of this species in seral environments have been discussed by Kushwaha, Ramakrishnan and Tripathi (1981), the present study concerns, itself, with growth and resource (biomass and nutrients) allocation pattern.
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 gniess, schists and granites. The soil is red sandy loam and of laterite origin. The pH ranges from 5 to 7. The angle of slopes generally range 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 and minimum temperatures are 33°C and 7°C respectively.

The tribal population of north-eastern hill region of India practise shifting agriculture which involves slash and burn of developing communities followed by mixed cropping at least for one year (Ramakrishnan et al. 1981); this whole process is locally referred to as 'Jhum'. After cultivation, the site is left abandoned for fallow development and is again cultivated after a few years. This cycle was fairly long ranging from 20 - 30 years; however, under present conditions of higher human population pressure and reduced acreage the cycle is often as short as 4-5 years. Eupatorium odoratum is an important early
successional species up to about 5-6 years of fallow development along with many other weedy species. However, in some of these fallows, Imperata cylindrica Beav. var. major may dominate due to its rapid multiplication vegetatively.

METHODS OF STUDY

Three fresh fallows (0 year) and one each of 2 years and 6 years age were selected for the purpose of the present study. Amongst the three fresh fallows, two were abandoned immediately after the burn. Of these two, one was a 20 year old field dominated by Dendrocalamus hamiltonii and the other was a 6 year old one dominated by Imperata cylindrica at the pre-burn stage (henceforth referred as F_1 and F_2 respectively). The third fresh fallow was one, where cropping was done for one year and then abandoned, but had a 20 year old community at the pre-burn stage (henceforth referred as F_3).

Three randomly placed quadrats (50 cm x 50 cm) in each site were harvested for Eupatorium odoratum at monthly intervals during the entire growing season starting from June, 1978 to January, 1979. Care was taken to include individuals derived from seeds only. In the fresh fallows (F_1, F_2, F_3), E. odoratum established through seedlings in May 1978 whereas the individuals considered in the older
fallow of 2 and 6 years were of that age. Below ground parts were carefully washed and the plants were separated into different compartments like root, stem, leaf, etc. The pedicels of inflorescence were included in the stem component. Fruits of *E. odoratum* are achenes, which are the ecological equivalents of seeds. Fruit biomass, thus, equals seed biomass (Harper, Lovell and Moore 1970). The fallen leaves and seeds were also included following Hickman (1975). The different components were dried at 80 ± 5°C for 48 hours and weighed. Leaf area estimations using a planimeter and leaf dry weight per unit area were based on three replicates and 50 leaves per replicate. Total leaf area per plant was computed using leaf biomass and leaf dry weight per unit area.

The growth functions: relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) (Hughes and Freeman 1967; Radford 1967) were calculated as:

\[
RGR = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}
\]

\[
NAR = \frac{(W_2 - W_1) (\ln A_2 - \ln A_1)}{(A_2 - A_1) (t_2 - t_1)}
\]

\[
LAR = \frac{(A_2 - A_1) (\ln W_2 - \ln W_1)}{(\ln A_2 - \ln A_1) (t_2 - t_1)}
\]

where \( W_1 \) and \( A_1 \) are the biomass per plant and leaf area per
plant respectively at time $t_1$ and $W_2$, $A_2$ are the same at time $t_2$.

The concentration of nutrients in different plant parts were determined following standard methods given in Allen (1974). Thus, nitrogen was analysed by micro-Kjeldahl method; phosphorus by molybdenum-blue method and potassium by flame photometry, after dry ashing.

Nutrient uptake efficiency was calculated as mg nutrient absorbed per g root biomass following Blair and Cordero (1978).

**RESULTS**

Fig. 8.1 shows the increment in biomass/plant in different fallows. In all the cases, accumulation of biomass took place up to the month of October, but was very pronounced in $F_1$ and $F_3$ fallows only compared to others. Significant differences in the biomass values between different fallows were observed and it was in the order 6 years $>$ 2 years $>$ $F_1$ $>$ $F_3$ $>$ $F_2$. However, there was no significant difference between the individual biomass in $F_1$ and 2 year old fallow, towards the end of the growing season. The plants in 2 and 6 year old fallows were of that age and therefore had a high biomass initially.

Leaf area increase also continued up to the month
Fig.8.1 Growth curves of *Eupatorium odoratum* in different fallows. Fresh fallows - F1, (●); F2, (□); F3, (○); 2 year old fallows, (▲); 6 year old fallow, (△). Vertical bars represent least significant difference at 0.005P.
Fig. 8.1

Leaf area (cm²/plant) vs. time period (months).

Biomass (g/plant).
Fig. 8.2. Nutrient accumulation in *Eupatorium odoratum* during growth in different fallows. Fresh fallows - F1, (●); F2, (◇); F3, (○); 2 year old fallow, (▲); 6 year old fallow (▲). Vertical bars represent least significant different at 0.005 P.
Fig. 8.2

Graphs showing the changes in phosphorus, nitrogen, and potassium levels over time periods (months).
Fig. 8.3  Nutrient concentration in the whole plant of *Eupatorium odoratum* during growth in different fallows. Fresh fallows - F₁, (●); F₂, (□); F₃, (○); 2 year old fallow, (▲); 6 year old fallow, (△). Vertical bars represent least significant difference at 0.005P.
of October in all the cases, except for F₂ and F₃ fallows where a slight increment occurred in the month of November also. It declined sharply in the months of December and January due to rapid leaf fall during this period. Leaf area in different fallows at the peak period was also in the same order as for biomass (Fig. 8.1).

Nutrient accumulation followed a pattern nearly similar to that of the biomass. Significant differences were also found in the quantity of nutrients/plant between different fallows. This varied depending upon the nutrient under consideration. While the amount of nitroten/plant was significantly higher in the 6 year old fallow than that in 2 year old one, the quantity of phosphorus/plant was higher during the early period of growth only. Potassium/plant was significantly higher in the 2 year old fallow than that in the 3 year old one only in the initial stages. The individuals of E. odoratum in F₁ fallow absorbed nutrients at such a fast rate that nitrogen and phosphorus/plant here equalled to that of 6 years and that of potassium was much higher in the F₁ towards the end of the growing season (Fig.8.2).

Fig. 8.3 shows the changes in nutrient concentration in the whole plant during growth in different fallows. A sharp decline during the early part of the growing season was observed for all the nutrients in the fresh fallows only. Further, the fresh fallows had always significantly higher concentration of nitrogen and potassium than older
ones, the differences being more pronounced for potassium whereas phosphorus concentration was significantly higher in the early part of the growth only. Amongst the fresh fallows, concentration of nitrogen and phosphorus was higher in F₁ fallow as compared to F₃, the differences being more pronounced in the later part of the growth whereas no such difference was noted for potassium concentration. 2 year old fallow always exhibited significantly higher nutrient concentration as compared to 6 year old one and the differences were more marked for phosphorus and potassium than for nitrogen (Fig.8.3).

Nutrient uptake efficiency was significantly higher in the fresh fallows compared to older ones for all the three nutrients (Table 8.1).

In general fresh fallows had higher values for all growth functions as compared to older fallows, the 6 year fallow giving the least values. Amongst the three fresh fallows F₂ fallow had significantly lower values of RGR and NAR but higher LAR compared to F₁ and F₃ (Table 8.2).

Fig.8.4 shows the allocation pattern of biomass and nutrients in different compartments, expressed as the percentage of the total capital. In the pattern of allocation of biomass and nutrients for different components, clear cut differences were observed between the fresh fallows and the older fallows of 2 and 6 years. In the former a
Table 8.1. Nutrient uptake efficiency (mg nutrient absorbed per g root biomass) of *Eupatorium odoratum* in different fallows.

<table>
<thead>
<tr>
<th>Fallows</th>
<th>Nitrogen</th>
<th>Nutrient uptake efficiency</th>
<th>Potassium</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Nitrogen</td>
<td>Phosphorus</td>
</tr>
<tr>
<td><strong>F₁</strong></td>
<td>71.02</td>
<td>9.21</td>
<td>72.40</td>
</tr>
<tr>
<td><strong>F₂</strong></td>
<td>60.62</td>
<td>9.02</td>
<td>82.40</td>
</tr>
<tr>
<td><strong>F₃</strong></td>
<td>57.60</td>
<td>6.30</td>
<td>70.80</td>
</tr>
<tr>
<td>2 year</td>
<td>1.82</td>
<td>1.30</td>
<td>5.74</td>
</tr>
<tr>
<td>6 year</td>
<td>1.40</td>
<td>0.72</td>
<td>4.70</td>
</tr>
<tr>
<td>L.S.D. (P = 0.01)</td>
<td>8.40</td>
<td>2.04</td>
<td>10.20</td>
</tr>
</tbody>
</table>
Table 8.2. Mean values (± S.E.M.) of growth functions of *E. odoratum* in different fallsows.

<table>
<thead>
<tr>
<th>Follows</th>
<th>Growth functions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>RGR ( \text{mg mg}^{-1} \text{d}^{-1} )</td>
</tr>
<tr>
<td>F₁</td>
<td>0.0359 ± 0.0154</td>
</tr>
<tr>
<td>F₂</td>
<td>0.0246 ± 0.0053</td>
</tr>
<tr>
<td>F₃</td>
<td>0.0350 ± 0.0151</td>
</tr>
<tr>
<td>2 year</td>
<td>0.0016 ± 0.0007</td>
</tr>
<tr>
<td>6 year</td>
<td>0.0008 ± 0.0004</td>
</tr>
</tbody>
</table>
Fig. 8.4 (a-d) Allocation of biomass and nutrients to different compartments (expressed as percentage of the total capital) during the growth of *Eupatorium odoratum* in different fallows. a, allocation of biomass; b, allocation of nitrogen; c, allocation of phosphorus; d, allocation of phosphorus.
Fig. 8.4: Allocation of biomass

- Seed
- Leaf
- Stem
- Root

% Total biomass vs. % Total biomass

6 year
2 year
Fig. 8.4 C

Allocation of Phosphorus

- Seed
- Leaf
- Stem
- Root

% Total Phosphorus

- F1
- F2
- F3

2 year
6 year
Fig. 8.4 d

ALLOCATION OF POTASSIUM

Seed
Leaf
Stem
Root

% Total Potassium

100 50 0

100 50 0

2 year

6 year
significant and continuous increase in allocation to root was noted throughout the period of observations whereas in the latter two fallows, there was an initial decline followed by an increase in subsequent months. The proportion allocated to stem increased significantly with the passage of time only in the case of fresh fallows while that for the leaves declined. No such clear cut pattern could be observed for older fallows. Comparing the allocation to different organs, it was found that this was more to the stem in the older fallows compared to that in the fresh ones and the reverse was the case for the leaf component. Comparing 2 and 6 year old fallows, it was found that the proportion of potassium in the root component was significantly higher in the latter compared to the former. The seed allocation was in the order of \( F_1 = F_3 > 2 \text{ year} > 6 \text{ year} > F_2 \). Further, in all the fallows, a substantially higher fraction of nitrogen and phosphorus than that of biomass was allocated to seed while the reverse was true for potassium. All the differences are significant at 0.01 \( \text{P (ANOVA)} \).

Reproductive effort, if considered as a percentage of current dry matter production or nutrients absorbed and then allocated to the seed component, a different pattern was noticed where older fallows of 2 and 6 years showed much higher values than the fresh ones. Amongst the fresh fallows, \( F_2 \) had markedly low reproductive effort compared to \( F_1 \) and \( F_3 \) (Table 8.3).
Table 8.3. Reproductive effort (allocation to seed as % of current dry matter production or nutrient uptake) of *E. odoratum* in different fallows.

<table>
<thead>
<tr>
<th>Fallows</th>
<th>Biomass</th>
<th>Reproductive Effort</th>
<th>Nitrogen</th>
<th>Phosphorus</th>
<th>Potassium</th>
</tr>
</thead>
<tbody>
<tr>
<td>F1</td>
<td>11.87</td>
<td></td>
<td>26.63</td>
<td>17.28</td>
<td>2.26</td>
</tr>
<tr>
<td>F2</td>
<td>1.47</td>
<td></td>
<td>2.65</td>
<td>2.15</td>
<td>0.19</td>
</tr>
<tr>
<td>F3</td>
<td>11.75</td>
<td></td>
<td>23.22</td>
<td>23.40</td>
<td>2.08</td>
</tr>
<tr>
<td>2 year</td>
<td>34.65</td>
<td></td>
<td>472.38</td>
<td>69.33</td>
<td>25.97</td>
</tr>
<tr>
<td>6 year</td>
<td>46.82</td>
<td></td>
<td>427.67</td>
<td>100.22</td>
<td>13.91</td>
</tr>
<tr>
<td>L.S.D. (P = 0.01)</td>
<td>4.21</td>
<td></td>
<td>11.56</td>
<td>15.20</td>
<td>6.45</td>
</tr>
</tbody>
</table>
DISCUSSION

Higher proportion of the available resources allocated to stem but lower proportion to leaf component was allocated in the older fallows as compared to the fresh ones, since the plants tended to grow taller and avoid shade in older fallows where light could be a limiting factor. On the other hand, allocation to seed was higher in the fresh fallows ($F_1$, $F_3$) than in the older ones. Similar shifts in the allocation pattern have been reported by a number of workers (Abrahamson and Gadgil 1973; Caines et al. 1974; Roos and Quinn 1977).

It has been shown for the colonizing species that vegetative reproductive effort is more plastic towards various environmental stresses (Ogden 1974; Thomas 1974; Abrahamson 1975a,b), while sexual reproductive effort according to them, remains nearly fixed regardless of the stress. While, such a type of strategy may operate in the perennials studied by these workers because of both sexual and vegetative multiplication alternatives available to such species, it may not be equally applicable for species exclusively dependent upon sexual mode of population expansion like the present species where significant reduction in sexual reproductive effort also occurred in the more stressful environments of older fallows.

Quantification of reproductive effort in perennials is problematic because, here, production of the previous years is added to that of the next year (Ogden 1974;
Hickman 1975; Kawano and Nagai 1975). It may be worth noting here that in the field studies, sexual reproductive effort in perennials has been always taken as the proportion of existing biomass or 'new growth' (in the cases where current growth is easily distinguished from the old growth e.g. overwintering of shoot every year) devoted for sexual reproduction and the importance of underground organs (Mooney and Billings 1960; Bradbury 1973; Jefford and Edelman 1973) is often ignored. Reproductive effort, if considered as the proportion of current gain of photosynthates or nutrients (net reproductive effort of Harper and Ogden (1970) i.e. ratio of propagule biomass and net production), was much higher in the older communities of 2 and 6 years than that in the fresh ones, suggesting that high seed production is maintained at the expense of vegetative development. It was interesting to observe that the quantity of nutrients devoted for sexual reproduction was much higher than the current uptake in the older fallows as compared to the fresh ones (nitrogen in 2 year old fallow and both of nitrogen and phosphorus in 6 year old fallow) indicating the extreme ruderal behaviour of this species. A number of experimental studies have shown the tendency of ruderals to sustain production of propagules when subjected to severe stress (Hodgson and Blackman 1956; Bunting 1956; Hickman 1975; Raynal and Bazzaz 1977; Van Andel and Vera 1977; Foulds 1978).

The lower nutrient uptake efficiency observed in
the older fallows may be accounted partly as due to losses from the system (Toky and Ramakrishnan 1981) and partly due to rapid absorption by pre-existing vegetation (Ramakrishnan and Toky 1981). The low accumulation capacity of potassium in older fallows compared to younger ones and the related meagre allocation of this element to seed component and its accumulation in the perennating organs may be an adaptive strategy to conserve this nutrient within the plant.

The nutrient stress in older fallows may be partly responsible for reduced growth rate and assimilation rate compared to the fresh fallows apart from competition. This has been reported by Grime (1977,1979), though no systematic studies have been done under successional environments.

The quantity of available nutrients is increased immediately after the burn. However, during the cropping period subsequent to burn, tremendous losses of nutrients occur through run-off and percolation due to heavy rainfall and the absence of adequate plant cover, resulting in a drastic reduction in the soil fertility (Ramakrishnan et al 1980; Ramakrishnan and Toky 1981) Such a lowering of soil fertility may be responsible for the reduced dry matter production and nutrient accumulation in the F_3 fallow as compared to F_1. However, no significant differences were observed between these two fresh fallows with respect to the allocation pattern. Ettershank et al (1978) also showed similar findings in *Larrea tridentata* where reproductive
allocation remained constant, though the species responded positively to high levels of nitrogen.

Species which establish through sprouts following fire like Imperata cylindrica have been shown to have immediate competitive advantage over the species coming through seedlings like E. odoratum (Keeley and Keeley 1977). In F2 fallow, E. odoratum exhibited much reduced growth probably because of the competitive superiority of I. cylindrica and, therefore, the limited available resources were utilized for the vegetative growth at the cost of reduced reproductive potential.

Thus, stresses of different nature and magnitudes, partly nutritional (Ramakrishnan and Toky 1981), partly competitive and partly increased shade (Kushwaha, Ramakrishnan and Tripathi 1981) as secondary succession progresses results in gradual replacement of E. odoratum after 5-6 years of fallow development (Ramakrishnan and Toky 1978; Ramakrishnan et al. 1981).
SUMMARY

Growth and resource partitioning of *Eupatorium odoratum*, an important early successional species were studied in the seral environments following slash and burn. Growth rates and nutrient uptake efficiency declined with the increasing age of the fallow. Concentration of potassium in the whole plant was much lower in older fallows as compared to fresh ones, while no such clear cut and marked differences were observed for nitrogen and phosphorus. Higher proportion of the available resources was allocated to stem but lower proportion to leaf compartment was allocated in older fallows compared to fresh ones. On the other hand, allocation to seed was higher in younger fallows than older ones. Reproductive effort, if considered as proportion of current increment in biomass or nutrients absorbed was much higher in older fallows compared to fresh ones. Growth was adversely affected by low soil fertility and severe competitive interference in the fresh fallows. Further, while the allocation pattern was not affected by reduced soil fertility; under the competitive environment, the limited resources were utilized for vegetative development at the cost of reduced reproductive potential. Adaptive strategy of this species is discussed.
CHAPTER IX

GROWTH STRATEGY AND ALLOCATION PATTERN
OF EUPATORIUM ODORAM AND IMPERATA
CYLINDRICA AT DIFFERENT FERTILITY
LEVELS OF SOIL

*****************************************************************************
INTRODUCTION

Rapid growth and multiplication are two important features of colonizing species (Gomez-Fompa 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 are available on 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 and Ogden 1970; Ogden 1974; Abrahamson 1975a,b; Hawthorn and Cavers 1977; Pitelka et al. 1977; Bell 1979). However, only recently attention is being given to the allocation pattern of nutrients (Andel and Vera 1977; Williams and Bell 1984) which may be equally important particularly in situations with a limited supply (Harper and 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 C4 photosynthetic pathway (Black 1971; 1973). However, the ecological implications of this photosynthetic strategy has been questioned by a number of workers (Bull 1971; Graford 1974; Baskin and 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. 1980). The former species is a C₃ plant exclusively dependent upon sexual reproductive strategy, while the latter is a C₄ 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 pre cambrian rocks are represented by gniess, schists and granites. The soil is red sandy loam and of laterite origin. The pH ranges from 5 to 7. The angle of slopes generally range 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 and minimum temperatures are 33°C and 7°C respectively.
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: (1) soil-sand mixture (1:1 volume) (ii) soil-sand mixture (2:1 volume) (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. 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 ± 5°C for 48 hours 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). Five replicates were done for all the treatments.

Nutrient concentration in different components was determined following standard methods as described by Allen (1974). Thus, nitrogen was analysed by micro-Kjeldahl method; phosphorus by molybdenum-blue method and potassium by flame photometry after dry ashing.

Nutrient uptake efficiency was calculated as mg
Fig. 9.1 Mean dry weight per pot of *E. odoratum* and *I. cylindrica* grown at three 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.
Fig. 9.1
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

Mean dry matter production given in Fig. 9-1 shows that at all the three fertility levels, \textit{E. odoratum} had better growth yield over \textit{I. cylindrica} in all harvests ($P < 0.01$) and this became more pronounced during the later harvests. Further, while marked increase in growth was observed between 180 days and 240 days in the case of \textit{E. odoratum}, it was significant in the case of \textit{I. cylindrica}. Biomass increased significantly ($P < 0.01$) with increase in the fertility level of the soil in the case of both the species, though this was more pronounced for \textit{E. odoratum} as compared to \textit{I. cylindrica}.

Allocation pattern of biomass and nutrients expressed as percentage of the total pool is shown in Fig. 9-2. A significant decline ($P < 0.05$) in the allocation to root was found in \textit{E. odoratum} at the beginning of sexual reproductive growth; followed by an increase towards the end of growth period. However, this decline was more pronounced at lower fertility levels while the increase was more conspicuous at higher fertility levels. \textit{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.
Fig. 9.2 (a-d) 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 are the harvests at different times during growth as given in Fig. 10.1).
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 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 the allocation to the stem, both in terms of biomass and nutrients, was noted.

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 towards the end of growth period.

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
Table 3.1. Nutrient efficiency (mg nutrient absorbed per g root biomass) of *E. odoratum* and *I. cylindrica* at different fertility levels.

<table>
<thead>
<tr>
<th>Nutrient uptake Efficiency</th>
<th>I</th>
<th>II</th>
<th>III</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. odoratum</em></td>
<td>41.40</td>
<td>57.02</td>
<td>74.88</td>
</tr>
<tr>
<td><em>I. cylindrica</em></td>
<td>54.23</td>
<td>71.61</td>
<td>115.77</td>
</tr>
<tr>
<td>Level of significance</td>
<td>P&lt;0.05</td>
<td>P&lt;0.05</td>
<td>P&lt;0.05</td>
</tr>
<tr>
<td>Phosphorus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. odoratum</em></td>
<td>5.31</td>
<td>6.63</td>
<td>9.25</td>
</tr>
<tr>
<td><em>I. cylindrica</em></td>
<td>7.26</td>
<td>11.87</td>
<td>18.77</td>
</tr>
<tr>
<td>Level of significance</td>
<td>P&lt;0.05</td>
<td>P&lt;0.05</td>
<td>P&lt;0.05</td>
</tr>
<tr>
<td>Potassium</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. odoratum</em></td>
<td>32.60</td>
<td>44.49</td>
<td>51.77</td>
</tr>
<tr>
<td><em>I. cylindrica</em></td>
<td>39.60</td>
<td>56.12</td>
<td>89.27</td>
</tr>
<tr>
<td>Level of significance</td>
<td>P&lt;0.05</td>
<td>P&lt;0.05</td>
<td>P&lt;0.05</td>
</tr>
</tbody>
</table>
Table 9.2. Nutrient use efficiency (mg dry matter production per mg nutrient absorbed) of *S. odoratum* and *I. cylindrica* at different fertility levels.

<table>
<thead>
<tr>
<th>Nutrient use efficiency</th>
<th>I</th>
<th>Fertility levels</th>
<th>III</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. odoratum</em></td>
<td>101.47</td>
<td>86.60</td>
<td>78.65</td>
</tr>
<tr>
<td><em>I. cylindrica</em></td>
<td>151.81</td>
<td>135.11</td>
<td>124.77</td>
</tr>
<tr>
<td>Level of significance</td>
<td>P&lt;0.01</td>
<td>P&lt;0.01</td>
<td>P&lt;0.01</td>
</tr>
<tr>
<td>Phosphorus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. odoratum</em></td>
<td>790.80</td>
<td>744.76</td>
<td>636.91</td>
</tr>
<tr>
<td><em>I. cylindrica</em></td>
<td>858.97</td>
<td>815.15</td>
<td>769.49</td>
</tr>
<tr>
<td>Level of significance</td>
<td>P&lt;0.01</td>
<td>P&lt;0.01</td>
<td>P&lt;0.01</td>
</tr>
<tr>
<td>Potassium</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. odoratum</em></td>
<td>118.03</td>
<td>116.10</td>
<td>113.70</td>
</tr>
<tr>
<td><em>I. cylindrica</em></td>
<td>162.88</td>
<td>164.11</td>
<td>162.14</td>
</tr>
<tr>
<td>Level of significance</td>
<td>P&lt;0.01</td>
<td>P&lt;0.01</td>
<td>P&lt;0.01</td>
</tr>
</tbody>
</table>
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 9.1).

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 9.2).

DISCUSSION

It has been often shown that vegetative reproductive effort of the colonizing species is more plastic towards various environmental stresses while sexual reproductive allocation remains nearly fixed in terms of percentage allocation regardless of the stress (Harper and 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 *R. 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 cascadense* 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 and Vera 1977; Austin and Blackwell 1979; Williams and Bell 1981).

Based chiefly upon the physiological studies under manipulated environments, the speculation has often been advanced that plants with C₄ photosynthetic pathway should be more productive than those having C₃ pathway (Black et al 1969; Black 1971). However, in the present case *R. odoratum* which is a C₃ plant accumulated significantly higher dry matter throughout its growth and at all fertility levels as compared to a C₄ plant like *I. cylindrica*, suggesting thereby that C₄ strategy may not be essentially superior to C₃ strategy (Wilson 1967; Slatyer 1970, 1971; Mooney et al 1976; Baskin and Baskin 1978). In an earlier study (Chapter VII) 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 the cases of other species.

Though low nutrient uptake efficiency observed at low fertility levels may be related to decreased availability of nutrients (Blair and Cordero 1978), both the species tended to compensate it through increased proportional allocation of biomass to the root system (Andel and Vera 1977; Bell 1979) and more efficient use of nitrogen and phosphorus, which are critical elements like the higher nutrient uptake and use efficiency of I. cylindrica (C₄) as compared to E. odoratum may be associated with the evolution of C₄ 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 to be 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.
SUMMARY

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.
SECTION C
NITROGEN MINERALIZATION

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CHAPTER X

RATE OF NITRIFICATION DURING SECONDARY SUCCESSION SUBSEQUENT TO SLASH AND BURN AGRICULTURE
INTRODUCTION

Nitrogen is the most important and often a limiting element in the terrestrial communities chiefly due to its extremely dynamic nature (Woodmansee 1978). Plants take up this nutrient in the form of NO$_3^-$ - N and NH$_4^+$ - N depending upon their genotypic make up and also on the prevailing ecological conditions (Epstein 1972; Haynes 1977; Haynes and Goh 1978).

A number of studies are available on the production of NO$_3^-$ - N in soil and its consequences under varying ecological conditions to evaluate the prediction of Odum (1969) that nutrient conservation efficiency is improved during vegetation succession. Rice and Pancholy (1972) showed that nitrification rate is drastically reduced in climax forest communities as compared to developing ones in Oklahoma and this was attributed to a variety of tannins and their derivatives inhibiting the growth and activity of the nitrifiers (Rice and Pancholy 1973; Lodhi 1974; Lodhi 1977). Similar patterns during vegetation development have been reported elsewhere also (Heiklejohn 1962; Robinson 1963; Levingston and Allensson 1963; Todd et al. 1975; Nakos 1977). However a number of diversions from such a normal pattern of nitrogen mineralization due to allelopathic chemical have also been demonstrated and the process has been found to be influenced by a number of other ecological factors like pH, soil phosphorus level and availability of NH$_4^+$ - N (Ellis 1974; Leak and Martin 1975; Vitousek and Reiners 1975; Johnson and Edwards 1979; Lamb 1980).
Fire is a tool utilized by the tribal population of north-eastern India for shifting agriculture, locally referred to as 'Jhum'. The pattern of nitrogen mineralization during cropping and natural succession is of prime importance in view of the intense rainfall and high potential for nutrient losses through leaching and run-off in the prevailing ecological conditions (Ramakrishnan et al. 1980; Toky and Ramakrishnan 1981). The present study analyses the nitrification process as affected during slash and burn agriculture and subsequent secondary succession in the jhum fallows and is related to a number of chemical characteristics of the soil.

STUDY AREA AND CLIMATE

The study was carried out in Darynhat 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 pH ranges from 5 to 7. The angle of slopes generally range 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 and minimum temperatures are 33°C and 7°C respectively.

METHODS OF STUDY

Three fresh fallows under a 4, 6 and 10 year Jhum cycles, which were slashed in the month of December, 1978 and freshly burnt in March, 1979 and three seral communities of 1, 3 and 20 year age (three replicates) were selected for the purpose of the present study. Under the three cycles, cropping was done for only one year, after which they were fallowed. The sites were identified on the basis of the local records of land use pattern. Soil samples from 0-10 cm horizon were collected 15 and 30 days before and after the burn. Subsequent sampling was done at monthly intervals between April and December. Simultaneously, sampling from the same horizon was also done from all the successional communities. Ten randomly collected soil samples were thoroughly mixed to give one composite sample after removing undecomposed litter. 150 g soil from each site was incubated at 30 ± 2°C and nitrification rate was measured as the amount of \( \text{NO}_3^- - N \) after 6 days of incubation. The moisture content in the soil during incubation was maintained at 75% of the water holding capacity.

Soil samples were also analysed for various chemical characteristics (Jackson 1967; Allen 1974). Thus, \( \text{NO}_3^- - N \) was analysed by phenol di sulphonic acid method, \( \text{NH}_4^+ - N \) by indophenol blue method, organic matter by
Walkley-Black method, available phosphorus by molybdenum blue method using Bray's extraction solution. pH was measured in a soil:water suspension (1:5) by a digital pH meter.

The effect of the additional supply of $\text{NH}_4^+ - \text{N}$ and organic matter was studied in the soil collected in the month of December/January at the end of the cropping period. The soil was mixed with ammonium sulphate or leaf powder of three species viz. *Eupatorium odoratum* L., *Aggeratum co-nyzoides* L., *Borreria articularis* (L.f.) Will. separately (30 ml of 0.01M ammonium sulphate or 2 g leaf powder per 150 g soil). Controls were supplied with distilled water only and moisture content was finally maintained at 75% of the water holding capacity in all the cases. Degree of nitrification was measured as the increase in $\text{NO}_3^- - \text{N}$ concentration after 8, 16, 24 and 32 days of incubation.

RESULTS

Rate of nitrification increased sharply after slashing the vegetation but declined soon after the burn up to the month of May. A gradual increase occurred in subsequent months reaching a maximum in September, again followed by a decrease in the following months up to December. Amongst the three cropped sites, nitrification rate was maximum under a 4 year cycle and minimum under a 10 year cycle. The differences were marked during the two peak periods of nitrification than at other times. The pattern of nitrification rate during the
Fig. 10.1 Temporal variation in the rate of nitrification in the Jhum sites and fallows of secondary succession subsequent to cropping. A, site under cropping; B, fallows. Time-period (days) before (-) and after the burn at different samplings is given additionally in case of the sites under cropping. '0' represents the day of the burn.
Fig. 10.1

A. 4 yr. Jhum cycle
   △ 6 yr. " "
   □ 10 yr. " "

B. △ 1 yr. fallow
   ○ 3 yr. " "
   □ 20 yr. " "

Nitrification rate (ppm/6 days)

Time period
Fig. 10.2 Temporal variation in the NO$_3^-$ - N concentration of soil in the Jhum sites and fallows of secondary succession subsequent to cropping. (Other details as in Fig. 10.1).
year in the successional communities was very similar to that under slash and burn agriculture except that the second peak was in the month of July. The rate of nitrification was slow for the older fallows but the differences between the fallows were more marked during the period of July to September (Fig.1o.1).

A sharp increase in the $\text{NO}_3^-$ - N concentration following slashing the vegetation and a decline after the burn was found in all the jhum sites. Soon after slashing, $\text{NO}_3^-$ - N concentration was maximum under a 4 year cycle and least under a 10 year cycle. This difference, though not very pronounced, was maintained 15 days after the burn. However, in subsequent months the concentration was least under a 10 year cycle. During cropping, $\text{NO}_3^-$ - N concentration was maintained at a low level in all the cases. $\text{NO}_3^-$ - N concentration in the three jhum fallows did not show as sharp fluctuation as during jhum, though the concentration was more during February to April after which it declined to a low and steady level. 1 year old jhum fallow had higher concentration of $\text{NO}_3^-$ - N whereas a 20 year fallow had the least, a 3 year fallow falling in between the other two (Fig.1o.2).

During jhum there was no marked change in the level of $\text{NH}_4^+$ - N immediately after cutting or burning of the vegetation. During early monsoon, in April-May it peaked followed by a decline reaching a low level in August, again
Fig.10.3 Temporal variation in the $\text{NH}_4^+$ - N concentration of soil in the Jhum sites and fallows of secondary succession subsequent to cropping. (other details as in Fig.10.1).
Fig. 10.4 Temporal variation in the organic matter of soil in the Jhum sites and fallows of secondary succession subsequent to cropping. (Other details as in Figure 10.1).
followed by a subsequent increase. While the peaking in April-May was more pronounced under a 4 year and 6 year jhum cycles, the dip in August was more marked under a 10 year cycle. Concentration of $\text{NH}_4^+$ - N was higher under a 4 year cycle compared to a 10 year cycle where the values were the least (Fig. 10.3). In the fallows, a sharp decline in $\text{NH}_4^+$ - N level was noted in February followed by a sharp increase during March-April which was maintained up to September in the case of 20 year fallow followed by a decline. In 1 and 3 year fallows, however, there was a sharp decline reaching very low concentration in July followed by another peaking in October. A 20 year old fallow had maximum concentration of this nutrient followed by 3 and 1 year fallows, the latter giving the least values (Fig. 10.3).

Under jhum, a continuous decline in the organic matter content was found up to the month of August with a steep decline after the burn. It increased in the month of September and was maintained at this level. The level of organic matter content was maximum under a 10 year cycle and minimum under a 4 year cycle throughout the year, but the differences were more pronounced during the relatively dry months of February-March and September to December (Fig. 10.4). The successional communities also showed nearly a similar pattern in the organic matter content level during the year, with maximum levels for a 20 year fallow and minimum for a 1 year fallow (Fig. 10.4).
Fig.10.5 Temporal variation in the pH of soil in the Jhum sites and fallows of secondary succession subsequent to cropping. (Other details as in Fig.10.1).
Fig. 10.6 Temporal variation in the level of available phosphorus in soil of the Jhume sites and fallows of secondary succession subsequent to cropping. (Other details as in Fig. 10.1)
pH of the soil increased sharply following the burn, under all jhum cycles, peaking during June but declined during July-August. An increase was again observed in the month of September where it was stabilized. Soil pH was always higher under a 10 year cycle followed by 6 year and 4 year cycles (Fig.10.5). In the case of the successional communities it declined gradually during the rainy season and increased during the subsequent relatively dry months. pH in a 20 year fallow was maximum followed by a 3 and 1 year old fallows (Fig.10.5).

The level of available phosphorus declined with the passage of time in all the slash sites under jhum. Under a 10 year cycle available phosphorus concentration was more than under 6 and 4 year cycles (Fig.10.6). The successional communities also exhibited nearly a similar pattern during the year. A 20 year fallow had much higher concentration as compared to the other two (Fig.10.6).

A conspicuous increase in the amount of NO₃⁻ - N produced was found in the soil incubated with ammonium sulphate but the increase was more pronounced in the initial stages. After 24 days of incubation, there were less marked differences in the amount of NO₃⁻-N produced amongst the different sites in the case of additional supply of NH₄⁺ - N while the differences were well marked in the controls. In the case of soils mixed with leaf material of different species, level of NO₃⁻ - N increased more sharply after 24 days.
Table 10.1 Increase in the concentration of $\text{NO}_3^- - N$ (ppm.) during soil incubation mixed with ammonium sulphate on leaf material.

<table>
<thead>
<tr>
<th>Sites and treatments</th>
<th>days of incubation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>8</td>
</tr>
<tr>
<td>Control</td>
<td></td>
</tr>
<tr>
<td>4 year (J)</td>
<td>2.00</td>
</tr>
<tr>
<td>6 year (J)</td>
<td>1.90</td>
</tr>
<tr>
<td>10 year (J)</td>
<td>1.80</td>
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<tr>
<td>1 year (F)</td>
<td>1.98</td>
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<tr>
<td>3 year (F)</td>
<td>1.86</td>
</tr>
<tr>
<td>20 year (F)</td>
<td>1.25</td>
</tr>
<tr>
<td>+ Ammonium sulphate</td>
<td></td>
</tr>
<tr>
<td>4 year (J)</td>
<td>13.36</td>
</tr>
<tr>
<td>6 year (J)</td>
<td>8.98</td>
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<td>10 year (J)</td>
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<td>5.34</td>
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<tr>
<td>20 year (F)</td>
<td>4.62</td>
</tr>
<tr>
<td>+ leaf of Ageratum conyzoides</td>
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</tr>
<tr>
<td>4 year (J)</td>
<td>1.70</td>
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<tr>
<td>6 year (J)</td>
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<td>20 year (F)</td>
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<tr>
<td>+ leaf of Eupatorium odoratum</td>
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<tr>
<td>4 year (J)</td>
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<td>Year</td>
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<tr>
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<tr>
<td>Leaf of Borrella articulatais</td>
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<tr>
<td>4 year (J)</td>
<td>1.80</td>
</tr>
<tr>
<td>6 year (J)</td>
<td>1.90</td>
</tr>
<tr>
<td>10 year (J)</td>
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<td>3.26</td>
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<td>3 year (F)</td>
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<td>20 year (F)</td>
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<td>9.02</td>
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J, Jhum site; F, fallow of secondary succession subsequent to Jhum.
of incubation as compared to that after 8 and 16 days. The concentration was found to be maximum in the soils mixed with *E. odoratum* followed by *A. cor-nyzoides* and *B. articularis*. In the controls and ammonium sulphate mixed soils, maximum nitrification was observed under a 4 year cycle followed by 6 year and 10 year cycles while the reverse trend was obtained in the soils mixed with leaf material. Similarly, for the fallows it was maximum in 1 year fallows followed by 3 year and 20 year fallows in the controls and ammonium sulphate treatment, but the reverse trend was found in the case of soils mixed with leaf powder (Table 10).  

**DISCUSSION**

The possible inhibition of nitrification due to the allelopathic chemicals (Rice and Pancholy 1973, 1974; Lodhi 1977) is expected to be maximum during the comparatively dry period due to higher concentration of these chemicals in a less moist soil. However, maximum nitrification was noted at this time which also happens to be the time of slashing the vegetation. This could be associated with the least competition for ammonium ions offered by the heterotrophs and thereby higher availability of these ions to the nitrifiers. Fire usually stimulates the activity of soil microorganisms because of a more favourable environmental conditions like higher pH, higher soil temperatures, greater availability of nutrients from the ash and moisture due to
reduced vegetational cover (Neal et al. 1965; Ahlgren and Ahlgren 1965; Bilmour and Chenoy 1968; Jorgensen and Wells 1971; Woodmansee 1978). Nitrification process has also been found to be enhanced after fire (Christensen 1973, 1977; Clark 1977). In contrast, nitrification rate was found to decrease sharply following the burn in the present study. It may be noted here that heterotrophic microbial population and also the heterotrophic activity in terms of CO₂ evolution tremendously increased following the burn (Deka, unpub.). It is likely that the low competitive vigour of the nitrifiers for NO₃⁻ - N as demonstrated by Jones and Richards (1977) may cause the reduced activity of the nitrifiers soon after the burn. Low heterotrophic activity due to the low levels of organic matter and nutrients and also the dilution of any allelopathic chemical because of intense rain may be accounted for another peaking in nitrification towards the later part of the year. The maximum rate of nitrification under 4 year cycle compared to that under 6 year and 10 year ones, may be explained as due to higher availability of NO₃⁻ - N to nitrifiers and conversely minimum heterotrophic potential because of relatively low levels of organic matter, available phosphorus, and pH which are the most critical factors for heterotrophic microbes (King and Webster 1971; McColl and Grigal 1977).

Decrease in nitrification rate with increasing age of the community may be accounted for a similar trend for
$\text{NO}_3^- - N$ and the reverse for $\text{NH}_4^+ - N$ as reported elsewhere also (Rice and Pancholy 1972; Todd et al 1975; Lodhi 1977). This may be explained partly as due to a less favourable environment of low energy regime for microbial activity and also due to more effective allelopathic interactions in the older fallows. However, the bulk increase in $\text{NO}_3^- - N$ concentration when incubated with an additional supply of $\text{NH}_4^+ - N$ clearly shows that availability of $\text{NH}_4^+ - N$ is more critical for nitrifying activity rather than the existence of any allelopathic inhibition in the prevailing ecological conditions.

The inhibition of nitrification in the initial stages, in case of the soils mixed with leaf powder may be associated with the immobilization of $\text{NH}_4^+ - N$ by the heterotrophs which act upon the added energy and may be associated with the immediate release of the inhibitors if present. It is possible that these chemicals are gradually mineralized and the higher amount of $\text{NH}_4^+ - N$ released as a by-product of decomposition of organic matter stimulates the activity nitrifiers as evident from a sharp increase in $\text{NO}_3^- - N$ concentration after 24 days of incubation. Further, the maximum rate of nitrification in case of the samples mixed with $E. \text{odoratum}$ leaf followed by $A. \text{conyzoides}$ and $B. \text{articululis}$ may be because of a similar trend of leaf nitrogen concentration (Chapter V) which determines the capacity of $\text{NH}_4^+ - N$ supply.
Low level of available phosphorus and pH have been shown to be associated with lower nitrification rates (Purchase 1974; Surathchandra 1978). However, no clearcut relationship could be detected in the present study indicating possibly that these factors may be more critical in the situations where competitions between heterotrophs and nitrifiers is not as severe as in the hot and humid climate prevailing in the present case.

It is evident from the present investigation that the possible inhibition of nitrification due to allelopathy may not essentially operate in all the environments. The activity of nitrifiers seems to be more related to the competitive interference offered by the heterotrophs particularly in the hot and humid climate of tropical regions as discussed by Lamb (1980) also.
SUMMARY

Rate of nitrification was studied under three Jhum sites (4, 6 and 10 year Jhum cycles) and 1, 3 and 20 year old fallows of secondary succession following the cropping. A sharp increase in the rate of nitrification after slashing the vegetation was found in the Jhum sites while a marked decline was noted soon after the burn. Another peak in the nitrification rate was found in the month of September again followed by a decrease in the following months. It was maximum under a 4 year cycle and minimum under a 10 year cycle. Successional fallows also showed nearly a similar pattern for nitrification rate during the year and it decreased with the increasing age of the community. Soil from all the sites showed higher rate of nitrification when incubated with an additional supply of NH$_4^+$ - N. Though in the initial stage the nitrifying activity was slow, in case of the soils incubated with leaf material, a sharp increase in the NO$_3^-$ - N concentration was found after 24 days of incubation. Nitrification activity in soil was found to be more critically associated with the availability of NH$_4^+$ - N rather than the allelopathic interactions.