

## Reproductive efficiency of secondary successional herbaceous populations subsequent to slash and burn of sub-tropical humid forests in north-eastern India

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**Abstract.** Three categories of secondary successional herbaceous communities subsequent to slash and burn, viz., early successional non-sprouting, early successional sprouting and late successional populations were investigated for their reproductive efficiency considering leaf component since it is the chief organ of photosynthesis. Early successional non-sprouting populations were found to be reproductively the most efficient whereas the early successional sprouting populations allocated more to vegetatively reproducing organs. While the high reproductive potential of early successional non-sprouting species was associated with vigour and production efficiency of the species, this relationship was stronger with the latter characteristic. On the other hand, early successional sprouting populations showed inverse relationship between vegetative and sexual reproductive effort. The strategy of late successional species seems to be to maximize vegetative growth in a closed habitat. The significance of these strategies is discussed in the paper.

**Keywords.** Growth strategies ; leaf area ratio ; reproductive effort ; successional communities ; adaptation.

### 1. Introduction

Slash and burn agriculture, locally known as 'Jhum', is the most prevalent form of cropping in the hill regions of north-eastern India. The early successional herbaceous communities constitute an important phase in the fallow development during secondary succession subsequent to cropping. This community, which holds the ground for about 5-6 years, often gets arrested at this stage due to the shortening of the Jhum cycle, the intervening period before the cropping is done on the same site (Ramakrishnan *et al* 1981).

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). Much is known about the resource 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 1975, 1979 ; Newell and Tramer 1978). While such an approach has yielded

valuable information, little effort has been made to relate the reproductive growth strategy with the leaf growth (McNaughton 1975; Bazzaz and Harper 1977; Primack 1979). This approach for evaluating the reproductive strategy of plants is more relevant because, leaf as an organ is the chief region of photosynthetic activity. In the present paper, early successional non-sprouting and sprouting, and late successional herbaceous populations have been compared for their growth and reproductive characteristics considering leaf as the sole organ responsible for energy capture and its overall distribution. The non-sprouting species, obviously, are all established through seeds alone. Sprouting species, though they may also come through seeds, are those that are established through sprouts alone.

## 2. Study area and climate

The study was carried out in Burnihat (26° N latitude and 91.5° E longitude) in the Khasi Hills about 90 km north of Shillong, on precambrian rocks which 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 slope generally ranges from 20° to 40°.

Climatically the year can be divided into three distinct seasons; the dry summer runs from mid-February to May and the rainy season extends from May to September with an annual rainfall of 2200 mm. The latter 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 (figure 1).

## 3. Methods of study

Four fallows which were slashed in January 1978 and freshly burnt in March 1978 and two 40 year old forested fallows were selected for this study. While

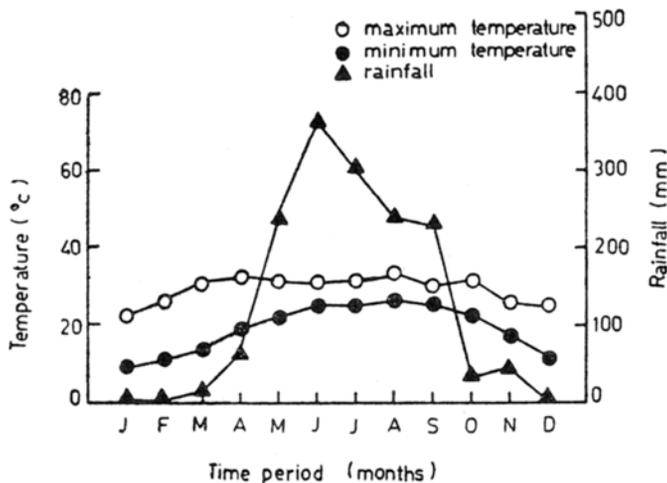


Figure 1. Ombrothermic diagram of the study area (1978).

mixed cropping is done normally at least for one year (Ramakrishnan *et al* 1981), for the purpose of the present study, the site was left directly as a fallow after the burn instead of being cultivated. The fire was a high intensity burn, since the slash burnt was derived from a 20 year regrowth. For each herbaceous species, phenological observations were made throughout the year using three permanent quadrats (50 cm × 50 cm) which were harvested at the fruiting stage. Those species which did not flower, were harvested at the end of the growing season. The samples were taken from uniformly monospecific patches of each species in order to minimize the variation due to micro-environment. Sample size ranged from 7 to 25 individuals. Below ground parts were carefully washed and leaf blade and seed components were detached. In situations where senescence started at flowering or fruiting stage, the fallen leaves and fruits or seeds were also included. Different components were dried at  $80 \pm 5^\circ\text{C}$  in a hot air oven, for 48 hours and then weighed.

Leaf area (by planimeter) and leaf dry weight were estimated using three replicates with 20 leaves per replicate. Total leaf area per plant was obtained by dividing total leaf biomass by dry weight per unit leaf area. Leaf area ratio was calculated as leaf area (cm<sup>2</sup>) per unit (g) biomass.

Density values for different species were estimated by using 50 randomly placed 1 m<sup>2</sup> quadrats in each fallow (Misra 1968). Twenty quadrats at random were harvested for estimating the average biomass per plant. This alongwith the density values were used for calculating biomass per m<sup>2</sup>. Each shoot was considered as a separate individual, in the case of the rhizomatous species. Community analysis was done at the end of the growing season.

#### 4. Results

Table 1 shows the density and biomass values of different species in the early and late successional communities. Amongst the early successional annuals, *Erigeron linifolius* was numerically the most dominant followed by *Panicum maximum* and *Cassia tora*. However, *C. tora* having the lowest density, contributed maximum to the herbaceous biomass. Six other annuals were present in a small proportion and therefore are considered together. Amongst the early successional non-sprouting perennials, *Eupatorium odoratum* was the most dominant. About 64% of the herbaceous biomass was contributed by the sprouting species in the early successional communities. *Thysanolaena maxima*, though having higher relative density than *Saccharum arundinaceum*, contributed lesser in terms of biomass compared to the latter. In the late successional herbaceous communities, *Oplismenus compositus* was the most dominant component.

Species like *Erigeron linifolius*, *Eupatorium odoratum*, *Saccharum arundinaceum* and *Thysanolaena maxima* which were the most dominant component in the early successional communities, had lower leaf area ratio compared to the less frequent species like *Euphorbia hirta*, *Borreria articularis*, *Digitaria adscendens* and *Mimosa pudica*. Leaf area ratio of the late successional species was generally much higher than the early successional species. Even *E. odoratum* and *P. maximum*, which are common in the early and late successional stages, exhibited higher leaf area ratio in the late successional communities. Reproductive effort which was

Table 1. Density and biomass of different species in the early and late successional herbaceous communities.

	Density (individuals/ m <sup>2</sup> )	Relative density (%)	Biomass (g/m <sup>2</sup> )	Biomass contribution (%)
<i>Early successional non-sprouting populations :</i>				
<i>Annuals :</i>				
<i>Erigeron linifolius</i>	3.45	10.11	6.38	0.19
<i>Panicum maximum</i>	1.96	5.75	13.52	0.40
<i>Cassia tora</i>	1.10	3.22	16.61	0.49
Others ( <i>n</i> = 6)	2.40	7.05	7.05	0.50
<i>Perennials :</i>				
<i>Eupatorium odoratum</i>	3.75	10.99	1087.35	32.03
<i>Panicum khasianum</i>	2.45	7.18	15.44	0.45
Others ( <i>n</i> = 4)	1.60	5.57	6.35	0.19
<i>Early successional sprouting populations</i>				
<i>Thysanolaena maxima</i>	9.05	26.53	728.53	21.46
<i>Saccharum arundinaceum</i>	6.20	18.18	1305.10	38.45
<i>Imperata cylindrica</i>	1.50	4.40	87.38	2.58
Others ( <i>n</i> = 2)	0.35	1.02	111.61	3.26
<i>Late successional populations</i>				
<i>Annuals :</i>				
<i>Panicum maximum</i>	5.62	16.11	3.37	3.59
<i>Oryza granulata</i>	1.85	5.30	12.21	13.02
<i>Perennials :</i>				
<i>Oplismenus compositus</i>	21.46	61.53	27.84	28.82
<i>Centotheca lappacea</i>	2.35	6.74	11.16	11.90
Others ( <i>n</i> = 7)	3.60	10.32	40.07	42.67

*n* is the number of species.

worked out in relation to leaf growth (seed (mg)/10 cm<sup>2</sup> leaf) indicates much higher values for species like *E. odoratum* and *E. linifolius* in early successional communities. Amongst the early successional sprouting perennials, *Imperata cylindrica* and *Grewia elastica* did not flower in the first post fire year and *M. pudica* had much higher reproductive effort than the others. The late successional species, on the other hand, had comparatively very low values for reproductive effort; in *Hedychium coccineum* and *Curculigo recurvata* flowering was not observed during the year of study (figure 2).

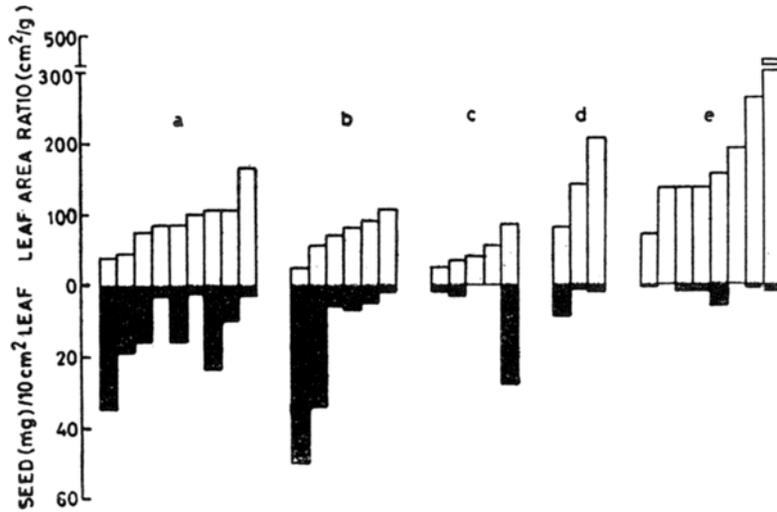


Figure 2. Leaf area ratio and reproductive effort (seed mg/10 cm<sup>2</sup> leaf) of secondary successional herbaceous populations. Non-sprouting early successional populations. (a) Annuals, (b) perennials, (c) sprouting early successional perennials. late successional populations, (d) annuals. (e) perennials. From left to right the different columns are: *Erigeron limifolius* Willd., *Rottboelia goalparensis* Bor., *Cassia tora* L., *Crossocephalum crepidioides* (Benth.) S., *Brachiaris distachya* (L.) Stapf., *Panicum maximum* Facq., *Euphorbia hirta* L., *Borreira articularis* (L.f.) Wild., *Mollugo stricta* L., *Eupatorium odoratum* L., *Setaria palmifolia* (Koen.) Stapf., *Paspalidium punctatum* (Burm.) A. Camus., *Panicum khasianum* Munro., *Manisuria granularis* L.f., *Digitaria adscendens* (H.B.K.) Henr., *Saccharum arundinaceum* Hook f., *Thysanolaena maxima* (Roxb.) O. Ketz., *Grewia elastica* Royle, *Imperata cylindrica* Beauv., *Mimosa pudica* L., *Oryza granulata* Nees et Arn., *Panicum maximum* Facq., *Rumex nepalensis* Spreng., *Eupatorium odoratum* L., *Hedychium coccineum* Ham. *Carex cruciata* Wahl., *Oplismenus compositus* Beauv., *Centothea lappacea* Deov., *Curculigo recurvata* Dryand., *Cyperus globosus* Allioni, *Chlorophytum arundinaceum* Baker.

These population characteristics were compared to assess their ecological importance. Pairwise comparison was made by Mann-Whitney's two sample rank test. Early successional non-sprouting category had significantly ( $P < 0.05$ ) lower leaf area ratio but higher reproductive effort than the late successional category. Early successional sprouting species showed significantly ( $P < 0.05$ ) lower leaf area ratio than those of the early successional non-sprouting and late successional types. However, its reproductive effort was not significantly different ( $P > 0.05$ ) from both the categories.

Regression analysis showed that while, reproductive effort was negatively correlated with leaf area ratio in the early successional non-sprouting category ( $r = -0.72$ ,  $P < 0.01$ ), positive correlation existed in the early successional sprouting category ( $r = 0.86$ ,  $P < 0.05$ ). Further, in the early successional non-sprouting category only, reproductive effort was positively correlated with leaf area per plant (figure 3). In the late successional category, no significant relationship could be detected between leaf characteristics and reproductive effort.

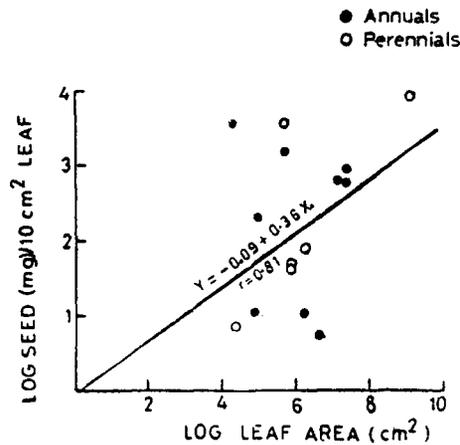


Figure 3. Relationship between leaf area (cm<sup>2</sup>)/plant and reproductive effort (seed mg/10 cm<sup>2</sup> leaf) in the non-sprouting early successional category.

Early successional non-sprouting populations when considered separately as annuals and perennials did not differ significantly between themselves for their leaf area ratio or reproductive effort. However, the negative correlation obtained for these categories, between leaf area ratio and reproductive effort, was more significant for the perennials ( $r = 0.93$ ,  $P < 0.01$ ) compared to the annuals ( $r = 0.65$ ,  $P < 0.05$ ). Reproductive effort was found to be positively correlated with absolute leaf area in the perennials only ( $r = 0.80$ ,  $P < 0.05$ ) and not in the annuals (figure 3).

## 5. Discussion

Leaf area ratio is an important structural concept as it expresses the proportion of assimilatory surface to respiratory mass (Evans 1972). Though the different species exhibit a range of variation, late successional populations which occupy the habitat of a low light regime, have higher leaf area ratio than the early successional ones as the adaptation in the former is to synthesize and maintain the maximum light interception surface whereas the latter occupying a productive and open environment divert their resource budget to other life purposes as growth and reproduction. Higher leaf area ratio in shaded environments compared to that in the open was also reported by Myerscough and Whitehead (1977) and Bazzaz and Harper (1977). Lower leaf area ratio of early successional sprouting species compared to that of the early successional non-sprouting types may be accounted as due to the preferential allocation of photosynthates to the underground organs of the former. The somewhat lower reproductive effort of the early successional sprouting populations compared to the non-sprouting ones, though not statistically significant ( $P > 0.05$ ), might have evolved due to the failure of their regeneration through seedlings (Wilson 1971).

Absolute leaf area of a plant gives an idea about its capacity of light interception and vigour while leaf area ratio, the ratio of light interception surface and total biomass ( $\text{cm}^2$  leaf area/g biomass) indicates the efficiency of dry matter production on leaf area basis. Significantly positive correlation of leaf area and negative correlation of leaf area ratio with reproductive effort in the early successional non-sprouting category show that high reproductive potential is associated with the vigour and also the production efficiency of the species. Comparatively stronger correlation of leaf area ratio with reproductive effort than that of the absolute leaf area with the reproductive effort in the early successional non-sprouting species indicates that reproductive success here depends more upon the production efficiency rather than the overall vigour of the plant. In contrast, early successional sprouting populations exhibited positive correlation of leaf area ratio with sexual reproductive effort. Thus a species like *Mimosa pudica* which has a high leaf area ratio allocates more for sexual reproductive effort. Also it so happens that this species is less vigorous in its vegetative regeneration compared to others like *Saccharum arundinaceum* and *Thysanolaena maxima*, and thus compensates more through sexual reproduction. Complete paucity of flowering in the first post-fire year, as in *Imperata cylindrica* and *Grewia elastica* has been shown for a number of shrub species (Gill 1975). This aspect of the problem is receiving our attention. Within the late successional group no significant ( $P > 0.05$ ) relationship between leaf characteristics and reproductive effort was found, suggesting that sexual reproduction is not related with production efficiency or vigour of the plant; the strategy seems to be to maximize vegetative-growth in a closed habitat.

Considering the annuals and perennials of the early successional non-sprouting category separately, certain differences are apparent. While reproductive effort seems to be dependent upon production efficiency in both the cases, it was positively correlated with absolute leaf area in the case of perennials alone indicating that the vigour of the plant is less critical for the annuals having a single possibility of flowering during their life-span.

MacArthur and Wilson (1967) pointed out that organisms in open environments are selected for greater reproductive capacity (*r*-strategy) while those in closed environments are selected for greater ability to compete for resources, though at the cost of lower reproductive potential (*K*-strategy). Grime (1974, 1977) has extended this argument by describing three primary strategies in plants which are related to their ability to withstand competition, stress and disturbance. Here, ruderal and stress tolerant strategies correspond to the extreme of *r*- and *K*-selection while highly competitive species of productive environments occupy an intermediate position. The findings of the present study clearly indicate that early successional non-sprouting populations are of ruderal type as they are equipped with the strategy to maximize seed production in order to colonize a disturbed habitat whereas early successional sprouting and late successional populations direct their synthetic capacity for competition and stress tolerance respectively by economizing on the reproductive growth. Vegetative reproduction has been looked merely as a growth in a horizontal plane (Harper 1977) and, therefore, is not considered in the present study.

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