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The pattern of resource allocation in wild herbs of early (chir pine) and late successional (oak) communities in Central Himalaya

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Abstract. Eight populations of four species of wild flowers characteristic of either early (chir pine) or late (oak) successional communities were analysed to determine patterns of dry mass allocation to component organs. The following patterns were determined: (1) The proportions of dry matter allocated to seed reproductive organs was greater in early successional populations than in late successional populations. (2) The herbs of late successional habitats allocated a greater proportion of their resources to leaves and belowground organs that herbs of early successional habitats.

The plant from the less mature site tends to allocate a greater proportion of their total mass to reproductive structures. Through this shift, these plants avoided the risk in the production of their next generation.

Keywords: herbs, resource partitioning

Introduction

Unlike most animals, plants exhibit extensive plasticity in response to environmental conditions. Because plants can not move to more favourable patches, this plasticity is essential if they are to produce progeny (Bradshaw 1972). The environment of a plant varies daily, seasonally, vertically and horizontally. The level of variability is determined by many factors including climate, geographical location, geomorphologic features, the nature site disturbances and the number and kind of species present (Bazzaz 1979).

Earlier Darwin (1859) stated populations of a plant species that are exposed to different environments might develop differences. Federer and Tanner (1969) revealed that the community dominants modify the environment of the herbaceous understory by reduction in the total radiation change in spectral distribution of the radiation and intercepting precipitation. Much of the attention has been directed towards the adaption of various environmental conditions (Gadgil and Solbrig 1972; Gaines *et al.* 1974; Hickman 1975; Ogden 1974). The theory of r- and K- selection was used by Gadgil and Solbrig (1972) to predict that reproductive effort will be greater in an environment which imposes a greater degree of mortality i. e., in a successionaly yong habitat. The variation in dry matter allocation pattern caused by genotypic and phenotypic effects within populations of plant species occupying diverse habitats has been the subject of the recent studies and considered from a variety of theoretical view points (Thompson and Stewart 1981; Evensen 1983; Bazzaz 1987).

In this study we have examined and analysed the resource allocation patterns in ground vegetation to describe the strategies in response to nature of dominant tree communities i. e., early (pine) and late (oak) successional communities.

Materials and methods

Himalayan, the great chain of mountains forming the northern most boundary of India, extend over a lenght of approximate 2,400 km and width varying from 250 to 400 km from North-west to the North-east with a mean elevation of the central axial range of 6,000 m (Valdia 1968). These chains of the mountains (latitudes 72-98° E) are aknowledged to be the youngest, the largest in the world and is divided into four well-marked parallel zone. The middle Himalaya (1,800-3,300) in which the present study area is being located. The present study was carried out in two dominant forests. These are characterised as a late successional community site (hereafter referred to as LS), oak forest (*Quercus lecotrichophora* A. Camus) and early successional community site (hereafter referred to as ES) chir-pine forest (*Pinus roxburghii* Sarg.) were located at 2,200 and 1,850m altitude respectively with 29°23´N lat. and 79°29´E long and both sites have south facing slopes.

There are three well defined seasons in a year, i.e., summer (April to mid-June), rainy (mid-June to September) and winter (November to February). May to June are the warmest months (27.4°C and 30°C - mean temperature) and December and January are coldest months (6.0°C and 3.5°C - mean temperature). The annual rainfall is 2,366 mm of which about 75% falls from mid-June to mid-September.

Parameters	Soil depth (cm)	*Q. lecotrichophora*	*P. roxburghii*
Fine soil	0 - 10	48.8 ±2.45	36.9 ±2.55
	10 - 20	41.1 ±2.39	33.0 ±2.30
	20 - 30	38.6 ±3.41	29.6 ±3.41
Water holding cap.(%)	0 - 10	67.12 ±0.67	49.6 ±31.57
	10 - 20	57.00 ±4.04	43.3 ±3.92
	20 - 30	54.00 ±2.88	38.9 ±3.12
pH	0 - 10	6.3 ±0.01	6.3 ±0.01
	10 - 20	6.0 ±0.00	6.1 ±0.01
	20 - 30	6.0 ±0.00	5.9 ±0.00
Nitrogen concentr. (mg/g)	0 - 10	5.1 ±0.03	2.4 ±0.03
	10 - 20	2.8 ±0.05	1.4 ±0.23
	20 - 30	2.2 ±0.11	1.1 +0.20

Table 1. Mean and standard deviation of physical and chemical properties of forest soils at late (*Q. leucotrichophora*)and early (*P. roxburghii*) successional sites.

Geologically soil of this area is chiefly forms of Volcanoes and Lauas (Valdia 1980). The main rocks responsible for the formation of the soil of this area consists of mainly massive dolomite, which is locally charity and phosohatic (P_2O_5 17.3%). The soil of this region is residual brown earth derived from limestone, quartzite, shale and sandy loam.

The oak forest of the study had a crown density of just about 80% and the chir-pine forest about 60% (Tewari *et al.* 1982). Fire is quite frequent almost in every summer of a year in pine forest but is rare in oak forest (Singh and Singh 1984). Shrubs were common in oak forest but are rare in pine forest, largely due to frequent fires. So grasses form a sizeable part of ground vegetation in chir-pine forest of this region and the difference between the two forest sites is given as Table 1. The water holding capacity, pH and total nitrogen concentration of soil were relatively higher in oak forest than chir-pine forest (Table 1). The four herbs species common to the two study sites (oak forest and chir-pine forest) were selected for on the basis of high density (4.0 individual/m^2) i.e., *Artemisia vulgaris* sensu. Hook F., *Artemisia concinnum* Schoot, *Gerbera gossypina* (Royle), Raizada and Saxena and *Onychium contiguum* Wall exhope.

Artemisia, an evergreen (Mehrotra 1998), erect growth form (Givnish 1987) with a tap-root belowground system, occurs on stony rocks where thin soil layers present; *Arisaema*, a deciduous species (Mehrotra 1998), belongs to special umbrella growth form (Givnish 1987) and generally, avoids open canopy areas; *Gerbera*, an evergreen (Mehrotra 1998), species belongs to basal growth form (Givnish 1987), occurs in shady sites but occasionally grows in dry slopes; *Onychium*, deciduous fern (Mehrotra 1998) of forest edges, which are rich in forest floor vegetation, and organic matter.

Herbaceous plant species of both chir-pine and oak forest were sampled during the peak of their growth (October). Eight populations of four species were harvested. In each population ten individuals were randomly selected. The plants for each species were carefully excavated from surrounding vegetation and separated into different components: belowground parts, stems, leaves, fruits and seeds. These components were dried at 80˚C to constant weight and weighed. The number of seeds per plant was determined for each of the ten individuals of all four species, individual seeds were weighed to the nearest 0.001 gm (the different data analysis has been done by measuring the dry weight of different components of a plant). The dry mass (among components) distribution ratios for individual population were used to calculate mean values for habitat type (Table 4).

Regression analysis was performed on dry mass of reproductive organ against total dry mass for population of ES and LS habitat populations.

Species	Below ground/shoot organs ratio	Percentage of total dry mass				Seed No./total dry mass	Weight of single propagule (mg)
		Below ground	Stem	Leaf	Reproductive		
			ES species (pine forest)				
A. concinnum	0.34 ±0.003	25.13 ±0.2	7.04 ±0.21	3.32 ±0.1	67.52 ±1.7	318.6 ±2.13	0.64 ±0.004
A. vulgaris	0.32 ±0.01	27.85 ±0.51	40.85 ±0.7	20.93 ±1.6	17.18 ±0.2	49.19 +2.09	0.053 +0.002
G. gossypina	1.23 ±0.06	54.95 ±1.13	23.12 ±0.5	21.83 ±0.7	-	-	-
O. contiguum	2.086 ±0.4	67.56 ±0.4	10.41 ±0.45	9.33 ±0.13	12.61 ±0.3	121.2 ±3.04	0.11 ±0.003
			LS species (oak forest)				
A. concinnum	0.67 ±0.01	40.09 ±0.27	9.45 ±0.5	5.0 ±0.1	46.50 ±1.4	148.4 ±2.09	0.45 ±0.006
A. vulgaris	0.60 ±0.01	37.69 ±0.28	44.54 ±0.4	15.11 ±0.38	2.65 ±0.05	11.76 ±0.24	0.018 ±0.0003
G. gossypina	1.21 ±0.02	54.84 ±0.15	15.60 ±0.42	29.56 ±3.5	-	-	-
O. contiguum	1.40 ±0.5	60.08 ±0.86	16.7 ±1.1	17.15 ±0.16	6.03 +0.14	51.48 ±0.90	0.05 ±0.008

Note: The reproductive phase was not observed in *G. gossypina*.

Table 2. Means and standard deviatios for resource allocation in eight populations and propagule weights of six populations from four species of herbs analysed.

Site	Below ground dry mass	Stem dry mass	Leaf dry mass	Reproductive dry mass	Shoot dry mass
ES	6.549 ±0.64	2.719 ±0.32	1.981 ±0.17	7.289 ±2.56	0.00097 ±0.0002
LS	10.439 ±0.85	4.495 ±0.52	3.091 ±0.25	5.032 ±1.82	0.0014 ±0.0003
Univariate anal. of variance	P<0.05	(NS)	P<0.05	P<0.05	

Table 3. Means and standard deviations for dry mass (gms) parameters of herbaceous plant populations at ES and LS sites.

Site	Total mass	Root/ shoot ratio	Below groud	Stem	Leaf	Repro-uctive organs
ES	18.392 ±3.072	1.046 ±0.180	43.891 ±4.1	20.109 ±0.67	14.209 ±1.896	22.208 ±6.227
LS	22.965 ±2.454	0.974 ±0.077	47.572 ±2.047	22.21 ±3.05	16.737 ±4.49	13.949 ±4.49

Table 4. Means and standard errors for five dry mass distribution ratios of the herbaceous plant populations characteristics of either ES and LS.

Results

The dry mass distribution expressed as percentage of total dry mass in below ground components, stems, leaves, seeds, reproductive organs, root/shoot ratio; and seed number/total dry mass, single propagaule weight in Table 2. Within each of species two groups, there was variability among populations in dry mass allocated to component organs. For example, at the early successional sites, the allocation to stem varied from 7.04% of the total dry mass in *Arisaema* to as high as 67.5% of total dry mass in *Onychium*.

Within each of these two groups, there was also variability in dry mass allocated to component organs from a population to population. For example, for low altitudinal populations, the allocation to stems varied from as low 7% of the total dry mass in *Arisaema* to as high as 41% of the total dry mass in *Artimisia*.

The correlation was particularly strong for the ES (r=0.99 between total mass and reproductive dry mass; Table 6). Table 4 gives the habitat means and standard deviations errors for dry mass in component organs for the two habitat types. There were significant differences in the absolute amounts of dry mass in stems, shoots and seed reproductive organs. In all cases there was more dry mass allocated to storage, supporting and assimilatory organs in LS than ES.

The ratio of seed dry mass/total dry mass was significatly lower for LS populations (14% of total dry mass) than for ES populations (22.2% of total dry mass; Table 4). The habitat mean ratio of stem dry mass/ total dry mass was slightly higher for herbs of LS community wood herbs (22.21% of total dry mass) than herbs for ES community field (20.1% of total dry mass; Table 5). Likewise the same pattern also was found for belowground mass and leaf components. However, the root/shoot ratio and the allocation to reproductive organs were greater for ES than LS.

The habitat means of seed number/plant and seed number/in total dry mass are given in Table 5. The herbs of ES community showed significantly higher ratio of each of these reproductive characteristic than herbs of LS community except ratio of seed mass:total mass.

Discussion

It is generally thought that environmental variability in open, early successional habitats is higher than closed, late successional ones (Bazzaz 1982). Both biotic and physical factors determined the growth of plant species in any habitats and the composition of plant communities. The relative importance of these two categories of factors may vary with the successional position of the community and the time scale in which it is considered (Bazzaz 1979).

Life histories are in part the result of selection for an optimal allocation of resources or energy for life activities such as maintenance, growth and reproduction (Harper and Ogden 1970).

A significant difference in the mean resource allocation pattern of ES and LS plants populations was observed in this study. Even though variability exists, there were clear trends evident from the data: (1) The proportion of dry matter allocated to reproductive organs was higher in ES populations. (2) The herbs of LS habitat allocated a higher proportion of resources to leaves, stem and belowground organs than did the ES herbs; and (3) there was a trend of more but smaller sized seeds in ES herbs as compared to LS herbs. The similar findings were reported by Hayashsi (1977) and he hypothesised

Site	Seed number/ plant	Seed number/g total dry mass	Seed mass/ total mass
ES	3,771.25 ±1,391.40	114.86 ±31.88	0.120 ±0.065
LS	1,762.00 ±6,646.00	52.36 ±15.03	0.128 ±0.050

Note: ES = early successional habitat, LS = late successional habitat

Table 5. Means and standard deviations for reproductive characteristic of herbaceous ES (N) and LS populations.

Independet character	Dependent character	Intercept (a)	Slope (b)	Correlation (r)
	Late successional			
Total dry mass	Shoot dry mass	4.256	0.103	0.048 (NS)
Total dry mass	Total leaf dry mass	4.478	-0.060	0.573 (NS)
Total dry mass	Reproductive dry mass	-11.809	0.733	0.800 (NS)
	Early successional			
Total dry mass	Shoot dry mass	2.572	0.008	0.082 (NS)
Total dry mass	Total leaf dry mass	2.32	-0.019	0.431 (NS)
Total dry mass	Reproductive dry mass	8.062	0.834	0.990 (NS)

Table 6. Allometric relatioships between total dry mass and different components of a herbaceous plant characteristic of LS and ES.

that plant species adapted to conditions of earlier stages of secondary succession. Bazzaz (1979) also stated that differences among the assemblages in the proportion of biomass in roots over nutrient gradient. Less than 20% of the total weight of early successional species was produced as roots and value did not changes with nutrient concentration and similar consistency for seed weight/total weight for early successional plants was found.

In our study the plant populations in early successional habitat allocated a greater proportion of their resources to seed components than population from late successional habitats. ES habitat showed allocation patterns indicating the importance of competitive ability and thus persistence on a site. Ross and Quinn (1977) and Abrahamson (1979) suggested that there is a phenotypic component to allocation patterns (which have a genetic basis).

The environment is variable both in time and in space; these wild species undoubtedly adjust their phenotype through physiological and developmental response so that the phenotype will be as close to optimum as possible for the prevailing situation. (E.g.) Hickman (1975); Nicolaus *et al.* (1976); Abrahamson and Hershey (1977); Abrahamson (1979) suggested that the distribution of biomass among the various vegetative plant organs should depend, to a large degree, on the nature of the limiting resources i.e. nutrient, water and light.

The patterns of allocation in our study are similar to those found in most analyses of single species (Abrahamson and Gadgil 1973). Hickman (1975) found similar patterns for reproductive allocation for *Polygonium cas-ceridense*. Greenhouse experiments with *Antropogon scopanrium* confirmed predicted shifts in vegetative biomass with shading (Ross and Quinn 1977). Newell and Tramer (1978) also found allocation shifts at the community level during succession similar to those in this study.

Comparison of the dry mass distribution ratios for each of the eight populations examined showed marked variability (Table 2). Much of this variability was still present often splitting the populations into early to late successional population. Variability in resource allocation are factors which should be basis for future studies: (1) It is known that differences exist in reproductive output due to life cycle (annual, perennials) (Salisbury 1942; Piletka 1977); (2) There may also be variability due to differences in seasonal cycles of species, e.g., spring to summer flowering (*G. gossypina*) versus rainy flowering (*A. concinnum* and *O. contiguum*).

The growth form of the plant will have a marked effect within a habitat type as well as between habitat types. Basal, rosette habits versus an erect branching stem will alter the resource allocation pattern detected by Abrahamson (1979). The many morphological differences (stem structure, leaf shapes) in tree species are also possible sources of variability.

The microclimate (light, temperature, etc.) of the individual plant may also be expected to modify its resource allocation pattern. For instance, a shaded plant may phenotypically shift to leaves at the expense of stem. Canopy effects the productivity and species composition of understory grasslands (Holland *et al.* 1980; Callaway *et al.* 1991). We predict that adaptive changes in dry mass allocation are significantly correlated to the enviroment.

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References

Abrahamson, W.G. 1979: Pattern of resource allocation in wild flower populations of fields and woods. *American Journal of Botany,* **66**: 71-79.

Abrahamson, W.G. and Gadgil, M.D. 1973: Growth form and reproductive effort in goldenrods (*Solidago compositae*). *American Naturalist,* **107**: 651-661.

Abrahamson, W.G. and Hershey, B. 1975: Reproductive strategies in dew berries. *Ecology,* **56**: 721-726.

Abrahamson, W.G. and Hershey, B. 1977: Resource allocation and growth of *Impatiens capensis* (Balsaminaceae) in two habitats. *Bulletin Torrey Botanical Club*, **104**: 160-164.

Bazzaz, F.A., Carlson, R.W. and Harper, J.L. 1979: Contribution to reproductive effort by photosynthesis of flowers and fruits. *Nature*, **279**: 554-555.

Bazzaz, F.A., Chiariello, N.R.O., Coley, P.D. and Pitelka, L.E. 1987: Allocating resources to reproduction and defence. *Bioscience*, **37**: 58-67.

Bazzaz, F.A. and Carlson, R.W. 1982: Photosynthetic acclimation to variability in the light environment of early successional plants. *Oecologia*, **54**: 313-316.

Bradshaw, A.D. 1972: Some evolutionary consequences of being a plant. *Evol. Biology*, **5**: 25-47.

Darwin, C. 1859: On the oringin of species by means of natural selection. Murray, London.

Evenson, W.E. 1983: Experimental studies of reproductive energy allocation in plants. In: *Handbook of Experimental Biology* (eds. E. Jones and R.J. Little)

Federer, C.A. and Tanner, C.B. 1966: Spectral distribution of light in the forest. *Ecology*, **47**: 555-561.

Gadgil, M.D. and Solbrig, O.T. 1972: The concept of r- and K- selection: experience from wild flowers and some theoretical considerations. *American Naturalist*, **106**: 14-31.

Gaines, M.S., Vogt, K.S., Hamrick, J.L. and Caldwell, J. 1974: Reproductive strategies and growth patterns in sunflowers (*Helianthus*). *American Naturalist*, **108**: 889-894.

Givnish, T.J. 1987: Comparative studies of leaf form: assessing the relative roles of selective pressure and phytogenetic constraints. *New Phytology*, **106 Suppl.**: 131-160.

Harper, J.L. and Ogden, J. 1970: The reproductive strategy of higher plants I. The concept of strategy with special reference on *Senecio vulgaris* L. *Journal of Ecology*, **58**: 681-698.

Hayashi, I. 1977: Secondary succession of herbaceous communities in Japan. *Jap. Journal Ecol.*, **27**: 191-200.

Hickman, J.C. 1975: Environmental upredictability and plastic energy allocation strategies in the annual *Polygonum cascadence* (Polygonaceae). *Journal of Ecology*, **63**: 689-701.

Mehrotra, P. 1998: Adaptive significance of leaf in relation to other parts of oak forest herbs. PhD. thesis, Kumaon University, Nainital (U.P.), India.

Newell, S.J. and Tramer, E.J. 1978: Reproductive strategies in herbaceous plant communities during succession. *Ecology*, **59**: 228-234.

Nichols, J.D., Conley, W., Batt, B. and Tipton, A.R. 1976: Temporally dynamic reproductive strategies and the concept of r- and K- selection. *American Naturalist*, **110**: 995-1005.

Ogden, J. 1974: The reproductive strategy of higher plants II. The reproductive strategy of *Tussilago farfara* L. *Journal of Ecology*, **69**: 291-313.

Pitelka, L.F. 1977: Energy allocation in annual and perennial lupines (*Lupinus*: Leguminosae). *Ecology*, **58**: 1055-1065.

Ross, F.H. and Quinn, J.A. 1977: Phenology and reproductive allocation in *Andropogen scoparius* (Graminae) population in communities of different successional stages. *American Journal of Botany*, **64**: 535-540.

Salisbury, E.J. 1942: The reproductive capacities of plants. Bell, London.

Singh, J.S. and Singh, S.P. 1984: An integrated Ecological study of eastern Kumaun Himalaya with emphasis on natural resources. Kumaun University, Nainital, India, Final report submitted to the Department of Science and Technology, New Delhi.

Tewari, C.K., Pandey, U. and Singh, J.S. 1982: Soil litter respiration rates in different micro-habitats of mixed oak-conifer forest and their control by edaphic conditions and substrate quality. *Plant and Soil*. **65**: 233-238.

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