anionic derivative, distributes primarily in the outer lipid monolayer, whereas, the cationic derivative TMA-DPH preferentially localizes in the inner lipid monolayer²¹. While the fluidity of the outer leaflet, as reported by DPH-PA, as well as that of the inner leaflet, as probed by TMA-DPH, were found to increase during the chemically-induced transition from dormancy to germination, it was only in case of the outer lipid monolayer that a significant correlation was observed between the fluorescence anisotropy value and T_{50} for each chemical (Table 1). However, it would be rather premature to suggest a causative relationship between membrane fluidity and dormancy breaking and the observed relationship could be described, with the data in hand, as correlative at best.

- Taylorson, R. B. and Hendricks, S. B., Planta, 1979, 145, 507-510.
- 2. Taylorson, R. B., Ann. Bot., 1991, 68, 337-340.
- Cohn, M. A., Jones, K. L., Chiles, L. A. and Church, D. F., Plant Physiol., 1989, 89, 879-882.
- 4. Bewley, J. D. and Black, M., Seeds: Physiology of Development and Germination, Plenum Press, New York, 1994.
- 5. Cohn, M. A., Seed Sci. Res., 1996, 6, 147-153.
- Adkins, S. W., Simpson, G. M. and Naylor, J. M., Physiol. Plant, 1984, 62, 18-24.
- Corbineau, F., Gouble, B., Lecat, S. and Come, B., Seed Sci. Res., 1991, 1, 21-28.
- Footitt, S. and Cohn, M. A., Plant Physiol., 1995, 107, 1365– 1370.
- Taylorson, R. B., in The Physiology and Biochemistry of Seed Development, Dormancy and Germination (ed. Khan, A. A.), Elsevier Biomedical Press, Amsterdam, 1982, pp. 323-346.
- 10. Taylorson, R. B., J. Exp. Bot., 1988, 39, 50-58.
- Di Nola, L., Mischke, C. F. and Taylorson, R. B., Plant Physial., 1990, 92, 427-433.
- 12. Amritphale, D., Curr. Sci., 1993, 64, 187-190.
- Amritphale, D., Dixit, S. and Singh, B., J. Exp. Bot., 1993, 44, 1621-1626.
- 14. ISTA, Seed Sci. Technol., 1985, 13, 299-513.
- 15. Sangster, J., J. Phys. Chem. Ref. Data, 1989, 18, 1111-1200.
- Hodges, T. K. and Mills, D., Methods Enzymol., 1986, 118, 41-54.
- Wheeler, J. J. and Boss, W. F., Plant Physiol, 1987, 85, 389-392.
- Fodor, E., Szabo-Nagy, A. and Erdei, L., J. Plant Physiol., 1995, 147, 87-92.
- Shinitzky, M. and Barenholz, Y., Biochim. Biophys. Acta., 1978, 515, 367-394.
- Freifelder, D., Physical Biochemistry, W.H. Freeman and Company, New York, 1982.
- 21. Haugland, R. P., Handbook of Fluorescent Probes and Research Chemicals, Molecular Probes, Inc., USA, 1996.

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Canopy effect on the dry matter allocation in different components of evergreen and non-evergreen forb species of Kumaun Himalaya

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Two forb species, Artemisia vulgaris and Arisaema concinuum occurring in both open and closed canopy forests have been selected for the study of resource allocation pattern under different light, moisture content and pH conditions to individuals of both species were randomly selected and harvested at peak of their growth. The distribution of dry mass in the underground, stem, leaves and in reproductive components were determined. In open canopy, both forb species had relatively greater dry mass invested in their reproductive activity than that of individuals occurring at the closed canopy site. However, the allocation of dry mass to supporting and assimilatory system of plants were adversely affected by direct sunlight, low moisture content, pH of soil and less fertile soil character of open canopy site than at close-canopy site. Regression analysis showed strong correlation between reproductive organ biomass and total biomass in individuals at the open canopy site.

THE knowledge of dry matter production by herbs is useful in studies of photosynthetic capture and dry matter production of the herb layer. For the tree seedlings, Madgwick et al. emphasized that the relative distribution of photosynthates to leaves, stems and roots of young tree seedlings, is related to the ultimate biomass production of the trees.

Canopy affects the productivity and species composition of understorey grasslands²⁻⁴. The pattern of biomass distribution to the various plant parts differs between individuals of the same species growing in different habitats⁵⁻⁸.

The distribution of biomass among various vegetative plant organs depends, to a large degree on the nature of the limiting resource(s), i.e. nutrients, water, light, etc. 9,10. Plant species from habitats that are less mature or more highly disturbed tend to allocate a great proportion of total biomass to reproductive parts when compared with plants of more mature or relatively less disturbed areas? Variation in allocation and morphology within individual species should follow patterns predicted for communities 11.

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Table 1. Comparison of characters at open and close canopy sites

Characters	Open-canopy site Close-canopy site			
Dominant forest	Pinus	Quercus		
	roxhburgii	leucotrichophora		
Altitude (m)	1850 m	2200 m		
Aspect	South	South		
Fire occurrence	Regular	Rare		
Tree crown density (%)	60%	80%		
Shrub density	Less	More		
Soil				
Fine soil (%) at 0-10 cm	36.9	48.8		
Depth				
pH	6.3 ± 0.011	6.8 ± 0.008		
Water holding capacity (%)	49.6	67.12		
Total nitrogen	2.4	5.1		
Concentration (%) (0.10 cm	depth)			

This paper describes how biomass allocation in two species influenced by variation in over canopy structures, i.e.: open canopy, (chir-pine site) and closed canopy, (oak site) of Kumaun Himalayas. We predict that adaptive changes in morphology and dry mass allocation are significantly correlated to the environment.

The closed canopy site (oak forest) (Quercus leucotrichophora A. Camus) and open-canopy site (chir-pine forest) (Pinus roxburghii Sarg.) were located at 2200 and 1850 m altitude respectively with 29°23' latitude and 79°29'E longitude 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 through June are the best 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 2366 mm of which about 75% falls from mid-June to mid-September. The oak forest had a crown density of just about 80% and the chir-pine forest about 60% (ref. 12). Fire is quite frequent in the pine forest but rare in the oak forest¹³ because of which shrubs were common in the oak forest but rare in the pine forest. Hence grass forms a sizeable part of ground vegetation in the chir-pine forests of this region and the soil here is residual brown earth derived from limestones, quartzite, shales and sandy loam. The difference between the two forest sites is given in Table 1. The water-holding capacity, pH and total nitrogen concentration of the soil were relatively higher in the oak forest than the chirpine forest (Table 1).

Two common forb species at two sites were studied, i.e. Arisaema concinuum Schoot (Araceae) and Artemisia vulgaris Sensu. Hook F. (Asteraceae). A. concinuum is deciduous forb species with 4.00 m⁻² (oak forest site) and 3.36 m⁻² (pine forest site) density, short above ground life span (130 days) and belongs to special-umbrella growth form¹⁴. A. vulgaris is an evergreen

(near about 327 days) with long above ground life span, has 4.00 m⁻² (in oak forest site) and 3.40 m⁻² (in pine forest site) density, with taproot system and belongs to erect growth form¹⁴. Herbaceous plant species characteristics of both chir-pine and oak forests were sampled during the peak of their growing season. Four populations representing two species were sampled. In each population, ten individuals were randomly sampled. The plants were carefully excavated from the surrounding and separated into different components, viz. belowground part, stem, leaves, fruits and seeds. These components were dried at 80°C till constant weight and weighed. The number of seeds per plant were determined for ten individuals of all species. Seeds were weighed to the nearest 0.001 g.

In this study we have examined and analysed the resource allocation patterns of evolutionarily unrelated herbaceous species characteristic of both open canopy and closed canopy communities. The primary objective in this study was to survey the generalized allocation patterns of forb components of open (chir-pine) and close (oak) canopy communities in situ.

The biomass distribution (expressed as percentage of total biomass in underground stems, leaf and seed reproductive organ and the belowground/shoot ratio), seed member/g total biomass, single propagule weight and life cycles for each of the two species examined are given in Table 2. Populations were characterized as either open canopy species or closed canopy species.

Within each of these two groups there was variability in biomass allocated to component organs for example, for open canopy population the allocation to stem varied from as low as 7.8% of the total biomass in A. concinuum to as high as 40.9% of the total biomass in A. vulgaris.

Regression analysis was performed on biomass of different components against total biomass, underground biomass and reproductive biomass for open canopy as well as closed canopy populations. The corelation was particularly strong for closed canopy forbs with all comparisons yielding r = 0.99, except r = 0.94 for flower reproductive mass regressed against total biomass. Open canopy population showed strong correlation of r = 0.98 for total biomass and belowground biomass; r = 0.99 for belowground biomass and reproductive biomass; and weak r = 0.96 for total biomass and shoot biomass (Table 3).

Table 4 gives the habitat means and standard errors for biomass in component organs, shoots and total biomass for the two habitat types. There were significant differences in the absolute amount of biomass in stems, shoots and reproductive organs. In all cases there was more biomass allocated in the closed canopy populations except reproductive components which had relatively more biomass allocated for the open canopy populations.

Table 2. Mean and standard deviations for resources allocation in four population and single seed weight of two species of forbs analysed. (E = Evergreen and N = Non-evergreen). The letters in parenthesis after species' names represent life cycle duration. The sum of biomass percentages for underground, stem, leaf and reproductive will be 100%

Species	Below ground/ shoot ratio	Below ground	Stem	Leaf	Repro- ductive	Seed no/g total biomass	Weight of single seed (mg)
Open-canopy site				- 70 - 7			
A. concinuum (N)	0.34 ± 0.003	25.13 ± 0.2	7.04 ± 0.21	3.32 ± 0.1	67.52 ± 1.7	318.60 ± 2.13	0.64 ± 0.004
A. vulgaris (E)	0.37 ± 0.01	27.85 ± 0.51	40.85 ± 0.7	20.93 ± 1.6	7.18 ± 0.2	49.19 ± 2.09	0.05 ± 0.002
Closed-canopy site							
A. concinuum (N)	0.67 ± 0.01	40.09 ± 0.27	9.45 ± 0.5	5.0 ± 0.1	46.50 ± 1.4	148.40 ± 2.09	0.05 ± 0.006
A. vulgaris (E)	0.60 ± 0.01	37.69 ± 0.28	44.54 ± 0.4	15.11 ± 0.38	2.65 ± 0.05	11.76 ± 0.24	0.02 ± 0.0003

Table 3. Allometric relation between dry mass, underground dry mass vs dry mass of different components

Component	a	b	c
SEE AACC	Oa	k forest	
Total dry mass vs underground dry mass	0.508	0.240	0.998
Total dry mass vs shoot dry mass	6.090	0.310	0.960
Total dry mass vs leaf dry mass	3.380	-0.040	0.960
Total dry mass vs reproductive dry mass	-10.200	0.890	0.999
Underground dry mass vs reproductive dry mass		3.710	0.999
ϵ	Pi	ne forest	
Total dry mass vs belowground dry mass	2.110	2.340	0.998
Total dry mass vs shoot dry mass	11.520	0.170	0.960
Total dry mass vs leaf dry mass	3.452	0.030	0.980
Total dry mass vs reproductive dry mass	-14.381	0.800	0.950
Underground dry mass vs reproductive dry mass	-12.600	1.873	0.995

The biomass distribution ratios for each individual population were used to calculate mean values for habitat type (Table 4), which showed that the open canopy populations are significantly different from closed canopy populations. The ratio of flower reproductive organ biomass/total biomass was significantly lower for closed canopy populations (26.0% of total biomass) than that for the open canopy population (39.2% of total biomass; Table 5). The habitat mean ratio of stem biomass/total biomass was not significantly different for close canopy forbs (27.0% of the total biomass) and open canopy forbs (23% of total biomass; Table 5). The mean leaf biomass/total biomass ratio was not very sharply different for populations of open canopy (13.15%) and close canopy (10.10%) (Table 5). The mean ratio of underground biomass/total biomass was significantly higher for close canopy populations (39.2% of total biomass) than open canopy populations (26.1% of total biomass; Table 5). Likewise, the ratio of underground biomass/ shoot biomass was not significantly different for both populations (Table 4).

The habitat means of seed number/plant, seed number/total biomass and seed mass/total mass are given in Table 6. The open canopy forbs showed significantly higher values for each of the reproductive characteristics than closed canopy forbs.

The interesting feature of this study is the significant difference in the mean resource allocation pattern of open and closed canopy plant populations. (1) The proportion of dry matter allocated to seed and fruit reproductive organs was greater in open canopy populations. (2) The forbs of closed canopy habitats allocated a greater population of their resource to the stem, and below ground but a lesser proportion of their resources to leaves than did the open canopy forbs. These results are consistent with the study of Hunt¹⁵. Who found that to grow quickly in height, stems must allocate relatively less above ground biomass to leaves under closed canopy. Givnish¹⁴ predicts that relative leaf allocation decreased with plant size. It may be possible that plants from disturbed or less mature sites, allocate a greater proportion of their total mass to reproductive structures because they do not want to take any risk in the production of their next generation. Abrahemsen and Gadgil⁷ and Gaines et al. 16 suggest that in habitats that are less mature or more highly disturbed, plants tend to allocate a greater proportion of their total mass to reproductive structure when compared to plants of more mature or less disturbed areas. Hickman¹⁷ found similar patterns for reproductive allocation for Polygonum cascadense green house experiments with Andropogon scoprium and confirmed predicted shifts in vegetative organ biomass in shading. (3) Fruit characters showed more and larger propagules in open canopy forbs as compared to closed canopy. This means that plant species adapted to conditions of open canopy habitat allocated a greater proportion of their resources to seed reproductive activity than plant species adapted to conditions of closed canopy habitat. A similar observation was made by Abrahamson, The open-canopy populations show and

Table 4. Means and standard means for biomass (g/m²) parameters of the forb populations character of open-canopy or closedcanopy sites

Site*	Below ground	Stem	Leaf	Reproductive	Shoot	Total	Root/Sheet
Open canopy	6 89 ± 1 53	3 93 ± 0.49	2.15 ± 0.33	13.76 ± 5.73		26.99 ± 4.79	0.36 ± 0.01
Closed canopy	11 89 ± 2.15	6 22 ± 0.90	2.44 ± 0.19	9.68 ± 4.10		29.99 ± 3.79	0.65 ± 0.02

^{*}Paired test indicated significant differences in underground, stem and reproductive biomass (P < 0.01) for open canopy and closed canopy sites. However, the tests showed that the biomass was not significantly different for leaf, shoot and also the total biomass (P, non-significant)

Table 5. Means and standard errors for biomass distributions of the forb populations characters of open canopy or closed canopy sites

Site*	Below ground	Shoot	Leaf	Reproductive part
Open-canopy	26.10 ± 0.66	23.11 ± 7.27	13.15 ± 4.37	39.39 ± 14.42
Closed-canopy	39.22 ± 0.63	27.14 ± 7.67	10.10 ± 2.32	26.04 ± 10.64

^{*}Paired t-test showed significant differences in biomass for different components (P < 0.05).

Table 6. Means and standard errors for reproductive characteristics of forbs at open and closed canopy (N = 2) sites

Site*	Seed number/plant	Seed number/total biomass	Seed mass/total mass	
Open-canopy	6863.5 ± 2783	184.03 ± 59.87	0.347 ± 0.130	
Closed-canopy	3227.0 ± 997.0	81.83 ± 31.06	0.236 ± 0.097	

^{*}Paired t-test showed significant differences in reproductive characteristics between two sites (P < 0.001).

allocation characteristics indicating the importance of competitive ability and thus persistence on a site. In this study, the inherited ability to show phenotypic variation is of considerable adaptive importance. The environment is not static but variable both in time and space. To occupy more than a point in time and space, the wild flowers 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 6.17-19. The microclimate (light, temperature, etc.) of the individual plant may also be expected to modify its resource allocation to leaves at the expense of the stem?

- Madgwick, H. A. I., White, E. H., Xydias, G. K. and Leaf, A. L. Forest Sci., 1970, 16, 154-159.
- Holland, V. L., USDA General Technical Report PSW-44, 1980, pp. 314-318.
- McClaren, M. P. and Bartalome, J. W., Madrono, 1989, 36, 141-153.
- Caliaway, R. M., Nadkarni, N. M. and Mahall, B. E., Ecology, 1991, 72, 1484-1499.
- 5. Snell, T. W. and Burch, D. G., Ecology, 1975, 56, 742-746.
- 6. Roos, F. H. and Quinn, J. A., Am. J. Bot., 1977, 64, 535-540.

- Abrahamson, W. G. and Gadgil, M. D., Am. Nat., 1973, 107, 651-661
- 8. Gadgil, M. D. and Solbrig, O. T., Am. Nat., 1972, 106, 14-31.
- 9. Abrahamson, W. G., Am. J. Bot., 1979, 66, 71-79.
- Bazzaz, F. A., Chirariello, N. R. O., Coley, P. D. and Pitelka, L. E., Biosci., 1987, 37, 58-67.
- 11. Menges, E. S., Am. J. Bot., 1987, 74, 551-563.
- Tewari, C. K., Pandey, V. and Singh, J. S., Plant Soil, 1982, 65, 233-238.
- Singh, J. S. and Singh, S. P., Forests of Himulaya, Structure, Functioning and Impact of Man, Gyanodaya Prakashan, Nainital, 1992.
- 14. Givnish, T. J., New Phytol., 1987, 106, 160.
- Hunt, R., Plant Growth Analysis, Edward Arnold, London, 1978.
- Gaines, M. S., Vogt, K. S., Hamrick, J. L. and Caldwell, J., Am. Nat., 1974, 108, 889-894.
- 17. Hickman, J. C., J. Ecol., 1975, 63, 689-701.
- Nichols, J. D., Conley, W., Bart, B. and Tipton, A. R., Am. Nat., 1976, 116, 995-1005.
- Abrahamson, W. G. and Harshey, Bull. Torrey Bot. Club, 1977, 104, 160-164.

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