

Phenological features in relation to growth forms and biomass accumulation in an alpine meadow of the Central Himalaya

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Abstract

Phenological records of 50 plant species were made during 1988–89 in an alpine meadow (30° 10'–30° 13' N lat. and 79° 39'–79° 41' E long.) of Central Himalaya located between 3100–3750 m elevation. The growth initiation occurred when temperature began to rise continuously and the resulting in snowmelt. The peaks of the various phenophases succeeded one after another in time, within a period of about four months (from May to September) which is longer than the period reported for the alpine sites of higher latitudes. The period of growth initiation appeared to be related to growth form, the species showing earlier growth initiation (when temperatures were lower) deployed leaves to lower heights, close to the ground. A majority of forbs completed growth cycle earlier than the grasses. For example, one group represented by *Trachydium roylei* reached peak growth a few weeks before did another group of species, represented by *Danthonia cachemyriana*, which is indicative of niche separation of the respective group of species. Activities of accumulation of live and dead shoot biomass were clearly separated in time in most communities, the former occurring from May to August, and the latter mainly in September.

Nomenclature: Osmaston (1926).

Introduction

Phenological studies are important to understand the plant responses as affected by competition, e.g. for light or pollinators. The effect of herbivory is also known to bring about changes in phenological behaviour of plant species (Crawley 1983). A little information on the phenology of alpine regions of the world is available. The major works include those of Bliss (1962), Chabot & Billings (1972), Billings (1973), etc. Few published reports

are also available on the phenology of forests (Ralhan *et al.* 1985a, b; Rawal *et al.* 1991) and alpine meadows of Central Himalaya (Semwal *et al.* 1981; Sundriyal *et al.* 1987; Ram 1988).

This study on Baideni-Ali bughiyal (a seasonally grazed alpine meadow from May to September) was undertaken with the objective to understand the community level plant phenology. Attempts were made to find out how do different growth forms phase their growth cycles within the short growing season of harsh climate.

Study site and climate

The study site (Baideni-Ali alpine meadow) was located ($30^{\circ}10' - 30^{\circ}13' \text{ N}$ lat. and $79^{\circ}39' - 79^{\circ}41' \text{ E}$ long.) between 3100–3750 m elevation in Chamoli district (India) of Central Himalaya. The site encompasses about 1000 ha area with most of the slope angles ranging between 5 and 65° . Monthly data of rainfall and temperature were collected from early May to late September (the snow-free period of the year). The total rainfall (average of 1988 and 1989) was 1557 mm which is comparable to that of the lower ranges in the Central Himalaya. The mean monthly minimum temperature in open ranges between 4.5°C in May and 9.5°C in June and the mean monthly maximum temperature between 12.5°C in September and 18.0°C in July (Fig. 1). Since these temperatures are markedly lower than in lower elevations, the precipitation effectiveness is to be relatively higher and conditions are more mesic at this site than in sites of lower elevations with similar precipitation values. Further, the snow-melt during April–May renders the soil moist, contrary to the lower ranges where the pre-monsoon summer (April to mid June) is dry (Singh & Singh 1987). At the Baideni-Ali site

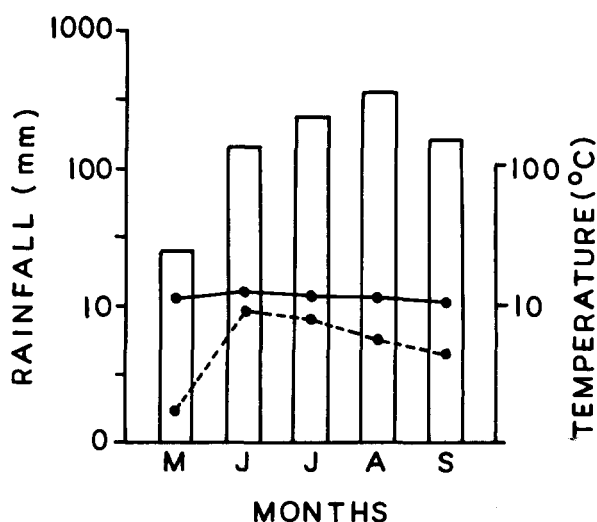


Fig. 1. Rainfall in mm (bars) and temperature in $^{\circ}\text{C}$ (curves) for average of two years, i.e. 1988 and 1989. ●—● represents mean maximum and ●--● represents mean minimum temperature.

cloud and fog formation was a regular feature even during the pre-monsoon summer period, contrary to lower ranges where clear sky is a characteristic feature of this period. Apart from the mesic condition throughout the summer season (April–May to September), a high wind velocity is a characteristic feature of the region.

The alpine belt established after the final uplift of the Himalaya during the early pleistocene. The rock types of the study site are quartzite, interbedded with metavolcanics, granite, gneisses and schists (Valdiya 1980).

Compared to soils of lower ranges, in general, the soil is deeper, black to blackish brown in colour with increasing depth, stone-free, and somewhat stratified (Singh 1991).

Community type

The vegetation of the site is identifiable into six natural communities (Singh 1991): mixed forb-tussock grass community, tussock grass community, tussock grass-forb community; *Trachydium roylei* dominated-forb community; sedge-tussock grass community; and low *Rhododendron-Cassiope* community (Table 1). With the exception of low *Rhododendron-Cassiope* community, in which the woody species *Rhododendron anthopogon* (a species of prostrate habit) was dominant, grass-sedge and forbs showed varying proportions of dominance in these communities.

Methods

After a thorough reconnaissance of the study area a total of 50 species (representing about 70% of the species), which accounted for about 95% of plant cover of the meadow distributed in the six plant communities, were observed from spring to monsoon in 1988–89 for phenological characters (Table 2). Tussock grass, sedge-tussock grass and low *Rhododendron-Cassiope* communities were found on steep slopes and therefore they are seldom grazed by the animals while the remaining

Table 1. List of species by growth forms, growth cycles, growth initiation categories and the communities where they were observed for various phenophases. (CSF = Cushion and sprawling forb; SF = Short forb; TF = Tall forb; G = Grass; S = Sedge; SUS = Shrub and undershrub).

Community/species	Growth form	Growth initiation category*	Growth cycle category**	Relative percent cover (n = 20)
1	2	3	4	5
<i>Trachydium roylei</i> dominated-forb				
<i>Agrostis munorana</i> Aitch et Hemsel	G	Early	Long	2 ± 0.12
<i>Carex alpina</i> Sweet	S	Early	Long	8 ± 0.48
<i>Oxygraphis polypetala</i> Hook. f.	CSF	Early	Short	7 ± 0.63
<i>Plantago major</i> L.	CSF	Early	Intermediate	6 ± 0.53
<i>Poa partensis</i> L.	S	Early	Long	4 ± 0.23
<i>Polygonum amphibium</i> L.	SF	Early	Long	4 ± 0.33
<i>Trachydium roylei</i> Lindl.	CSF	Early	Long	48 ± 0.22
<i>Swertia cuneata</i> D. Don	TF	Late	Long	3 ± 0.11
<i>Parnassia nubicola</i> Wall.	CSF	Late	Intermediate	1 ± 0.11
<i>Senecio chrysanthemoides</i> DC.	TF	Early	Long	2 ± 0.12
<i>Bupleurum longicaule</i> Wall.	SF	Late	Intermediate	3 ± 0.18
<i>Epilobium roseum</i> D. Don	SF	Early	Intermediate	1 ± 0.15
<i>Sibbaldia cuneata</i> Hornem.	SF	Late	Long	4 ± 0.41
<i>Saxifraga diversifolia</i> Wall.	SF	Late	Intermediate	1 ± 0.11
<i>Lactuca bractata</i> Hook f.	CSF	Late	Short	2 ± 0.12
<i>Ranunculus hirtellus</i> Royle	CSF	Early	Long	1 ± 0.11
<i>Trifolium repens</i> L. White	CSF	Late	Intermediate	1 ± 0.11
Mixed forb-tussock grass				
<i>Geranium wallichianum</i> D. Don	CSF	Early	Long	4 ± 0.33
<i>Geum elatum</i> Wall.	TF	Early	Long	12 ± 0.25
<i>Juncus concinnus</i> D. Don	G	Early	Long	4 ± 0.13
<i>Jurinea macrocephala</i> Clarke	CSF	Late	Long	7 ± 0.18
<i>Pedicularis tubiformis</i> Klotzsch.	SF	Early	Intermediate	4 ± 0.13
<i>Potentilla nepalensis</i> Hook.	TF	Early	Long	7 ± 0.18
<i>Primula denticulata</i> Smith	CSF	Early	Intermediate	4 ± 0.33
<i>Polygonum filicaule</i> Wall.	SF	Early	Intermediate	1 ± 0.11
<i>Potentilla peduncularis</i> D. Don	CSF	Late	Intermediate	2 ± 0.22
<i>Tanacetum longifolium</i> Wall.	CSF	Late	Long	2 ± 0.12
<i>Veronica biloba</i> L.	CSF	Early	Intermediate	1 ± 0.11
Tussock grass-forb				
<i>Euphorbia stracheyi</i> Boiss.	SF	Early	Long	6 ± 0.23
<i>Rhododendron lepidotum</i> Wall.	SUS	Early	Intermediate	1 ± 0.11
<i>Allium stracheyi</i> Baker	TF	Early	Intermediate	1 ± 0.11
<i>Polygonum amplexicaulis</i> D. Don	TF	Late	Intermediate	2 ± 0.23
<i>Polygonum polystachya</i> Wall.	TF	Late	Long	2 ± 0.23
<i>Euphrasia officinalis</i> L.	SF	Late	Short	1 ± 0.11
<i>Gypsophila cerastioides</i> D. Don	CSF	Early	Intermediate	1 ± 0.11
Tussock grass				
<i>Anaphalis contorta</i> Hook. f.	TF	Late	Long	6 ± 0.23
<i>Cynanthus lobatus</i> Wall.	CSF	Early	Long	1 ± 0.11
<i>Viola biflora</i> L.	CSF	Early	Early	2 ± 0.21

Table 1. Continued.

Community/species	Growth form	Growth initiation category*	Growth cycle category**	Relative percent cover (n = 20)
1	2	3	4	5
<i>Danthonia cachemyriana</i> Jaub. et Spach.	G	Early	Long	69 ± 0.19
Sedge-tussock grass				
<i>Polygonum vacciniifolium</i> Wall.	SF	Late	Long	7 ± 0.28
<i>Sedum linearifolium</i> Royle	SF	Late	Intermediate	4 ± 0.25
<i>Senecio kunthianus</i> Wall.	SF	Late	Intermediate	2 ± 0.21
<i>Kobresia dutheii</i> Clarke	S	Early	Long	45 ± 0.29
<i>Ophiopogon intermedius</i> D. Don	G	Early	Intermediate	2 ± 0.21
Low <i>Rhododendron-Cassiope</i>				
<i>Rhododendron anthopogon</i> D. Don	SUS	Early	Intermediate	49 ± 0.28
<i>Salix lindleyana</i> Wall ex Andersson	SUS	Late	Intermediate	4 ± 0.25
<i>Polygonum viviparum</i> L.	SF	Late	Long	3 ± 0.20
<i>Cassiope fastigiata</i> D. Don	SF	Late	Long	10 ± 0.15
<i>Potentialla microphylla</i> D. Don	CSF	Early	Long	2 ± 0.21
<i>Taraxacum officinale</i> Wigg.	CSF	Early	Long	4 ± 0.28

* Early growth initiation category = growth initiation before 30 May; and late = growth initiation after 1 June.

** Long growth cycle category = more than four months; intermediate = 2–4 months; and short = less than two months.

three communities were enclosed to exclude grazing. Detailed phenological observations on various species were made in the communities where they had their maximum cover. Phenological records were collected from the end of April, when the study sites had not become completely free from snow cover to end of September, when senescence had set in. Observations were made at

Table 2. Percent similarity on the basis of growth forms across the plant communities: 1 = Tussock grass; 2 = Tussock grass-forb; 3 = Sedge-tussock grass; 4 = Mixed forb-tussock grass; 5 = *Trachydium roylei* dominated-forb; 6 = Low *Rhododendron-Cassiope*.

	Communities					
	1	2	3	4	5	6
1	100					
2	91	10				
3	70	72	100			
4	82	86	66	100		
5	80	83	60	91	100	
6	74	77	52	71	75	100

weekly intervals when growth was initiated and at biweekly/monthly when plants had mature and the changes were slow. We collected data on the following phenophases: growth initiation, flowering, fruiting, fruit maturation, and senescence. If a given phenophase was observed in 10 to 30% individuals (depending upon the abundance of species) of a species, the species was considered to be in that phenophase. When most (80–90% or more) individuals of a species population were in a given phenophase was considered to peaking for that species. When green tissues became first visible as a result of sprouting of propagules and germination of seeds in a species, growth was considered to have initiated in that. The fruit maturation stage was differentiated from fruiting stage by colour and hardness of fruits and seeds. The onset of senescence was recognizable due to rather abrupt change in colour of leaves which preceded the death of shoots.

The species were categorized into the following growth forms: (i) shrubs and undershrubs, (ii) tall forbs, (iii) short forbs, (iv) cushion and sprawling

forbs, (v) grasses, and (vi) sedges (Table 1). Cushion and sprawling forbs formed small patches of sprawling mats and bore small leaves. Generally, short forbs were 10 cm or less tall plants with leaves arranged in a short umbrella-like structures with or without arching stems. Tall forbs were more than 10 cm high plants with scattered leaves all along the erect stems. They showed continuous leaf-shedding, starting from the portion close to the ground. With respect to length of growth cycle periods (from growth initiation to the beginning of senescence) the species were arbitrarily divided into three categories: (i) short, completing growth cycle within 2 months, (ii) intermediate, completing growth cycle in 2–4 months, and (iii) long, completing growth cycle in more than 4 months. Species were also classified according to the periodicity of growth initiation. In one group, the early-growth species growth was initiated before May 30, and in the other, the late-growth species it was initiated after 1 June. Since, the individuals of a species showed a strong synchronization for various activities, it was easy to identify the above stages.

The total above-ground plant biomass (live and dead shoots) was harvested as close to the ground as possible in 5 randomly selected 1×1 m quadrats from each of the six communities at 30 days intervals from 25 May to 25 September for 1988–89. Plant samples of each quadrat were oven-dried and weighed separately (for details see Singh 1991). Net accumulation rate (average of 1988 and 1989) in terms of dry weight ($\text{g m}^{-1} \text{day}^{-1}$) was calculated as: $(w_2 - w_1)/(t_2 - t_1)$; where w_2 and w_1 are total shoot biomass values (gm^{-2}) at time t_1 and t_2 .

Importance value was obtained for each growth form in a community by summing up the relative percent cover of all species in that community which were members of that growth form. These importance values for different growth forms were then used to calculate percent similarity between the communities by double-standardizing them as given in Bray & Curtis (1957) before computing for the percent similarity: $\text{PS} = \frac{\sum \text{Min}(x, y)}{\sum \text{Max}(x, y)}$; where (x, y) is the smaller of the two values for a given species in community x and y (lower val-

ues for each species were summed to determine similarity values between communities).

Results and discussion

Growth cycle and growth initiation

In general, the growth initiation occurred in the last week of April towards the lower altitudinal limits of the meadow (3100–3750 m), where mixed forb-tussock grass community occurred, while toward the higher altitudinal limits with tussock-grass and sedge-tussock grass communities, the growth initiation was delayed until mid May.

Percent similarity indicated that the tussock-grass and tussock grass-forb communities were most similar to the remaining communities (Table 2), indicating that they represented an intermediate habitat in the meadow. The low *Rhododendron-Cassiope* community was most different from the other communities (Table 2) and it occupied an extreme habitat, characterized by steep-slope and thin soil layer, toward the higher elevational limit of the meadow.

Of the species examined, about 8% belonged to short-growth cycle category, 44% species to intermediate-growth cycle category, and 48% species to long-growth cycle category (Table 3).

Competition for light is an important selective pressure on leaf height, and where community biomass is high, competition favours increased leaf height which prevents overtopping. Consistent with this, percentage of species belonging to tall forbs and grasses (also of larger dimension) was higher in sites with larger community biomass (Table 1). Within a site of temperate region where species composition of herb layer (non-graminoids) changes seasonally within an annual cycle, tall forbs are reported to occupy the warmest period of the year, while the species of relatively shorter forms occur as spring ephemerals, evergreen or winter annuals (Givnish 1987). Occurrence of tall forbs, predominantly in lower elevations of this study, i.e. in warmer habitat is consistent with this observation. Favourable tem-

Table 3. Number of species of different growth forms of all the communities belonging to a growth cycle category. Values in parentheses indicate percentage of total species in a growth form.

Growth cycle category	Total species	Growth forms				
		Tall forbs	Short forbs	Cushion forming and sprawling forbs	Grasses and sedges	Shrubs and undershrubs
Long	24 (48)	6 (75)	3 (25)	9 (45)	6 (86)	0
Intermediate	22 (44)	2 (25)	8 (67)	8 (40)	1 (14)	3 (100)
Short	4 (8)	0	1 (8)	3 (15)	0	0

perature conditions seem to enable most of tall forbs (6 out of 8) to maintain growth and long-growth cycle and to deploy leaves at a greater height on stem (Table 3). The tall forbs were equally divided between early and late categories of growth initiation. The short forbs showed an early-growth initiation at the sites of low elevation and late-growth initiation at sites of higher elevation. Most of the grasses showed early-growth initiation and long-growth cycle, regardless of the elevation they occupied. In the graminoids leaves emerge right from the base and grow much in horizontal space, close to the ground which represents warmest microenvironment in the meadow. This growth habit enables grasses to initiate growth earlier in the season even in higher

elevations than many tall forbs, which mainly grow in height. In regard to growth initiation, cushion and sprawling forbs, which deploy their leaves on the ground surface, resemble grasses. About two-third of the forbs showed early-growth initiation and intermediate- or short-growth cycles. They deployed most of their leaves before tall forbs and were able to attain any sizeable length. Thus they exploited resources of the meadow when conditions were less favourable (cold-conditions), and by doing so, escaped the competitive influence of tall forbs, which could easily overtop them.

Most alpine plants of higher latitudes are reported to complete their growth cycles within 2-4 months (Bliss 1966; Billings & Mooney

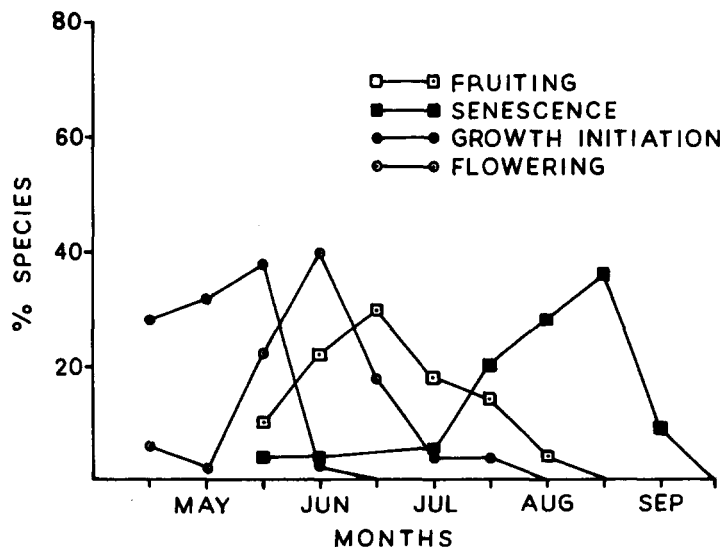


Fig. 2. Percentage of total species (50) under different phenophases in different months.

1968). A longer than four months growth cycle for 48% species in this alpine site may be due to the favourable moisture conditions, throughout the snow-free period.

General phenophases

Figure 2 shows the percentages of the 50 species studied under different phenophases in different months. Across the species the growth initiation occurred over a two-month period and peaked in later half of May to early June when temperatures were more warmer. *Oxygraphis polypetala*, *Primula denticulata*, *Trachydium roylei*, *Taraxacum*

officinale (all cushion and sprawling forbs) were among the first to show the growth initiation, in the first week of May when snow-melt had begun and *Euphrasia officinalis* (a short forb) was the last to exhibit its growth initiation (in the last week of June). *O. polypetala*, put out leaves and flowers at the same time even when still under snow cover. *P. denticulata* began to flower in the first week of May thus soon after the initiation of vegetative growth when snowmelt was not yet complete. The number of flowering species increased from June and by mid July a majority of the species were flowering. Short forbs, such as *Bupleurum longicaule*, *Epilobium roseum* and *Polygonum amphibium* were blossoming in the latter half of

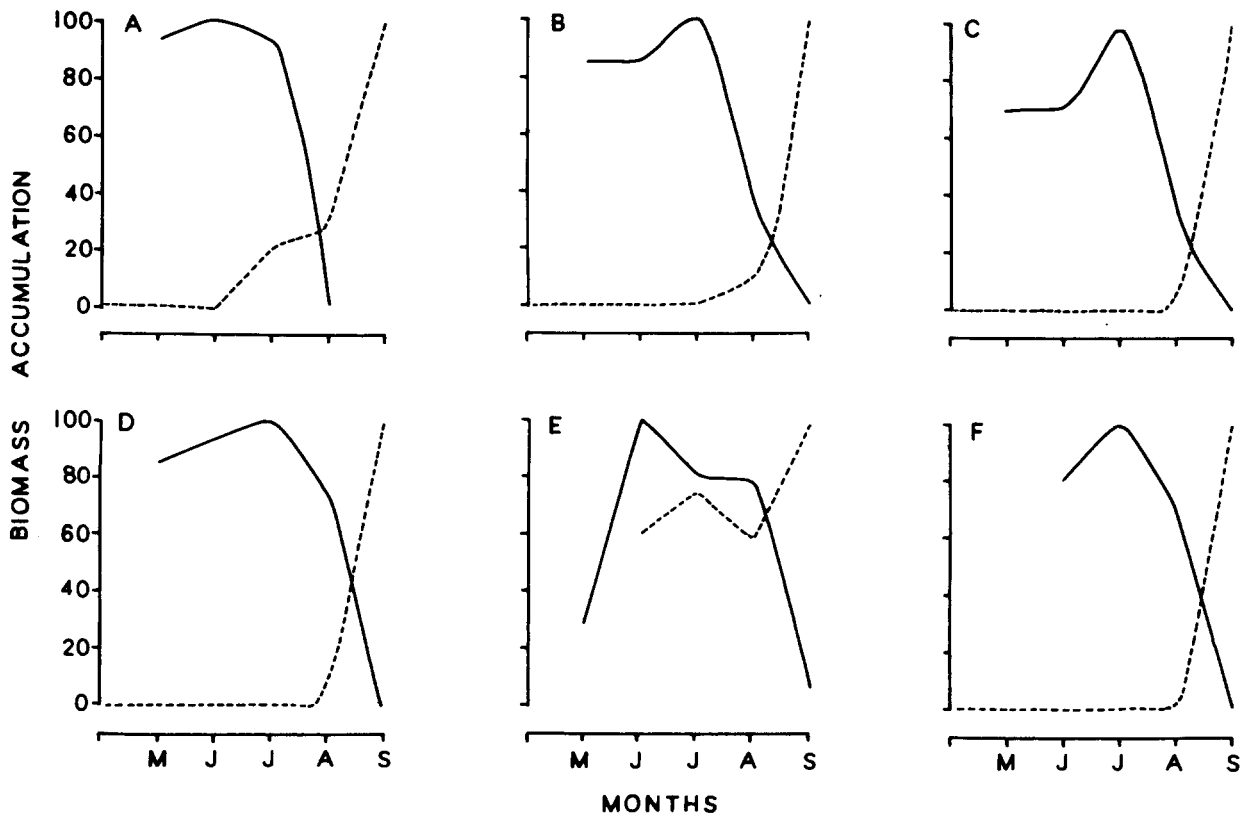


Fig. 3. A representation of periodicity of biomass accumulation at community level. The peak value in each case is taken as 100 and all other values are computed as a function to that. The peak values for live shoot biomass accumulation (solid lines) and dead attached biomass (broken lines) accumulation ($\text{g m}^{-2} \text{ day}^{-1}$) are 1.8 and 1.4, respectively in *Trachydium roylei* dominated-forb community (A); 2.3 and 2.4 in mixed forb-tussock grass community (B); 3.7 and 2.0 in tussock grass-forb community (C); 3.7 and 2.7 in tussock grass community (D); 1.5 and 0.9 in sedge-tussock grass community (E); and 1.5 and 0.2 in low *Rhododendron-Cassiope* community (F).

July; in *Jurinea macrocephala* (a cushion and sprawling forb) it was delayed until mid August when some species were already in the senescence phase. In all the three woody species and in a few forbs (e.g. *Allium stracheyi*, *Anaphalis contorta*, *Geum elatum*) fruiting began in the last week of June. However, 70% of species were in peak fruiting during mid July to mid August. Most of the species bore mature fruits within one month of fruit formation with the exception of a few forbs (e.g. *B. longicaule*, *Trifolium repens*). Grasses were among the last to bear mature fruits.

The senescence occurred gradually from first week of August, peaked during late August to early September; by late September most of the species were in senescence, with the exception of *Cassiope fastigiata* and *T. longifolium* (both forbs). By the end of September a few species were with green tissues. The sudden decline in temperature in last week of September did not allow the normal form of senescence in which a gradual yellowing of leaves occurs, as noticed for the vegetation of lower elevations in the Central Himalaya (Ralhan *et al.* 1985a & b; Negi 1989). Instead, it was manifested by sudden death and darkening of tissues and gave an impression of frost injury.

Aboveground biomass accumulation

In *Trachydium roylei* dominated-forb and tussock grass communities the rate of live shoot biomass accumulation was consistently high from May to July (Fig. 3). In low *Rhododendron-Cassiope* community it rose sharply from May to June then declined gradually until August, whereafter the decline became rapid. In the remaining three communities the rate of live shoot biomass accumulation increased clearly from June to July, and then declined sharply. In all communities, the rate of dead shoot (attached) biomass accumulation peaked in September. However, the communities differed markedly from one another with respect to monthly rate of the dead shoot biomass accumulation that occurred before September (Fig. 3). In short, May to July was the main period of accumulation of live shoot biomass and September was the main period of dead shoot biomass accumulation. Only a narrow overlap in the periodicities of live and dead shoot biomass accumulations occurred in August in all except low *Rhododendron-Cassiope* community, in which the time overlap was broader. This situation in the woody community was somewhat similar to that

Table 4. Average net accumulation rate ($\text{g m}^{-2} \text{day}^{-1}$) for different growth forms in Baideni-Ali alpine meadow. Values in parentheses indicate the range of net accumulation rate across all the communities.

Growth forms	Months				
	April–May	May–June	June–July	July–August	August–September
Cushion and sprawling forbs	0.39 ± 0.218 (0.0 – 1.30)	0.37 ± 0.151 (0.02 – 0.81)	0.34 ± 0.146 (0.0 – 0.76)	–	–
Short forbs	0.08 ± 0.071 (0.0 – 0.43)	0.17 ± 0.033 (0.03 – 0.26)	0.24 ± 0.057 (0.03 – 0.40)	–	–
Tall forbs	0.19 ± 0.077 (0.0 – 0.47)	0.22 ± 0.062 (0.0 – 0.36)	0.42 ± 0.053 (0.0 – 0.53)	–	–
Grasses	0.80 ± 0.415 (0.0 – 2.43)	0.83 ± 0.443 (0.0 – 2.71)	0.85 ± 0.440 (0.0 – 2.80)	1.01 ± 0.502 (0.0 – 3.13)	–
Sedges	0.11 ± 0.034 (0.0 – 0.20)	0.22 ± 0.091 (0.03 – 0.66)	0.24 ± 0.097 (0.03 – 0.71)	0.30 ± 0.111 (0.03 – 0.83)	–
Shrubs and undershrubs	–	–	0.15 ± 0.145 (0.0 – 0.87)	0.19 ± 0.188 (0.0 – 1.13)	0.02 ± 0.016 (0.0 – 0.10)

of the low-altitude forest communities, where the period of maximum leafing shows a broad overlap with the period of leaf senescence (Ralhan *et al.* 1985a). Roughly, during one-third of the snow-free period, generation of dead shoot was the predominant activity. In the tussock grass, dead shoots formed in one year are carried over to next year (Ram 1988), and therefore dead shoots, litter and associated organisms remain important in the community over a considerable period.

The influence of temperature and moisture on plant growth has been well documented by several workers (e.g. Dewald & Steiner 1986; Walter 1973). A comparison of different growth forms for biomass increment in different months indicate that cushion and sprawling forbs showed decline in net accumulation rate from May to July while the other growth forms showed increase in net accumulation rate from May which continued upto July–August (Table 4). Thus the rate of net accumulation in cushion and sprawling forbs was negatively related to rainfall ($r = -0.970$; $P < 0.01$) as opposed to the positive relationship ($r = 0.882-0.995$; $P < 0.05$) found with the remaining growth forms. Cushion and sprawling forbs attained peak net accumulation rate immediately after the snowmelt during May when the temperatures were minimum (mean monthly temperature = 8.8°C) and rainfall was low. Among the remaining growth forms, short forbs and tall forbs showed peak net accumulation rate in July (early monsoon period), while grasses and sedges had peak net accumulation rate in August. Out of the 12 most important species (two most important species from each community) all forbs (except *T. roylei* and *J. macrocephala*) viz., *E. stracheyi* ($0.14\text{ g m}^{-2}\text{ d}^{-1}$), *A. contorta*, *P. amplicaulis*, *P. vacinifolia* (each $0.68\text{ g m}^{-2}\text{ d}^{-1}$), *G. elatum* ($0.49\text{ g m}^{-2}\text{ d}^{-1}$) and *C. fastigiata* ($0.30\text{ g m}^{-2}\text{ d}^{-1}$) showed peak growth rate in July when temperature (mean monthly temperature = 12.9°C) and rainfall were favourable. *T. roylei* ($0.97\text{ m m}^{-2}\text{ d}^{-1}$) and *J. macrocephala* ($0.30\text{ g m}^{-2}\text{ d}^{-1}$) showed peak net accumulation rate in May and June, respectively. *D. cachymeniana* ($3.13\text{ g m}^{-2}\text{ d}^{-1}$), *K. duthei* (0.83 g m^{-2}

d^{-1}) and *C. alpina* ($0.26\text{ g m}^{-2}\text{ d}^{-1}$) showed peak net accumulation rate in August.

The snow-free part of the year of this alpine belt is the period when varied activities occur rapidly. The species peaks for the various phenophases succeeded one after another in time within a short period of about four months from May to September. This is made possible as a result of subtle differentiation among the species with regard to growth form, phenology and leaf height. Variation in height, manner of leaf deployment, such as vertical vs. horizontal spread of shoots and periodicity of leafing enabled a number of species to occupy the same site, by reducing competition for vital resources.

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