

**An exploration on the phenology of different growth forms of an alpine expanse of North-West Himalaya, India**

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**Abstract:** Phenological behavior of different growth forms was observed in an alpine pasture of North – West Himalaya (Tungnath), India. Total 103 species were identified which were categorized in 10 different growth forms. In the majority of the growth forms, growth initiation was recorded in May whereas senescence in October. Flowering occurred in July- August in most of the growth forms. In different growth forms, stoloniferous forbs exhibited maximum percent contribution in comparison to tussock graminoids and stoloniferous graminoids. On the basis of growth cycle pattern, long growth cycle plant species contributed maximum percentage in comparison to short growth cycle plant species. Phenological characters *viz.*, initiation, flowering, fruiting etc. depends on the climate of the particular regions. Currently, most of the species initiate after snow melt in alpine regions (April – May) and in near future because of predicted global climate changes, phenology of many plant species may get altered which in turn will be the factor responsible for their acclimatization in changed environment. The present study deals with the phenological characters of different growth forms of an alpine expanse which will be fruitful in this respect. [New York Science Journal. 2009; 2(6):29-42]. (ISSN: 1554-0200).

**Key words:** Alpine, flowering, growth cycle, growth forms, phenology, Tungnath

**Introduction:** Phenology is the study of the timing of chronic biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species (Leith, 1974). The word is derived from the Greek *phainomai* - to appear, come into view, and indicates that phenology has been principally concerned with the dates of first occurrence of natural events in their annual cycle. Examples include the date of emergence of leaves and flowers, the first flight of butterflies and the first appearance of migratory birds, the date of leaf coloring and fall in deciduous trees, the dates of egg-laying of birds and amphibia, or the timing of the developmental cycles of temperate-zone honey bee colonies. In the scientific literature on ecology, the term is used more generally to indicate the time frame for any seasonal phenomena, including the dates of last appearance (Mier, 2007 and Menzel *et al.*, 2006). In arctic and alpine tundra, the growing season is extremely short, and its duration varies strongly among years (Molau, 1993; Tho'rhallsdo'ttir, 1998).

In this biome, the timing of the onset of flowering is crucial to the reproductive success of flowering plants. In late - flowering species, the entire seed production is often lost in summers colder or shorter than the average (Molau, 1993, Henry and Molau, 1997). In alpine habitat, seedlings are uncommon, though seedlings may be abundant in certain high favorable environmental conditions scattered randomly. However, it has been widely perceived that vegetative reproduction predominates by underground parts in an alpine biome (Bliss, 1971). Flowering time varies from species to species, because

photoperiodic and thermo periodic responses are different. At higher elevations, temperature is the most important factor in different phenological stages (Holway and Ward, 1965).

Dickinson and Dodd (1976) observed that although there is annual variation in phenological progression within a species in response to variation in weather, there appears to be little variation of the species sequence between growing seasons. Plant phenology in alpine region is strongly influenced by variation in microenvironments related to micro topography (Bliss, 1956, 1966; Percy and Ward, 1972 and Fareed and Caldwell, 1975). Phenological and phenomenological variations of the plants are the product of interaction between genotype and environment. The growth of a species during early and late growth season shows the ability of plants to absorb water at low temperature. The phenological pattern of the species within and among community may differ from each other (Mooney and Billings, 1960).

### Methodology

**Study area:** The present study was carried out in Tungnath, situated at 30° 14' N Latitude and 79° 13' E Longitude and between altitudes of 3200 m and 3750 m above MSL (Figure 1). The present alpine region ends at two popular summits namely, Rawanshila (3400 m) and Chandrashila (3750 m). The timberline in this area reaches upto an elevation of 3200 m. The meadows here are gentle at the base, becoming gradually steeper until they form summits. Meadows with deep soil cover are seen in northern aspects, while the southern faces generally have large rock spurs and crevices are either barren or have a few lithophytes. Important species at the timber line are *Quercus semecarpifolia*, *Abies pindraw* and *Betula utilis* (Sundriyal and Bisht, 1988). *Rhododendron campanulatum*, *Sorbus* and *Berberis* are common shrub species at treeline. Above and beyond the tree line, most of the plants are small with a dwarf-rosette growth structure.

The study was conducted in the alpine garden of High Altitude Plant Physiology Research Centre (5 ha) and area adjacent (10 ha) to the field station was surveyed randomly from April – November, 2008. After species emergence, the species were identified and categorized into different growth forms on the basis of their growth behavior as per Körner (1999) viz., tussock graminoids, stoloniferous graminoids, mat forming forbs, rhizomatous forbs, stoloniferous forbs, tuberous forbs, bulbous forbs, shrubs and under shrubs, creeping dwarf shrubs and prostrate creeping dwarf shrubs and, on account of the length of growth cycle as per Nautiyal *et al.* (2001) viz., short growth cycle (species completing their life cycle within two months), intermediate growth cycle (species with a span of 2-4 months) and long growth cycle (species completing their life cycle in more than 4 months). Monthly phenological observations were made for individual plant species.

**Meteorological observations:** Average maximum temperature was recorded in August (21.23 °C) wherein minimum in October (6.06 °C). Maximum rainfall was recorded in August (1550.31 mm) wherein minimum in May (139.81 mm). Likewise, maximum humidity was recorded in August (59.19 %) wherein lowest in May (48.22 %).

### Results

**Selection of growth forms:** Total 103 species were identified in the study area and further were categorized into different growth forms. Out of 103 species, 3 species were identified as tussock graminoids, stoloniferous graminoids and creeping dwarf shrubs, 6 species as mat forming forbs, 25 species as rhizomatous forbs, 30 species as stoloniferous forbs, 11 as tuberous forbs, 7 species as bulbous and shrubs and under shrubs and 8 species as prostrate creeping dwarf shrubs.

Generally, growth initiation occurred in May wherein senescence in October in different plant species of different growth forms. In different growth forms maximum flowering was occurred in the month of July - August and minimum in the month of April - May. Dominant flower colour was observed as yellow followed by white, purple and blue whereas minimum as red color (Table 1 and Figure 2).

Table 2 depicts that percent contribution of different species on the basis of growth forms was recorded maximum for stoloniferous forbs (29.13 %) followed by rhizomatous forbs (24.27 %) wherein minimum for tussock graminoids, stoloniferous graminoids and creeping dwarf shrubs (2.91 %).

In tussock graminoids, stoloniferous graminoids and shrubs and under shrubs, all related species of these growth forms were identified as long growth cycle plant so that 100 % contribution was recorded for long growth cycle plants in these growth forms. In mat forming growth form 2 species were identified as short growth cycle, 4 species as long growth cycle. In rhizomatous forbs growth form 17 species were identified as long growth cycle, 1 as short growth cycle and 7 as intermediate growth cycle. In stoloniferous

forbs 14 species were identified as long growth cycle, 15 as intermediate and 1 as short growth cycle plant. In case of tuberous forbs 7 species were identified as long growth cycle, 3 as intermediate and 1 as short growth cycle plant. In bulbous growth form 3 species were identified as long and intermediate growth cycle and 1 species as short growth cycle. In creeping dwarf shrubs 2 species were identified as long growth cycle and 1 species as intermediate growth cycle. In prostrate creeping dwarf shrubs 4 species were identified as long growth cycle and 2 species as intermediate and short growth cycle plant. Overall in different growth forms maximum contribution was recorded for long growth cycle plant species and minimum for short growth cycle plant species (Table 3).

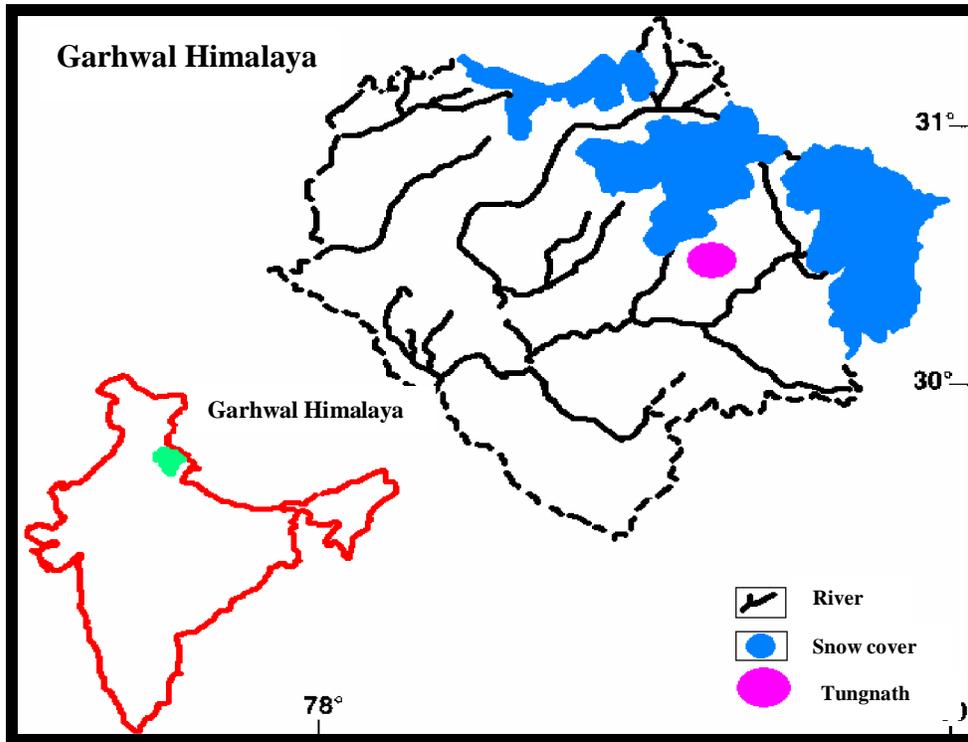
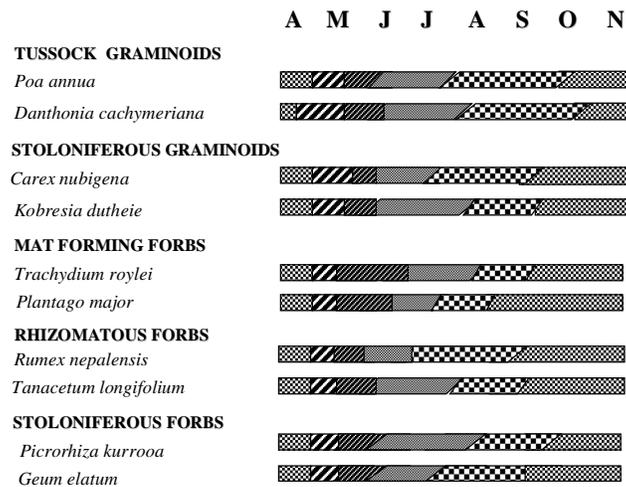


Figure 1. Location map of the study area



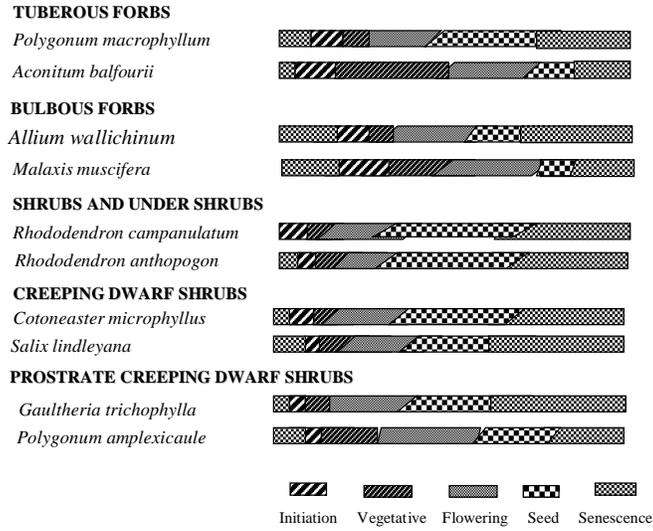


Figure 2. Phenophase spectra of dominant species in different growth forms

Table 1. Phenological observations of different growth forms

S. No.	Growth forms	Species	Growth initiation	Flowering	Flower color	Fruiting	Senescence
1	Tussock Graminoids	<i>Agrostis munroana</i> Ait. Et Hemsl.	May	August-September	Creamish	September-October	October-November
2		<i>Danthonia cachymeriana</i> Jaub. & Spach.	May	August-September	Creamish	September-October	October-November
3		<i>Poa annua</i> L.	May	June- July	White	August-September	October
1	Stoloniferous	<i>Carex nubigena</i> D. Don	May	June- July	Dark brown	July-August	October-November
2	graminoids	<i>Cyperus</i> spp.	May	July-August	Dark brown	August-September	October-November
3		<i>Kobresia dutheie</i>	May	June - July	Brown-black	July-August	October
1	Mat forming forbs	<i>Gentiana argentic</i> (D. Don.) Cl.	May	May- June	Blue	July-August	September
2		<i>Plantago depressa</i>	May	June- July	Light brown	August-September	September
3		<i>Plantago major</i> non L.	May	June- July	Light brown	August-September	September
4		<i>Trachydium roylei</i> Lindl.	May	July-August	White	August-September	October
5		<i>Viola biflora</i> L.	May	May- June	Yellow	July - August	September
6		<i>Oxygraphis polypetala</i>	April	April-May	Whitish blue	June-July	July
1	Rhizomatus forbs	<i>Anemone obtusiloba</i> D. Don.	May	May- June	Light purple	July-August	August-September
2		<i>Anemone rivularis</i> Buch. - Ham. Ex DC.	May	May- June	White	July-August	August-September
3		<i>Anemone tetracephala</i>	June	May- June	White	July-August	August-September
4		<i>Angelica archangelica</i>	May	July - August	White	September-October	October-November
5		<i>Angelica glauca</i>	May	July - August	White	September-October	October-November
6		<i>Arnebia benthami</i>	May	August-September	White	October	October
7		<i>Bergenia stracheyi</i>	May	July - August	Light pink	August-September	October
8		<i>Corydalis cashmeriana</i>	May	May- June	Blue	July-August	September
9		<i>Corydalis longipes</i>	May	June - July	Yellow	July - August	September
10		<i>Jurinia macrocephala</i>	June	August-September	Brown	October	October
11		<i>Ligularia amplexicaulis</i>	June	July - August	Yellow	September-October	October
12		<i>Ligularia arnicoides</i>	June	July -	Yellow	September-	October

				August		October	
13		<i>Morina longifolia</i>	June	July - August	Pinkish purple	August-September	October
14		<i>Nardostachys jatamansi</i>	May	July-August	Pink	September-October	October
15		<i>Podophyllum hexandrum</i>	May	May- June	White	July-August	October
16		<i>Polygonum affine</i> D. Don.	June	June- July	Purple	August-September	October
17		<i>Polygonum alpinum</i> All.	June	July-August	Pinkish white	September-October	October
18		<i>Polygonum rumicifolium</i> Royle ex Bab.	June	June- July	Reddish	August-September	September
19		<i>Rheum emodi</i>	May	June- July	White purple	August-September	October
20		<i>Rheum moorcroftianum</i>	May	June- July	White purple	August-September	October
21		<i>Rumex nepalensis</i> Spreng.	May	June- July	Reddish	August-September	October
22		<i>Selinum candolli</i> DC.	May	July-August	White	September-October	October
23		<i>Selinum vaginatum</i> (Edgew.) CLl.	May	July-August	White	September-October	October
24		<i>Tanacetum longifolium</i> Wall. ex DC.	May	July-August	White	September-October	October
25		<i>Taraxacum officinale</i> (Weber) Wiggers	May	July-August	Yellow	August-September	September
1	Stoloniferous forbs	<i>Anaphalis cuneifolia</i> Hook f.	May	June- July	White	September-October	October
2		<i>Anaphalis margaritacea</i>	May	June- July	White	September-October	October
3		<i>Arenaria</i> spp. L.	June	June- July	White	July-August	September
4		<i>Caltha palustris</i> Linn.	May	May- June	Yellow	July-August	September
5		<i>Chrysanthemum</i> spp.	June	July-August	White	August-September	September
6		<i>Doronicum roylei</i> DC.	June	August-September	Yellow	September-October	October
7		<i>Epilobium latifolium</i>	June	July - August	Dark mehroon	September-October	October
8		<i>Eregiron multiradiatus</i>	June	July-August	Light purple	August-September	October
9		<i>Fragaria nubicola</i> Linn.	May	May- June	White	July-August	September
10		<i>Geranium wallichianum</i>	May	July-August	Purple	August-September	October
11		<i>Geum elatum</i> Linn.	May	June- July	Yellow	August-September	October
12		<i>Impatiens thomsonii</i>	May	July - August	Pink	August-September	September
13		<i>Inula grandiflora</i> Willd	June	August-	Yellow	October	October

				September			
14		<i>Juncus bracteatus</i> Buchen	May	June- July	White	July- August	September
15		<i>Meconopsis aculeata</i>	May	June- July	Blue	July- August	September
16		<i>Meconopsis robusta</i>	May	June- July	Yellow	July- August	September
17		<i>Oxyria digyna</i>	June	July - August	Reddish	September- October	October
18		<i>Parnassia nubicola</i> Wall. Ex Royle	June	July - August	White	August- September	September
19		<i>Phlomis bracteosa</i>	May	June - July	Mehroon	August- September	October
20		<i>Picrorhiza kurrooa</i> Royle ex Benth.	May	June- July	Light purple	September- October	October
21		<i>Potentilla</i> <i>atrosanguinea</i> Lodd.	May	May- June	Red	July- August	September
22		<i>Potentilla cuneata</i> Wall. ex Lehm.	May	June- July	Yellow	July- August	September
23		<i>Potentilla fulgens</i> Wall. ex Hook.	May	June- July	Yellow	July- August	September
24		<i>Ranunculus hirtellus</i> Royle, Bot.	May	May- June	Yellow	July- August	September
25		<i>Senecio alatus</i> Wall. ex DC.	June	July- August	Yellow	August- September	October
26		<i>Senecio</i> <i>chrysanthemoides</i> DC.	June	July- August	Yellow	August- September	October
27		<i>Swertia cuneata</i>	June	July - August	Creamish	August- September	September
28		<i>Swertia speciosa</i> D. Don.	June	July- August	White	September- October	October
29		<i>Thalictrum alpinum</i>	May	July- August	Yellow	September	October
30		<i>Rubus nepalensis</i>	May	June- July	Pinkish white	July- August	September
1	Tuberous forbs	<i>Aconitum balfourii</i>	May	August- September	Light Blue	October	October- November
2		<i>Aconitum</i> <i>heterophyllum</i>	May	August- September	Creamish	October	October- November
3		<i>Cypripedium</i> <i>himalaicum</i>	May	June - July	Pinkish- white	September- October	October
4		<i>Gymnedia spp.</i>	May	June - July	Purple	September- October	October
5		<i>Orchis chusua</i>	June	July - August	Purple	September	September
6		<i>Orchis latifolia</i>	May	June - July	Purple	September- October	October
7		<i>Polygonatum</i> <i>cirrhifolium</i>	May	July - August	Yellowish- white	September- October	October
8		<i>Polygonatum</i> <i>geminiflorum</i> Decne.	June	June- July	Yellowish white	August- September	October
9		<i>Polygonatum</i> <i>verticilatum</i>	May	July - August	Yellowish- white	September- October	October

10		<i>Polygonum macrophyllum</i> D. Don.	May	June- July	Light magenta	August-September	September
11		<i>Roscoea purpurea</i> J. C. Sm.	May	June- July	Purple	August-September	October
1	Bulbous forbs	<i>Allium stracheyi</i>	July	July-August	White	September	October
2		<i>Allium wallichinum</i>	June	July-August	Light purple	September	October
3		<i>Fritillaria roylei</i>	May	May- June	Cree mish	September-October	October
4		<i>Iris kumaonensis</i>	June	August-September	Purple	September-October	October-November
5		<i>Malaxis muscifera</i>	June	August-September	White	October	October
6		<i>Nomacharis oxypetala</i>	June	June- July	Light yellow	July-August	September
7		<i>Trillium govianum</i>	May	June - July	White	July - August	September
1	Shrubs and	<i>Berberis lonicera</i>	April	July-August	Yellow	September-October	October-November
2	under shrubs	<i>Piptenthus</i>	April	June- July	Yellow	August-September	October
3		<i>Potentilla polyphylla</i>	April	July - August	Yellow	August-September	October
4		<i>Rhododendron anthopogon</i>	May	May- June	Creamish	July-August	October
5		<i>Rhododendron campanulatum</i> D. Don.	April	April-May	Pinkish white	July-August	October
6		<i>Rhododendron lepidotum</i>	April	May- June	Light pink	July-August	October
7		<i>Rosa brunonii</i>	April	July-August	White	August-September	October-November
1	Creeping	<i>Cotoneaster microphyllus</i>	May	May- June	White	July-August	October-November
2	dwarf shrubs	<i>Euphorbia stracheyi</i>	June	June - July	Light pink	July - August	September
3		<i>Salix lindleyana</i>	May	June - July	Creamish	July - August	September
1	Prostrate creeping	<i>Gaultheria tricophylla</i> Royle	May	May- June	Pinkish white	July-August	September
2	dwarf shrubs	<i>Hypericum spp</i>	June	July-August	Yellow	August-September	October
3		<i>Pedicularis gracilis</i> Wall. ex Benth.	May	June- July	Dark purple	July-August	September
4		<i>Pedicularis pectinata</i>	May	June- July	Purple	July-August	September
5		<i>Polygonum amplexicaule</i> D. Don.	May	July-August	Dark purple	September-October	October
6		<i>Polygonum vacciniifolia</i>	June	July - August	Pinkish-white	August-September	October

7		<i>Primula denticulata</i> Sm	April	April-May	Dark pink	June- July	August-September
8		<i>Primula radii</i>	April	May- June	Light yellow	June- July	August-September

Table 2. Percentage contribution of different species on the basis of growth forms

Growth forms	% contribution
Tussock graminoids	2.91
Stoloniferous graminoids	2.91
Mat-forming forbs	5.83
Rhizomatous forbs	24.27
Stoloniferous forbs	29.13
Tuberous forbs	10.68
Bulbous forbs	6.80
Shrubs and under shrubs	6.80
Creeping dwarf shrubs	2.91
Prostrate creeping dwarf shrubs	7.77

Table 3. Percentage contribution of different species on the basis of growth cycle

Growth forms	Growth cycle	% contribution
Tussock graminoids	3 L	100
Stoloniferous graminoids	3L	100
Mat-forming forbs	4 L	66.67
	2 S	33.33
Rhizomatous forbs	17 L	68.00
	7 I	28.00
	1S	4.00
Stoloniferous forbs	14L	46.67
	15 I	50.00
	1S	3.33
Tuberous forbs	7 L	63.64
	3 I	27.27
	1 S	9.09
Bulbous forbs	3L	42.86
	3 I	42.86
	1 S	14.29
Shrubs and under shrubs	7L	100
Creeping dwarf shrubs	2L	66.67
	1I	33.33
Prostrate creeping dwarf shrubs	4 L	50
	2 I	25
	2S	25

### Discussion

Phenology is the study of periodically occurring natural phenomenon and their relation to climate and changes in season is a central focus of several aspects of ecology (Wieder *et al.*, 1984). Seasonal timing events can be critical for survival of life and reproduction. Phenology of different populations of the same species is determined by environmental parameters and allowed for genetic exchange (Ratchke and

Lacey, 1985). Phenological observations also provide a background to functional rhythms of plant communities (Rawal *et al.*, 1991).

Plant Phenology in alpine region is strongly influenced by variation in microenvironments related to micro topography Bliss, (1956, 1966), Percy and Ward (1972) and Fareed and Caldwell (1975). Sorenson (1941) and Mooney and Billings (1961) described the phenology of Tundra vegetation. Phenological and phenomenological variations of the plants are the product of interaction between genotype and environment. However, these modifications in plants may be reversible when plants are grown under diverse climatic conditions (Bhatt and Purohit, 1984). Ram *et al.* (1988) studied the community level phenology of grassland above tree line in Rudranath in the central Himalayan region. They observed the developmental stages of about 142 plant species. Their study simply adds to the fact that in the unfavorable environment of the high elevations the primary plant strategy is to complete the growth cycle rapidly in order to assure species survival.

Among the ecological studies phenological studies are important to understand the plant responses as affected by competition *e.g.* for light or topographic position. The climate, topography, weather of an area and the intensity of biotic interference are the most important ecological factors determining the type of plants that could occur there. Plants of alpine regions have various morphological and physiological means of adaptations against adverse climatic conditions. Each plant initiates and completes its vegetative phases with the commencement of favorable temperature and soil water accessibility. Accordingly, phenology is associated with plant growth rate (Taylor, 1972), nutrient transfer (Sosebee and Wiebe, 1973), thermal requirement (Ram *et al.*, 1988; Negi *et al.*, 1992), plant water relationship (Blaisdell, 1958) and evolutionary change (Kikuzawa, 1995).

In the present investigation total 103 species were identified out of which, 3 species were identified as tussock graminoids, stoloniferous graminoids and creeping dwarf shrubs, 6 species as mat forming forbs, 25 species as rhizomatous forbs, 30 species as stoloniferous forbs, 11 as tuberous forbs, 7 species as bulbous and shrubs and under shrubs and 8 species as prostrate creeping dwarf shrubs. Depending on the heterogeneity of the environmental gradients, the pattern of phenological stages between communities and within a community can vary from species to species. Dickinson and Dodd (1976) have stated that, although annual variations occurs in phenological progression within a species in response to variation in regional weather, there appears to be little variation of the species sequence between growing season.

Growth initiation occurred in May wherein senescence in October in different plant species of different growth forms, respectively. In different growth forms maximum flowering was occurred in the month of July - August and minimum the month of April - May. Dominant flower color was observed as yellow followed by white, purple and blue and minimum as red color. The early availability of moisture, a great majority of the species at the alpine site initiate growth and do not wait for the onset of the monsoon. The factor which decides growth initiation is snow melt, which not only supplies soil water but also indicates rise in temperature (Ram *et al.*, 1988). In response to early growth initiation, the species number for vegetative phase is in the alpine area peaked in June compared to August in the herbaceous communities of the lower ranges (Rana, 1985). The species of smaller forms generally began to grow earlier than the larger forms. This also has in avoiding competition for resources, particularly for light and possibly for available nutrients. Consequently, in all growth forms, flowering and seed setting peaks occurred over a relatively short period of time compared to this, in the vegetation of lower elevations these Phenophases are spread over most of the year. Interestingly, the peak for flowering in alpine plants occurred during the wet period of the year (July - August). In contrast to the trees and shrubs of the lower elevations, which show peak flowering during the dry summer season (Ralhan *et al.*, 1985).

The early growing species (cushion form) can have an unusual water absorbing ability at low soil temperatures, which is perhaps related to high levels of soluble carbohydrates in root stocks. In the study area, more abundant roots occurred in the upper soil layers, where temperatures were relatively higher or where the water requirement for early growth was low. The shallow root system of some species *viz.*, *Oxygraphis polypetala*, *Gentiana argentic*, *Primula denticulata* etc. also favor early growth because they restrict water use in the upper soil layer, moreover, they need little water because of their small size (Oberbauer and Billings, 1991). Flowering time varies from species to species because photoperiodic and thermoperiodic responses are different. At higher elevations, temperature is the most important factor in different phenological stages (Howlay and Ward, 1965).

Percent contribution of different species on the basis of growth forms was recorded maximum for stoloniferous forbs wherein minimum for tussock graminoids, stoloniferous graminoids and creeping dwarf

shrubs which could be accredited to the type of perennating organs and adaptation features of particular species. Underground parts accumulate more biomass and secondary metabolites, resulting in greater production. Harvesting after seed shedding provide opportunities to grow new plants of the same species and to maintain the species population, many of these species are threatened because of overexploitation and illegal exploitation. Different phenophase time will provide information about morphological and functional attributes that is useful in understanding adaptation features. After a long period of winter dormancy, alpine plants initiate their growth as soon as air temperature becomes favorable and soil begin to thaw, however the pattern of growth varies with life form and micro-environment (Billings and Mooney, 1968). Billings *et al.* (1965) showed that long photoperiod with high temperature was responsible for breaking dormancy in perennating buds of alpine plants.

Among different growth forms long growth cycle plant species contributed maximum proportion wherein minimum proportion was contributed by short growth cycle plant species. Nautiyal *et al.* (2001) also had reported that short growth cycle plants contributed minimum percentage to total species wherein maximum was reported for intermediate growth cycle. Similar observations were reported by Ram *et al.* (1988). Körner (2003) also has focused on such type of studies on growth forms with reference to perennating organs.

Phenophases of species provides information about morphological and functional attributes, which are useful to understand adaptation features (Nautiyal *et al.*, 2001). While, phenophases of the same species may vary from one region to another and yet in different macro - habitats because of environmental factors, the required germplasm can be collected from unapproachable areas in the Himalaya in accordance with the developmental stages of these species. Present study demonstrates the value of comparing and synthesizing results of multiple field methods within a single study. This also highlights the robust community wide trends, species specific responses of phenology to climate change and temperature related aspects of climate change which lead to long - term irregularities in interspecific interactions which in turn potentially alters the population and evolutionary dynamics, community structure and ecosystem functioning.

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