Flowering phenology on altitudinal gradient in the Himalaya

Priority of alpine research in the tropics and subtropics is towards documentary works on the flora and life condition. Consequently, functional ecology of alpine plants is largely underrepresented in the literature and most often not even the simplest base data are available[1]. The Himalayan 'high altitude' is no exception to this and despite the largest altitudinal gradient in the world there are few reports that have studied the effect of altitude on different aspects of plant life.

Flowering is an important aspect in the life history of angiosperm species, with both ecological and evolutionary consequences[2]. For successful presence (in time and space) in any environment a species has to time its flowering phenophase in such a way that conditions are optimal to flower. During this time pollinators should generally be abundant (considering most of the species are dependent on pollinators) and there should be low competition with other flowers for pollinators. Different phenophases of plants, of which flowering is one, at the population or ecosystem level are ultimately a product of selection acting on variation among individuals[3] and the phenology adapted and exhibited today by a species has evolved as the best fit for the prevailing environmental conditions.

Sub-alpine and alpine zones in the Garhwal Himalaya range between 3000 and 5400 m amsl, but this stretch of about 2400 m, considered as 'high altitude' here, is not a uniform habitat as regard to the duration of the growing season, species composition, flowering phenology, vegetation type, etc. due to continuously changing environmental conditions on the altitudinal gradient. This land includes the uppermost montane zone, subalpine zone and alpine zone. Here, the rich seed plant diversity of the montane zone gradually reduces to zero through the treeline ecotone, alpine zone, nival zone and the rate of elevational reduction is 24–28 species/100 m (ref. 4).

In contrast to the tropical alpine zones where plants can theoretically flower all year round, in the extratropical high altitudes of the Himalaya, the year is distinctly divided into two seasons – one 'dormant season' with snow cover over the land surface, and the other 'growing season' without snow cover over the land surface in which growth and develop-

ment are possible in the plant species (Figure 1 a–c). This growing season is restricted to April–October at 3000 m altitude, reduces upwards and remains hardly for two months at 5400 m altitude[5,6]. But even in this shortened growing period different species show different phenological behaviour, particularly flowering phenology, as the flowering periods are highly species-specific and even the flowering periods of closely related species are different[7].

In the Himalayan high altitudes, studies regarding phenology have been

made by some workers[8,9]. However, studies regarding flowering phenology are few and the overall effect of altitude on flowering phenology is not reported. Therefore, an attempt has been made here to assess the effect of altitude on flowering phenology of plants, particularly in the 'high altitude'.

Flowering starts early in the lower part of the high altitude and is delayed gradually with increasing altitude. However, to study the overall effect of altitude on flowering phenology, a specific approach has been used here in which the whole of
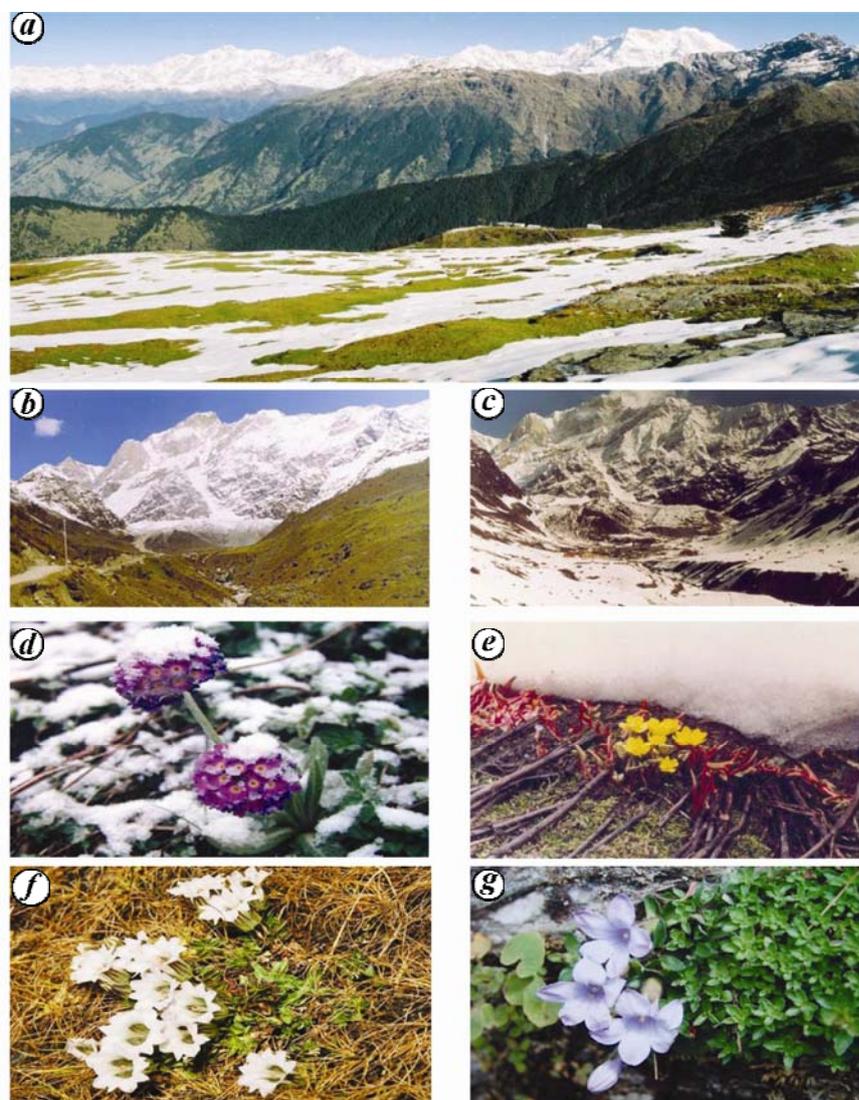
Figure 1. *a*, Panoramic view of high-altitude area in Garhwal Himalaya during October; *b*, *c*, Alpine zone during growing and dormant season; *d*, *e*, *Primula denticulata* and *Caltha palustris*, early flowering species; *f*, *g*, *Gentiana stipitata* and *Cyananthus integer*, late blooming species.
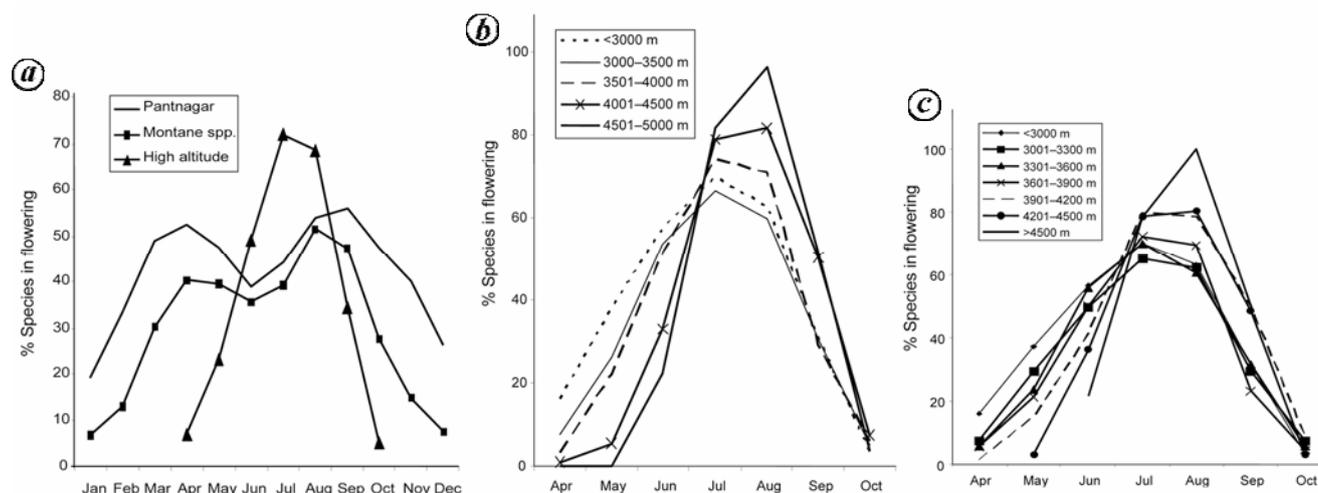
Figure 2. *a*, Flowering phenology in three zones. *b*, *c*, Flowering phenology in high altitude at 500 and 300 m interval.

the altitudinal stretch, from 3000 to 5400 m, is divided into different altitude classes, viz. 3000–3300 m, 3300–3600 m, 3600–3900 m, 3900–4200 m, 4200–4500 m and above 4500 m. Accordingly, the species observed above 3000 m are assigned to different altitude classes on the basis of their centre of altitudinal distribution (CAD). The uppermost and lowermost altitudinal limits of any species represent its maximum tolerance range to environmental factors changing with changing altitude and at these two extremes few individuals will manage to survive. But as we move upwards from the lower limit of distribution or downwards from the upper limit, the abundance of individuals will increase in response to more favourable environmental conditions till to an altitude where maximum favourable conditions are available (theoretically). Obviously, CAD of a species is the altitude where maximum probability of its occurrence exists. Though this point called CAD here, cannot be a sharp altitude as boundaries in nature are never so sharp, it is a useful point theoretically possible while considering a species as montane, alpine or treeline ecotone. A similar approach has also been used by Lenoir *et al.*[10] and termed as 'altitude of maximum probability of presence' or 'optimal elevation' for studying the upward shift in plant species. Based on its CAD a species is assigned to a particular altitude class where its centre of distribution lies. For example, *Dactylorhiza hatagirea* (D. Don) Soo is assigned to the 3600–3900 m class as its centre of distribution is 3700 m. Similarly, *Thylacospermum*

caespitosum (Cambess.) Schischk. is assigned to the 4500–4800 m class as its centre of distribution is 4750 m. These categorizations are done with the assumption that a species assigned to a particular class will be mainly distributed in its altitude class and thus represent the flowering phenology of that particular altitude zone. Overall phenology of all species belonging to a particular altitude class will be the representative phenology of this altitude class. Accordingly, 681 species observed above 3000 m in Garhwal Himalaya are categorized into different altitude classes. Because many species mainly distributed below 3000 m also occur in high altitudes, these are all categorized in the class 'below 3000 m'. Similarly, as very few species are mainly distributed above 4800 m in the alpine zone (only seven species), these are clubbed with those of 4501–4800 m and are called 'species above 4500 m'. Similarly, all 681 species of the high altitude are also categorized in bigger altitude classes of 500 m, viz. 3000–3500 m, 3501–4000 m, 4001–4500 m and above 4500 m, to check the trends obtained, at a larger scale. Flowering periods of observed species in Pantnagar (220 m amsl, 357 spp.) are based on our observations during 2007–2011. Mid-altitude (500–3000 m amsl, 463 spp.) distributions and flowering periods are based on Gaur[11] and those of high altitude (above 3000 m amsl, 681 spp.) are based on our studies and literature[8,12–19]. Finally, percentage of species flowering in a month in a particular area (Pantnagar, mid-altitude or high altitude) or altitude class is plotted against the months as

reported in the literature[1,8,20] to obtain flowering phenology of the entire growing season.

The results are shown in Figure 2. When overall flowering phenology of high altitude is compared with that of mid-altitude (submontane and montane zone) and Pantnagar (subtropical zone), few changes are evident – (i) at lower (subtropical) and mid-altitude flowering phenology is a two-peak phenomenon (first in spring, i.e. April, and second in late monsoon period, i.e. September), but compression of growing season at higher altitude (sub-alpine–alpine) results in single flowering peak (in July or August); (ii) flowering peaks at lower altitude (Pantnagar, mid-elevation) involve low percentage of species, but at higher altitude it involves higher number of species; (iii) with increasing altitude monsoon season peak becomes more and more pronounced. Within high altitude the important changes along the altitudinal gradient are – (a) number or percentage of species flowering in April reduces with increasing altitude and reaches zero above 4200 m, indicating melting of snow cover after April and consequent reduction in the growing season; (b) peak flowering involves more number or percentage of species with increasing altitude till no temporal choice is left, except for synchronous flowering and all species present are involved in peak flowering above 4500 m; (c) peak flowering occurs in July up to 4200 m, beyond which it shifts to August. The results are similar when species are classified in more broader altitudinal bands of 500 m (i.e. <3000 m, 3000–3500 m, 3501–

4000 m, 4001–4500 m and above 4500 m; Figure 2 c), indicating the constancy of trend. The duration of possible flowering season is about seven months for the lowest five classes (3000–4200 m), 6 months for the 4200–4500 m class and only 4 months or less above 4500 m.

The timing of many phenological events is the result of a complex interplay among the genes of an organism and several external environmental factors[3]. These factors, such as photoperiod, temperature and precipitation may directly control the timing of biological events or they may act instead as cues that set the internal biological clock of the organism[21]. In the tropics, variation in precipitation is more likely than temperature to drive phenological patterns[22] and for trees it is a single peak phenomenon in the dry season[23]. Similar flowering in trees is also known in this subtropical part of the Himalaya, and for herbs and shrubs flowering is a two-peak phenomenon at low and mid elevations[24]. With increasing altitude seasonality climate becomes more pronounced and reduction in temperature, moisture availability and length of growing season is obvious. Under such conditions, temperature and precipitation become important drivers than aridity and spring flowering diminishes while rainy season flowering becomes more pronounced. In the alpine zone, the timing of seasonal flowering is under tight environmental control with temperature and photoperiod playing important roles[1].

In high altitudes length of the growing season reduces with increasing altitude due to delayed snow melt and spring flowering is not possible. At high altitudes and latitudes flowering time and insect activity can be strongly, and apparently linearly, correlated with timing of snow melt[25,26]. Therefore, the snowmelt timing becomes an important driver of flowering by controlling the pollinators, and most of the flowering plants are pollinator-dependent. Characteristically, in this shortened growing season there is a phenological mid-domain effect of flowering diversity[2], which shows a peak in richness at the mid point of the flowering season. It is obvious that the flowering periods and altitudinal range of species also increase with increasing elevation and clear separation of flowering periods in different species is temporally not possible. This pattern of flowering showing mid-domain richness is found constant in all altitudinal classes in high altitude. But, some of the species may separate their flowering periods from majority of species by blooming very early in the season at different altitudes. In fact, there are 47 species flowering in April. Among them, species like *Caltha palustris* L. (Figure 1 *e*), *Oxygraphis endlicheri* (Walp.) Bennet & Sumer Chandra, *Primula* spp. (Figure 1 *d*), *Corydalis* spp., *Ranunculus* spp., *Bergenia stracheyi* (Hook.f. et Thoms.) Engl. and *Rhododendron campanulatum* D. Don are able to flower as soon as snow melts owing to their prefabricated flower or inflorescence buds. Such preformation is mentioned in 111 alpine plant species and more than 70% of them show opportunistic early flowering within one month of snow release[6]. This opportunistic nature of species is a ubiquitous arctic–alpine adaptation[27], which indicates that these species adopt the 'reproduce first grow later' tactics[28] and pollinators tend to favour peak or earlier flowering[29]. This can be seen as a strategy to separate their flowering period from other mid-season bloomers, though these species may face pollen-loss risk due to freezing temperatures in the early season[30].

Corresponding to the early bloomers, there are some species like *Aconitum violaceum* Jacquem. ex Stapf, *Delphinium* sp., *Sedum ewersii* Ledeb., *Chaetoseris cyanea* (D. Don) C. Shih., *Cyananthus integer* Wall. ex Benth. (Figure 1 *g*), *Gentiana stipitata* Edgew. (Figure 1 *f*), *G. prostrata* Haenke, etc. which are true late bloomers starting their flowering as late as September. Obviously, these species may be able to find pollinators, but face a seed-loss risk due to lack of sufficient time for maturation of fruits/seeds[30] or pre-dispersal seed predators which tend to favour off-peak or late flowering[29]. It becomes evident in *Aconitum violaceum* and *Cyananthus integer*, as these late bloomers do not produce seeds profusely. The case of *A. violaceum* and *C. integer* indicates that the 'grow first and reproduce later' tactics may not be as successful as the 'reproduce first grow later' tactics in the short growing season of high altitude. Though there are 35 species flowering in October, most of them do so by only prolonged flowering lasting up to October.

In the 3000–3900 m altitude zone, the possible flowering season is longer due to early snow melt and late arrival of snow cover. Consequently, the possible flowering season is longer up to 7 months in this zone. Here species have choice of early flowering, mid-season flowering or late-season flowering, as flowering periods are highly species-specific[1] and choices are possible. The trend of flowering phenology shows that flowering starts in April and peaks in July. But even at peak time the number of species involved in peak flowering is comparatively lower than that at higher altitudes because a large number of species occupy this altitude range and different species adopt different flowering strategies (early, mid or late-season flowering). However, with increasing altitude the duration of flowering season decreases, being 6 months long in the 4200–4500 m altitude range and 4 months (or less) long above the 4500 m altitude range. Therefore, choice to flower in a specific period is gradually narrowed with increasing altitude. Above 4500 m altitude a species has to flower between July and September and this results into gradual increase in flowering peak (% species involved in peak flowering) from 65.13% at 3000–3300 m range to 100% above 4500 m altitude range. Korner[1] schematically presented the effect of increasing latitude on percentage of species contributing to peak flowering, where he has shown that increasing latitude causes increase in the number of species contributing to peak flowering and maximum 80% of the species are involved in peak flowering in the alpine zone at 30° latitude; beyond 30°, it reduces up to 65% at 70°. In the present study a similar effect has been observed due to increasing altitude in the Himalaya. Our results further support Korner's calibration that even at 30° lat. (most of the sub-alpine–alpine zones in Garhwal Himalaya are between 30°N and 31°N lat.), variation in altitude affects the number of species contributing to peak flowering. It is 65% in the 3000–3300 m altitude zone and gradually increases to 100% above 4500 m altitude. Similar elevation of flowering peak with increasing altitude has been reported from Central Chilean Andes highlands[31].

Thus, increase in altitude or latitude has a similar effect, to great extent, on the number of species contributing to peak flowering in high-altitude areas, though the effect of altitude can elevate peak flowering to 100% at 30–31°N lat. in the Himalaya.

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Additional site for pollen germination in carrot

In angiosperms, pollination – either self or by various agents – mediates the transfer of pollen grains from the anther to the stigma, the site where pollen grains land; the compatible among these hydrate and subsequently germinate to produce pollen tubes that facilitate fertilization of the egg. However, in a few species, besides germinating on the surface of the stigma, pollen grains have been observed occasionally to germinate at other sites also, including the anther[1], intra-floral parts[2], ovary wall[3] and nectary[4]. In plants of *Daucus carota* L. ssp. *sativus*, the cultivated carrot, we observed pollen grains germinating at a hitherto unreported site, i.e. the stylopodium, the bulbous base of style, capping the epigynous ovary. Presence of the stylopodium is a characteristic feature of the family Apiaceae. It harbours a nectary. The observation is important as it puts on record one more site within the flower that has the potential of receiving the pollen grains and providing the necessary environment for them to germinate and produce pollen tubes. More significant is the observation that the pollen tubes formed at this site reach the ovules, leading to the formation of fruit.

D. carota, a biennial umbellifer, is represented by two subspecies, namely *sativus* and *carota*, in Jammu and Kashmir. The former is cultivated for its swollen napiform root and the latter grows wild. The wild forms were studied and collected from natural populations inhabiting Kud and Batote area. Plants of the cultivated form were grown in the Botanical Garden of the University of Jammu through seeds procured from the market. Both subspecies are andromonoecious and protandrous, exhibiting strong dichogamy[5].

Anthesis follows a sequential and centripetal order both at the level of umbellet and umbel. The stamens and petals are curved inwards in a bud and thereafter spread out as the flower opens gradually. As the anthers curve out, they dehisce and the process takes 2–3 days. There comes a time during anthesis when the anther is positioned in such a way that the self-pollen can easily fall on the stylopodium (Figure 1 *a*). Thus, some of the self-pollen invariably land on the stylopodium. Once the anthers have emptied their contents, the female phase begins. By the time the stigma becomes receptive, the pollen grains of the self-flower and every other flower in the same umbel are mostly dispersed, and the stylopodium is loaded with pollen grains belonging to the self-flower. Thus the stigma has the chance to receive cross-pollen only, whereas the stylopodium that is already loaded with self-pollen can be contaminated by cross-pollen also if an insect visits the flower.