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Developmental adaptation of leaves in *Podophyllum hexandrum* for effective pollination and dispersal

In alpine ecosystem, reproductive behaviour such as seed production and new plant establishment may be ineffective due to infrequent germination and low seedling survival^{1–3}. On the other hand, clonal plants from alpine habitats reveal similar genetic variation as lowland species, suggesting that at least occasionally there is recruitment from seeds. Plant phenology can be a useful tool in describing micro-environmental differences between various habitats. Bliss⁴ reported that many species in a specific habitat break dormancy, flower and fruit together, whereas the same species exhibits different cycles of development in other habitats. This shows the control of local micro-environmental factors on the pattern of plant development. Plants growing in alpine regions show unique phenology due to extreme environmental conditions. Temporal differences in snow disappearance determine the time of flower initiation and available growth period which affect reproductive success through the pollination process and the season length for fruit development^{5–8}. Because air temperature changes as the season progresses, plants exposed by melting of snow at different times of the season experience different temperature regimes through the life cycle.

The activity level of pollinators has been shown to decrease significantly with increasing altitude, and diversity of insects species declines rapidly in the high temperate mountains. These findings have led to the hypothesis that predicts lower outcrossing rates and higher amount of autogamy or apomixis at

high altitude, especially near the upper vegetational limits. Low temperatures and short snow-free periods which constrain the abundance and activity of insect pollinators^{8,9}, characterize arctic and alpine habitats. Thus, a relatively high proportion of arctic and alpine flowering plant species may have evolved autogamy and self-compatibility in response to poor cross-pollination opportunities. Self-compatibility co-evolves with changes in morphological or phenological traits of flowers that promote self-pollination¹⁰.

Podophyllum hexandrum Roxb. ex Kunth. is a rhizomatous herb found growing in the sub-alpine region of the Himalayas. The distribution of this species varies from 2000 to 4000 m asl and the habitat ranges from alpine meadows and understorey of cedrus forest. The phenology of *P. hexandrum* is similar to that of other alpine and sub-alpine plants, where leaf emergence is at the onset of snow melt and dispersal of seed at the onset of winter. During winter, the plant is in its dormant condition and perenniates in the rhizomatous form. In spring, the plant has to produce flowers, successfully pollinate and reproduce/disperse seeds within a short span of 4 months. For effective propagation of this endangered species, it has an unusual combination of traits related to sexual reproduction. Most notably, it does not reward its native pollinators. The flower is large (3–6 cm in diameter), white, fragrant, bowl-shaped, with six petals, six stamens and a single, unilocular pistil with 50–150 ovules. The flower lacks nectar, but has abundant pollen. The flowers are protandrous; the

anthers often dehisce before the flower has opened, stigmas remain receptive even as the stamens and petals abscise from the flower, approximately 1–2 weeks after anthesis. Factors such as prolonged stigma receptivity in plants at high elevation can offset reduction in pollination rates and make it comparable to pollinations at lower-elevation plants. For adaptation and perpetuity, the plant formulates effective adaptation, developmental modification for effective pollination and dispersal.

Immediately after the onset of snow melt, the rhizome sprouts and develops into first leaf (Figure 1a) with a rich anthocyanin pigmentation which may function as a UV protectant or protect from herbivores since the leaf may not be visible due to the reflection of anthocyanin and also the leaf may not palatable. Within a few days the lobed leaves become greenish (Figure 1b) and productivity is more during this stage (through podophyllotoxin production, pers. obs.). Later, the young green leaf forms a dark pigment from the centre (Figure 1c) towards the periphery and is wholly pigmented within a few days of the first leaf formation. The pigmented secondary leaves develop from the base of the first leaves along with the flower (Figure 1d). At this time only a prominently bright, white flower is visible with a dark, pigmented shrunken leaf providing contrasting background suitable for attracting pollinators. Within 3–4 days of anthesis, the petals and stamen wither-off and gynoecium remains 3–4 days after anthesis to receive more pollen, since the number

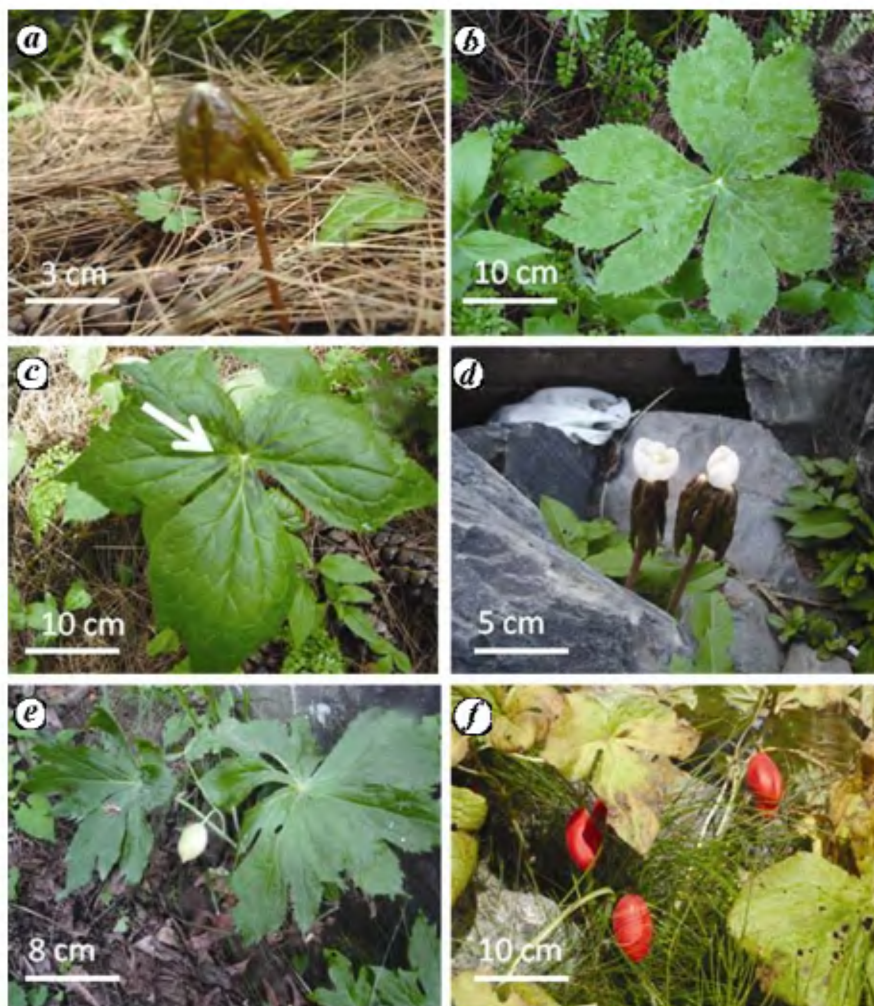


Figure 1. Adaptation and modification of leaves during different developmental stages. *a*, Young leaves; *b*, Vegetative; *c*, Vegetative with pigment formation; *d*, Flowers; *e*, Young fruit, and *f*, Matured fruits.

of ovules is higher and they produce viable seeds only when cross-pollinated. After fertilization, the immature fruit develops simultaneously along with a third leaf and the young fruit is then hidden with the help of large green leaves (Figure 1 *e*) for possible protection from herbivores. After maturation the fruit turns reddish and the leaves become yellowish due to loss of pigment; hence the

fruit is more prominently visible (Figure 1 *f*). The fruits are fleshy and edible at maturity and seed coat is hard, which explains the possibility of seed dispersal through herbivores. In conclusion, the developmental stages of *P. hexandrum* protect it from herbivores at the first leaf emergence stage and also at the early fruit formation stage, and thereafter attract herbivores at fruit ripening stage.

During flowering, the plant attracts pollinators with its bright, white-coloured flowers and a background of pigmented dark-coloured leaves.

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