

# Flowering phenology of tree rhododendron along an elevation gradient in two sites in the Eastern Himalayas

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**Abstract** Flowering phenology of tree rhododendron (*Rhododendron arboreum* Sm.) was monitored in situ along elevation gradients in two distinct ecological settings. Observations were carried out in Gaoligong Nature Reserve (GNR) in China and in the Kanchenjunga Conservation Area (KCA) in Nepal. Using the crown density method, flowering events of the selected species were recorded. Flowering duration and synchrony were determined within each site and along the elevation gradient in each study area. Our observations showed high synchrony throughout the elevation gradient, especially for peak flowering. Mean 15-day soil temperature,

soil parameters (soil moisture, nitrogen, organic matter and pH), age of the observed trees, and site characteristics (litter cover, canopy cover, inclination) were related to mean initial and peak flowering dates using partial least squares regression (PLS). Results differed between the two sites, but winter temperature was the most important variable affecting the regression model for both initial flowering and peak flowering at both sites. After temperature, soil moisture was the most important variable for explaining initial flowering dates. The distribution of tree rhododendron indicates that it is able to grow in a wide range of habitats with different environmental conditions. The recent trend of rising winter-spring temperature and the detected bloom-advancing effect of high temperatures during this period suggest that tree rhododendron might expand its distributional range in response to global warming.

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## Introduction

Human-induced climate change is one of the most influential drivers of changes in the distribution of biodiversity and the timing of biological events (Parmesan and Yohe 2003; Root et al. 2003; Walther et al. 2002). High elevation environments are characterized by limited photosynthetic activity and a very short growing season, which may be associated with snow or ice (Inouye and Wielgolaski 2003). Ecologically, high elevation environments include alpine and montane areas with temperate climates, where the annual life cycle of plants is determined by weather-related events, such as snowmelt, soil thawing and the

fulfillment of chilling requirements (Inouye and Wielgolaski 2003; Körner 2003; Luedeling et al. 2011). Global climate change is affecting phenology in these high elevation environments (Inouye and Wielgolaski 2003).

Various studies have detected biological changes in relation to recent climate change (Bertin 2008; Parmesan and Yohe 2003; Root et al. 2003), especially for spring phenology in temperate regions (Ibanez et al. 2010; Menzel et al. 2006). There is documentation of several factors that affect plant phenology. Temperature, sunshine duration, humidity (precipitation and soil moisture) and winter chilling are chief among them (Blake and Harris 1960; Jackson and Bliss 1984; Johansen et al. 1985; Kalbarczyk 2009; Körner and Basler 2010; Lucier and Hinckley 1982; Robbirt et al. 2010; Seghieri et al. 2009), along with soil nitrogen, organic matter, canopy cover and other environmental factors (Blake and Harris 1960; Dahlgren et al. 2007; Joiner and Gruis 1959; Kudo et al. 2008; Ma et al. 1997; Nord and Lynch 2009; Wielgolaski 2001). Dahlgren et al. (2007) mention canopy cover, plant density, slope and soil characteristics, such as depth, temperature, water content, pH, nutrient concentrations and litter layer as critical environmental factors. Among these factors, temperature is typically considered the most critical driver of the early stages of the growing season (Miller-Rushing and Primack 2008; Min 2000). Dozens of studies have established the effects of air temperature on plant phenology and demonstrated shifts in plant phenological events in response to rising temperature (Sparks et al. 2000; Fitter and Fitter 2002; Menzel et al. 2005; Primack and Miller-Rushing 2011). The impacts of climate change are predicted to be most pronounced in high-elevation environments (IPCC 2007), where these changes are a serious threat to biodiversity. In high-elevation environments, several above-mentioned factors besides temperature may influence flowering phenology, and the processes controlling flowering phenology in trees remain poorly understood.

In high mountain regions, flowering phenology changes along elevation gradients, with plants at lower elevations typically flowering earlier than plants of the same species that grow at higher elevations (Bertiller et al. 1990; Ziello et al. 2009). A similar pattern of phenology change is reported by Fielding et al. (1999) in insects (*Neophilaenus lineatus*) with no difference in developmental rates between lower and higher elevations. Generally, air temperature in mountainous regions decreases strongly with increasing elevation at a lapse rate of about 0.6 °C every 100 m (Barry 1992; Du et al. 2007; Fang and Yoda 1988). This temperature gradient is a crucial factor in the timing of biological events. Atmospheric circulation pattern, precipitation and sunshine duration vary strongly in mountainous regions due to variation in aspect and inclination. This creates strongly variable microclimates within mountain regions, which lead to differences

between phenology at high altitudes compared to lower sites (Inouye and Wielgolaski 2003).

Soil temperature is driven at least partly by variation in air temperature (Chudinova et al. 2006) and it changes with elevation. Soil temperature may change water and nutrient availability by altering soil moisture or organic matter inputs (Körner 2006; Nord and Lynch 2009). In addition to soil temperature, soil pH also determines plant growth through effects on nutrient uptake (Fageria and Zimmermann 1998). Soil pH may affect phenology (particularly growth) by effects on nutrient availability, which is lowered at high pH for many essential elements. The phenology of understory plants depends on the amount of light that newly emerged leaves can intercept, before the canopy of the upper story vegetation closes (Kudo et al. 2008). Similar to the canopy layer, the litter layer is also important in high elevation environments. Its slow decomposition rate reduces soil moisture loss from evaporation and buffers the amplitude of soil temperature by insulating the surface (Sato et al. 2004; Scopel et al. 2004). Rhododendron leaf litter decomposes very slowly, thereby shortening the time during the winter, when soils are frozen. Rhododendrons are reported to flower earlier under water deficit conditions (Sharp et al. 2009) and prevention of soil moisture loss by leaf litter might prevent water stress. All the above-mentioned conditions are interlinked, creating unique micro-environments in mountains. Besides these factors, the age of trees also affects flowering time (Yelemou et al. 2009). Yelemou et al. (2009) found that both flowering and fruit formation occurred earlier in older than in younger trees. Therefore, it is worth checking for a response of flowering phenology to these parameters along elevation gradients.

Species-level phenological studies are useful for elucidating plant responses to various micro-climatic factors, as the rhythm of plant phenology is attuned to environmental seasonality. The rates of warming in the Eastern Himalayas and adjoining regions are significantly higher than the global average (Shrestha 2009). It is therefore important to monitor changes in phenology in this region in response to climatic changes, but no long-term observations have been conducted there. Located in geologically young, unstable and rugged terrain, remoteness and inaccessibility are characteristic of these mountains. A dearth of previous phenological records and adequate research facilities are further constraints to long-term species-level observation, especially in Nepal. Lack of long-term phenological monitoring makes it impossible to correlate phenological change with temperature change, but research designed along elevation gradients can produce baseline information regarding climate and phenology. With a lapse rate of 0.6 °C / 100 m of elevation, a plant population spread over 500 m of elevation range will experience mean temperature differences of c. 3 °C. This is comparable with the temperature

increases predicted to occur as a result of global warming (Fielding et al. 1999).

#### The *Rhododendron arboreum* complex

The response of ecological systems to climate can best be characterized by focusing on ecologically important keystone species. The Eastern Himalayas and adjoining regions are the center of *Rhododendron* diversity, with unparalleled richness and dominance of the genus. *Rhododendron* is one of the keystone species at higher elevations (Singh et al. 2009). The *Rhododendron arboreum* complex is one of the most widely distributed species in this region occurring from 1200 to 3700 masl. It is one of the most important components of the ecosystem as different individuals tend to bloom from early spring to early summer, maintaining pollinator populations with their profuse flowering over a wide variety of habitats in the temperate to subalpine regions. The *Rhododendron arboreum* complex is distributed from Kashmir (NW India) to Yunnan (China) throughout the Himalayas. Flowering onset in this complex is regarded as an indicator of the arrival of spring by the aboriginal people of the Himalayan foothills. For the above-mentioned reasons, we selected *R. arboreum* Sm. for the present study. Sub-species of *Rhododendron arboreum* (source: Sekar 2010 and GRIN Taxonomy for Plants) are as follows:

- *R. arboreum* Sm. subsp. *arboreum*
- *R. arboreum* Sm. subsp. *roseum* Lindl.
- *R. arboreum* Sm. subsp. *cinnamomeum* (Wall. ex G. Don) Tagg
- *R. arboreum* Sm. subsp. *delavayi* (Franch.) D. F. Chamb.
- *R. arboreum* Sm. subsp. *nilagiricum* (Zenker) Tagg (endemic to South India)
- *R. arboreum* Sm. subsp. *zeylanicum* (T. J. Booth) Tagg (endemic to Sri Lanka)

The taxonomic status of *R. arboreum* subsp. *delavayi* is in debate; Chamberlain referred to it as sub-species of *R. arboreum* (Chamberlain 1982) while the Flora of China describes it as *R. delavayi* (Fang et al. 2005). It is described as eastern *R. arboreum* in the world's major taxonomic database (e.g. IPNI, GRIN Taxonomy for Plants accessed on Sept 2011), which keeps it as a sub-species of *R. arboreum*. Flowering of all sub-species and varieties occurs around the same time and highly overlaps for individuals at similar altitude. In the present paper, we describe this group as *R. arboreum* complex. At the study sites in Nepal, the most common species is *R. arboreum* subsp. *cinnamomeum*, whereas individuals at study sites in China are mostly *R. arboreum* subsp. *delavayi*.

The purpose of this study was in-situ monitoring of phenology events in the *R. arboreum* complex at temperate

and subalpine regions, to track the flowering synchrony across an elevation gradient, to determine the most influential environmental factors that drive flowering phenology, and to compare *Rhododendron* phenology at two ecologically different sites.

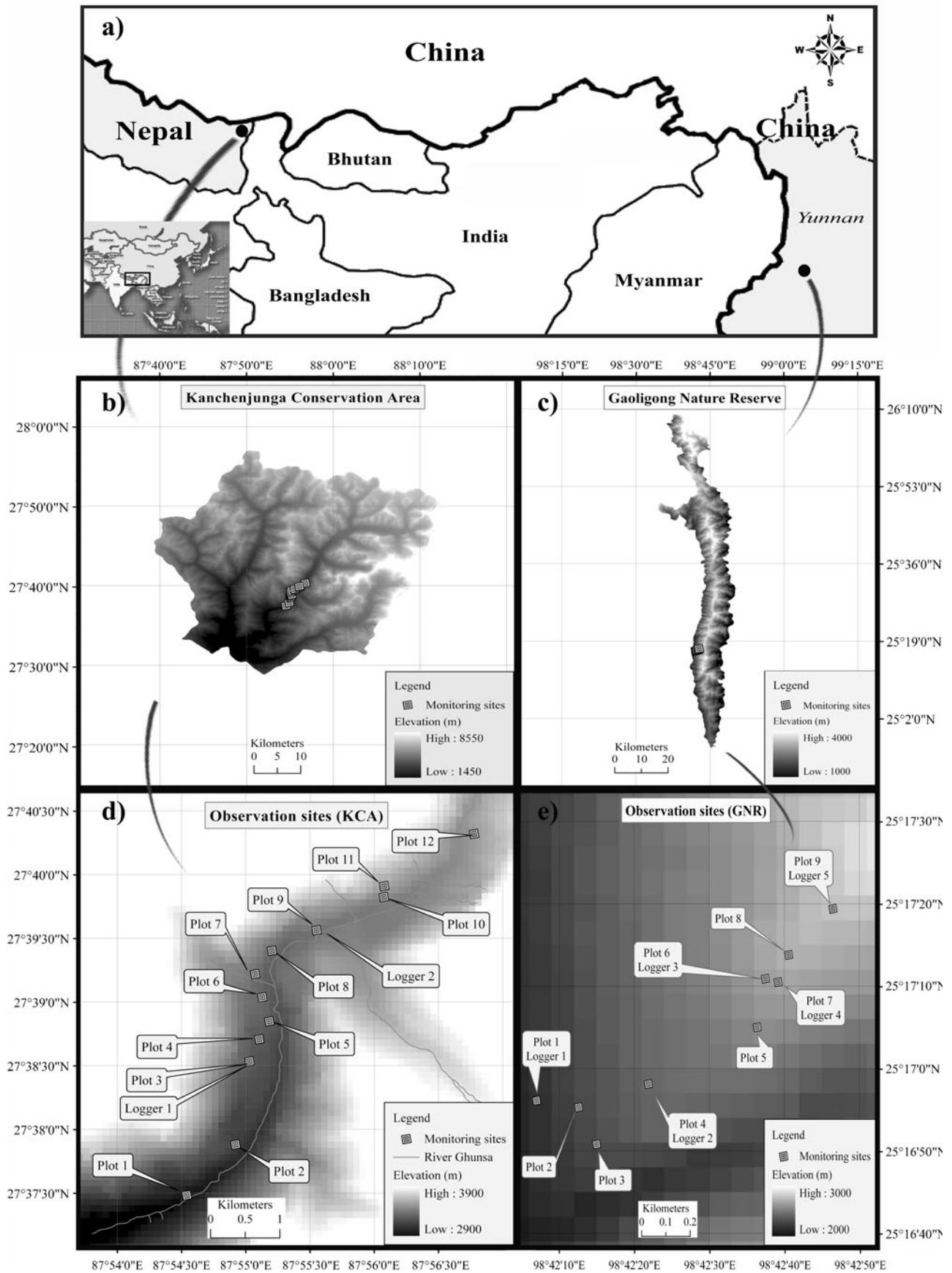
## Materials and methods

### Study site

Elevation gradients covering the local distribution ranges of the *R. arboreum* complex were chosen in Gaoligong Natural Reserve (GNR) and Kanchenjunga Conservation Area (KCA).

**Yunnan site (GNR)** The surveyed sites in China were located in the southern part of the Gaoligong Mountains in western Yunnan (Fig. 1a, c and e). The Gaoligong mountain range lies at the intersection of the Eastern Himalayas and the Hengdong Mountains of China. The sites were about 25 km from Tengchong County, where the nearest meteorological station lies (at c. 2000 masl). The climate of the study area is characterized by high rainfall and humidity, under the influence of the Indian Ocean Monsoon. The Yunnan site receives monsoonal rains from the southwest. Annual average precipitation recorded at the meteorological station is 1400 mm and rainfall occurs throughout the year (Li 2003). The observation sites are in warm temperate climate. The natural vegetation is mixed broad-leaf forest, dominated by species such as *Alnus nepalensis*, *Lyonia ovalifolia*, *Symplocos paniculata*, *Betula alnoides*, *Schima khasiana*, *Myrica esculenta*, and in some sites *Pinus yunnanensis*.

**Nepal site (KCA)** Observation sites in Nepal were in the Ghunsa river valley in northeast Nepal near the base of Mount Kanchenjunga (Fig. 1a, b and d). The sites were about 45 km from the district headquarters at Taplejung, where the nearest meteorological station is located (at c. 1700 masl). High rainfall and humidity are brought from the southeast by the Indian Ocean Monsoon. Meteorological recordings show average annual precipitation of 1350 mm, with about 80 % of the rainfall received during the monsoon (mid-June to September) (GoN 2008). The observation sites represent cool temperate and sub-alpine climate types, and mild to heavy snowfall occurs during November to February. Typical vegetation is mixed broad-leaf forest, composed mainly of species like *Quercus semicarpifolia* and *Lyonia ovalifolia* at lower elevation, *Rhododendron campanulatum*, *R. barbatum*, *Larix griffithiana* and *Juniperus recurva* at mid-elevation and *Betula utilis* and *Juniperus indica* at the higher elevation.



**Fig. 1** a Locations of the two selected areas in Taplejung, Nepal and Tengchong, China. b, c Kanchenjunga Conservation Area (KCA) and Gaoligong Nature Reserve (GNR), with squares showing the phenological monitoring sites. d, e Phenology monitoring sites along altitude in KCA and GNR with the position of temperature loggers (detailed characteristics in Table 1)

Temperature records in both study areas show warming trends (after 1998) following similar patterns (Fig. 2). At the Nepal site, the warming trend was stronger than in Yunnan for winter and spring temperatures (Fig. 2). Over the last two decades, average seasonal (winter + spring) temperature change per decade was  $+0.47\text{ }^{\circ}\text{C}$  at Tengchong (GNR) and  $+0.57\text{ }^{\circ}\text{C}$  at Taplejung (KCA).

#### Field data collection

Phenology monitoring plots of  $20\times 20\text{ m}^2$  were selected based on the relative distribution of the *R. arboreum* complex along the elevation gradient. Detailed site characteristics are presented in Table 1. At the GNR site in Yunnan, nine study plots were chosen spanning 680 m of elevation (2150 masl to 2830 masl) along a 2-km transect on a southwest-facing slope (Fig. 1e). At the KCA site in Nepal, 12 sites were distributed over an elevation gradient of 621 m

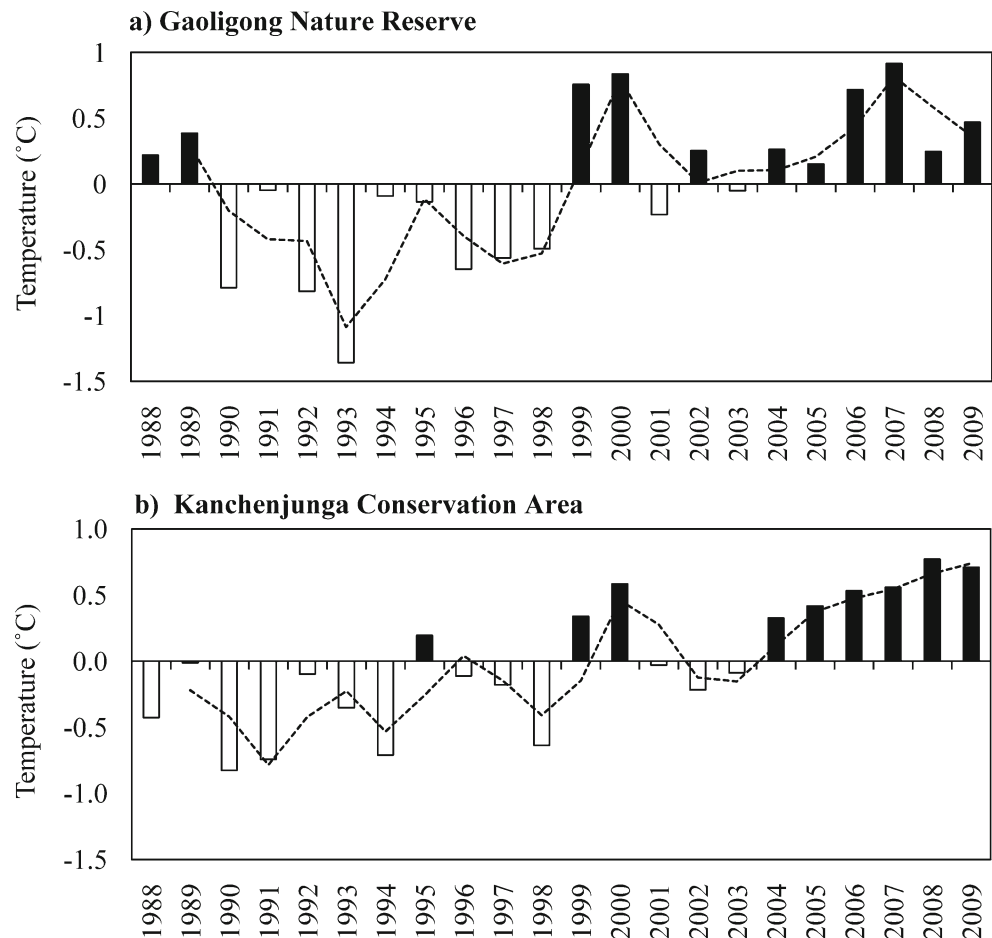
(2976 masl to 3597 masl) on an 8-km transect on a southeast-facing slope (Fig. 1d). The two study sites were about 1100 km apart, and separated by 800 m in elevation.

Soil samples were collected before flowering began from observation plots at both study areas. Sampling was done at two different depths (0–15 cm and 15–30 cm) from each corner and center of the observation site. All soil samples from each plot were mixed to arrive at one set of soil parameters per plot. Soil samples were sent to laboratories for determination of soil nitrogen, organic material, moisture content and pH. Temperature loggers were installed at a depth of 10 cm to record soil temperature along the elevation gradients. Five loggers were installed at the Yunnan site and two at the Nepal site (Fig. 1d and e). Temperature recording was started in May 2010 in China and in April 2010 in Nepal.

#### Phenological observation

The crown density observation method (Koelmeyer 1959) was adopted for phenological observations. In this method, distributions of distinct phenophases across the whole tree crown are scored on a linear scale, for instance, 0–4, with 0 representing absence of the phenophase and 4 representing maximum intensity. Values of 3, 2 and 1 represent three-

**Fig. 2** Temperature anomaly during winter and spring as recorded at the meteorological station in Tengchong (a) (China; 25 km from the study site) and Taplejung (b) (Nepal; 45 km from the study site) from 1988 to 2009. The running means (annual temperature) indicate increasing winter and spring temperature since the early 1990s in both areas



**Table 1** Site characteristics in the Gaoligong Nature Reserve, Yunnan, China (GNR) and the Kanchenjunga Conservation Area, Nepal (KCA)

Site	Ele	Lat	Long	Inc	Lit	Can	Exp	Asp	Snowfall	SM	N	OM	pH	Other feature
GNR 1	2150	25.2820	98.7035	45	90	80	PS	SW	NA	34.38	0.545	8.07	5.37	
GNR 2	2250	25.2823	98.7019	40	90	80	PS	SW	NA	37.915	0.655	8.32	5.07	M
GNR 3	2350	25.2808	98.7042	50	40	70	PS	SW	NA	30.155	0.785	11.09	4.375	LM
GNR 4	2410	25.2828	98.7061	15	90	70	Sh	S	NA	37.51	0.75	10.27	4.08	M
GNR 5	2500	25.2847	98.7101	45	100	70	Sh	SE	NA	33.35	0.825	11.25	4.08	
GNR 6	2680	25.2864	98.7104	60	90	90	Sh	SE	NA	35.23	0.36	5.845	5.135	PR
GNR 7	2700	25.2863	98.7109	20	40	55	Su	S	NA	38.895	0.42	6.525	5.28	M
GNR 8	2750	25.2872	98.7113	30	25	50	PS	SW	NA	30.8	0.34	5.255	5.12	LM
GNR 9	2830	25.2887	98.7129	30	50	80	PS	SW	NA	22.2	0.285	4.46	5.39	LM
KCA1	2976	27.6247	87.9090	25	40	35	Su	SW	Little	57.6	1.03	11.64	5.6	Close to river
KCA 2	3143	27.6314	87.9153	45	35	25	Su	SE	Medium	43.5	0.85	9.91	5.28	HD
KCA 3	3169	27.6422	87.9172	40	30	25	Su	SW	Medium	23.7	0.53	6.1	5.33	PR
KCA 4	3228	27.6451	87.9184	35	10	10	Su	SE	Medium	13.7	0.6	7.02	5.52	PR
KCA 5	3250	27.6506	87.9188	30	10	85	Sh	SE	Medium	19.7	0.54	6.3	5.3	PR
KCA 6	3291	27.6475	87.9197	40	20	30	PS	NE	Medium	29.5	0.65	7.63	5.21	
KCA 7	3301	27.6537	87.9179	10	20	30	Su	SW	Medium	37.4	0.3	3.47	5.79	HD
KCA 8	3373	27.6567	87.9201	15	25	65	PS	SE	Heavy	30	0.24	2.74	5.9	HD
KCA 9	3409	27.6594	87.9259	10	40	90	PS	SE	Heavy	39.2	0.8	9.15	5.02	Close to river
KCA 10	3503	27.6637	87.9346	20	30	80	Su	SE	Heavy	33.3	0.85	9.91	5.15	HD
KCA 11	3546	27.6720	87.9463	15	30	50	PS	SE	Heavy	29.6	0.16	1.83	5.87	HD
KCA 12	3597	27.6652	87.9347	35	40	70	Sh	SW	Heavy	32.2	0.75	8.76	5.04	

*Ele* elevation (m), *Lat* latitude (°), *Long* longitude (°), *Inc* inclination (°), *Lit* litter (%), *Can* canopy coverage (%), *Exp* exposure, *Asp* aspect, *SM* soil moisture, *N* soil nitrogen, *OM* organic matter, *M* moist, *LM* less moist, *PR* pure rhododendron, *HD* human disturbance, *PS* partly shady, *Sh* shady, *Su* sunny, *SW* southwest, *S* south, *SE* southeast, *NE* northeast

quarters, half, and one-quarter of the maximum intensity, respectively. Where a certain phenophase occurred on a tree but amounted to less than a quarter of the maximum intensity, a score of 0.5 was assigned. The sum of all phenophase scores can never be greater than the maximum value, but it can be lower because not all trees attain maximum intensity. This was carried out at 15-day intervals, from the beginning of flowering until the end of the monsoon. The following flowering stages were recorded: (1) bud, (2) bud opening (but still no petals visible), (3) >5 % flowering (petals opening) in inflorescence, (4) fruiting. In this paper, we only discuss observations on stage 3. Phenophases were scored based on their coverage ratio for each of the above-mentioned stages in each tree. Branches without buds were not considered during measurement and scoring. Trees that did not flower in the observation year were excluded from the analysis even though tagged for observation. Data on one season of flowering phenology for 113 trees from nine plots in GNR and for 97 trees from 12 plots in KCA were used for analysis.

#### Phenology data treatment

Phenophase scores were expressed as percentages of coverage and averaged for each study plot. For each individual,

phenology was characterized by (a) initial flowering date (day of the year at which >5 % flowering in inflorescence), (b) peak flowering date (day of the year with highest percentage of flowers in full bloom), and (c) bloom duration (number of days the plant remained in bloom). In addition we calculated flowering synchrony  $S_i$  for a given individual  $i$  by applying the formula of Augspurger (1981) in the modified version used by Giménez-Benavides et al. (2007):

$$S_i = \frac{1}{(n-1)} \sum_{j=1}^{n-1} \left( \frac{a_{ij}}{b_{ij}} \right)$$

where  $n$  is the number of plants, ' $a_{ij}$ ' is the number of days individuals  $i$  and  $j$  are simultaneously in bloom, and ' $b_{ij}$ ' is the number of days when at least one of them is in bloom. Synchrony ranges between 1, when flowering completely overlaps, and 0, when there is no overlap. Synchrony was calculated for individual trees within each plot and averaged to obtain one synchrony value per plot. Average bloom overlaps between plots were also examined. For this, first and last flowering dates in each observation plot were determined and these values were used to calculate bloom overlapping between the plots.

Initial flowering dates were averaged over all individuals in each plot. The resulting mean values were then

correlated with environmental factors for the plot, namely, soil moisture, soil pH, mean age of trees (see section 2.6), soil nitrogen, organic matter, and site characteristics (litter, canopy coverage, and slope). Partial least squares (PLS) regression was used to analyze the data (Luedeling and Gassner 2012). Fifteen-day interval temperature data from September 2009 to August 2010, soil parameters, average age of trees per plot, and plot characteristics were used to explain mean initial and peak flowering dates for each plot. Variable importance in the projection (VIP) and standardized model coefficients were used to interpret results of the PLS regression (Luedeling and Gassner 2012; Nokels et al. 2010). The VIP statistic reflects the importance of terms in the model both with respect to dependent and other independent variables (Hladysz et al. 2011). The VIP scores are based on a weighted sum of squares of the PLS loadings and calculated for each variable. Standardized model coefficients, and their 95 % confidence interval were used to interpret the direction (Nokels et al. 2010; Tenenhaus et al. 2005), in which certain independent variables affected bloom dates (advancing or delaying). Independent variables with  $VIP \geq 0.8$  and standardized coefficient confidence intervals significantly different from zero were considered important (Nokels et al. 2010; Wold 1995) for explaining bloom dates. For statistical analysis and preparing illustrations, we used XLSTAT, the statistical add-in extension of Excel; and REXcel, the statistics package R from within Excel.

#### Temperature and lapse rate

Air temperature ( $T_a$ ) obtained from the nearest meteorological station was averaged and plotted against mean soil temperature ( $T_s$ ). The resulting linear regression equations [ $T_s = 0.8006(T_a) + 0.5998 (R^2 = 0.95, p < 0.001; SE = 0.77)$  for GNR and  $T_s = 0.8333(T_a) - 2.9633 (R^2 = 0.61, p < 0.001; SE = 1.35)$  for KCA] were used to calculate soil temperature for the observation sites at lowest elevation for the duration when temperature recording was not available at the observation site

(September 2009 to April 2010). For the period, for which records for both soil temperature at the sampling sites and air temperature at weather stations were available, predicted temperatures, when averaged for 15 day intervals, closely matched observations. From 15-day means of temperatures recorded at different altitudes between September 2009 and September 2010, lapse rates for temperature were calculated for both study areas (Table 2). From calculated temperature and lapse rates in the study area, we interpolated soil temperatures for each observation plot.

#### Diameter based age determination

Cores were collected from several marked trees based on stem diameter (bigger and smaller) as representative of each observation site. Ages of the representative trees were determined from collected cores in a dendrochronology laboratory at the Ecological station, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, China. Average annual increments of the representative trees were determined and used to calculate the average age of trees at each observation plot:

$$\text{Average age of trees} = \sum_i^n [DBH_i / (2 \times aai \times n)]$$

where  $DBH_i$  is the diameter of tree  $i$  at breast height (cm),  $aai$  is the average annual increment (cm) and  $n$  is number of individuals.

## Results

#### Flowering duration and synchrony along elevation gradients

At the Yunnan site, flowering commenced in late January and lasted until the last week of April. At the Nepal site, flowers appeared in the third week of March and lasted until

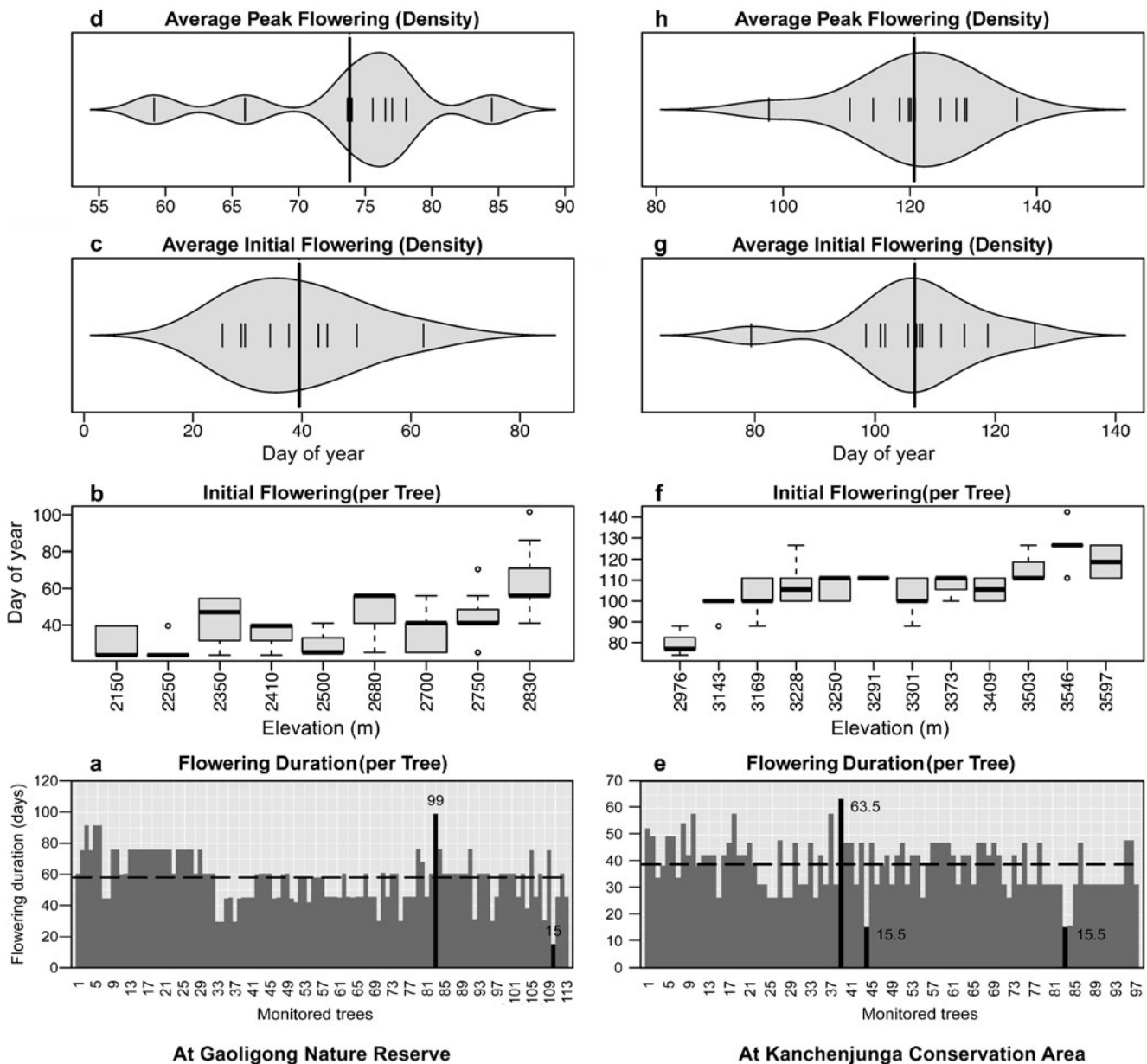
**Table 2** Fifteen-day interval temperature lapse rate calculated for each 100-m elevation difference based on the highest and lowest elevation of temperature recording

Location	Month													
	1-Sep	16-Sep	1-Oct	16-Oct	31-Oct	15-Nov	30-Nov	15-Dec	30-Dec	14-Jan	29-Jan	13-Feb	28-Feb	
GNR	0.54	0.55	0.55	0.57	0.59	0.61	0.63	0.66	0.66	0.63	0.64	0.61	0.59	
KCA	-0.04	0.07	0.25	0.55	0.64	0.87	0.91	1.09	1.21	1.13	1.18	1	0.66	
Location	15-Mar	30-Mar	14-Apr	29-Apr	14-May	29-May	13-Jun	28-Jun	13-Jul	28-Jul	12-Aug	27-Aug	11-Sep	
GNR	0.58	0.57	0.57	0.55	0.55	0.55	0.55	0.55	0.55	0.54	0.54	0.54	0.55	
KCA	0.29	0.22	0.13	0.11	0.05	-0.07	-0.19	-0.14	-0.18	-0.23	-0.12	-0.13	-0.01	

GNR Gaoligong Natural Reserve, KCA Kanchenjunga Conservation Area

the first week of June. In some observed trees flowering duration was very short, with all branches blooming at the same time and most flowers shed simultaneously. In other trees flowering duration was substantially longer. The mean duration of the flowering phases over all individuals was 19 days longer at the Yunnan site [mean 57.6 (SE = 1.47) days, range 15–99 days;  $n=113$ ] than at the Nepal site

[mean:38.76 (SE = 0.97) days, range 16–64 days;  $n=97$ ] (Fig. 3a and e). Flowering pattern and duration varied from tree to tree within each plot (Fig. 3a, b, e and f). In some trees, all branches were in bloom simultaneously, while in others bloom was staggered. Simultaneous flowering shortened bloom duration, while in the latter case it was extended (Fig. 3b and f).



**Fig. 3** a and e Flowering duration recorded for individual trees at monitoring plots. Individual trees with highest flowering and lowest flowering duration were plotted in *bold bars*, and average flowering duration for all the observed trees plotted in *dashed lines*. b and f Initial flowering date recorded in individual trees within each plot along the elevation gradients. Lack of clear quartiles in the box plots is because of simultaneous flowering (shortening bloom duration) in some trees and consecutive flowering (extending bloom duration) in some trees

within each observation plot. c and g Average initial flowering time in the observation plots. d and h Same as 'c' for average peak flowering. In plots c, d, g and h *bulge parts* represent duration with a high density of flowering activity. *Black lines* stand for average flowering dates in each observation plot, and the *bold line* is the average of all observation plots. More than one *bulge part* indicates that flowering activity was not uniformly distributed, as well as synchronized flowering activity in adjacent plots. 'Day of year' are the days of the year in 2010



**Table 3** Flowering dates of tree rhododendron averaged for each observation plot along the elevation gradient in the Gaoligong Nature Reserve, Yunnan, China

Flowering	Elevation								
	2150 m	2250 m	2350 m	2410 m	2500 m	2680 m	2700 m	2750 m	2830 m
Initial	28-Jan	25-Jan	12-Feb	3-Feb	29-Jan	19-Feb	6-Feb	13-Feb	2-Mar
Peak	14-Mar	5-Mar	15-Mar	13-Mar	28-Feb	17-Mar	16-Mar	18-Mar	24-Mar
End	18-Apr	4-Apr	29-Mar	29-Mar	23-Mar	8-Apr	15-Apr	10-Apr	21-Apr

In the Yunnan plots (GNR), most of the observed trees started flowering between late January and early March, but some trees only showed first flowers in mid-April (Fig. 3b). Mean initial flowering dates occurred during the first and second week of February (Fig. 3c and Table 3). Peak flowering lasted from late February until late April (Fig. 3d and Table 3). At KCA, flower initiation varied between mid-March and early-May (Fig. 3f), whereas peak flowering occurred between mid-March and late-May (Fig. 3g and h; and Table 4). Mean flowering synchrony for individual trees within observation plots ranged from 0.649 to 0.914 at GNR and 0.629 to 0.871 at KCA (Table 5). Bloom overlap between plots ranged from 0.649 to 0.974 [lowest value in a plot at the highest elevation and highest value in middle elevation (plot 5); see Fig. 1e] at GNR (Table 5). At KCA the bloom overlapping range was 0.531 at the lowest elevation (plot 1; see Fig. 1d) to 0.906 at middle elevation (plot 5; Fig. 1d). Mean overlapping value for both study areas were greater than 0.85 (Table 5), indicating high levels of overlap between bloom of individual trees at both locations. At both sites, initial flowering dates were generally delayed with increasing elevation, but due to high variation among individual trees, there was no significant trend. In addition to slight delays in initial bloom, flowering periods were contracted at high elevations.

#### Environmental controls on flowering dates

Among soil parameters, 15-day averages of soil temperature and mean age of trees, the PLS regression analysis identified those variables with the greatest influence on initial and

peak flowering dates. It also explored the direction in which high values for the respective variables pushed flowering dates at the two sites.

#### Gaoligong Nature Reserve (Yunnan, GNR)

The most important variables for explaining initial flowering dates at GNR were temperatures during the winter months (Dec, Jan and Feb) followed by temperature in late-Autumn (Nov) and early-Spring (Mar). Temperatures throughout the year were identified as important variables, along with soil moisture, nitrogen and organic matter (Fig. 4). For peak flowering, VIP values indicated that nitrogen, organic matter, litter and winter temperatures (Dec and Jan) were most important, followed by temperature of other seasons, soil moisture and soil pH (Fig. 4a). Interestingly, soil nitrogen, organic matter content and litter cover were found to strongly influence peak flowering at GNR (Fig. 4b). Standardized PLS model coefficients (Fig. 4a and b) showed that high soil pH (for peak flowering only) had positive effects (delaying bloom dates), whereas for the remaining important variables, high values had advancing effects on bloom dates. The main factors responsible for early bloom dates were thus high temperatures, low pH (for peak flowering), as well as high soil moisture, soil nitrogen and soil organic matter content. Model coefficients were significantly different from zero for temperature and soil parameters (moisture, nitrogen, and organic matter) for initial flowering, while only parameters for soil nitrogen, organic matter, litter and temperature during early and mid-winter were significantly different from zero for peak flowering (Table 6 and Fig. 4). For all other factors, even some identified as important by the VIP statistic, coefficients were

**Table 4** Flowering dates of tree rhododendron averaged for each observation plot along the elevation gradient in the Kanchenjunga Conservation Area, Nepal

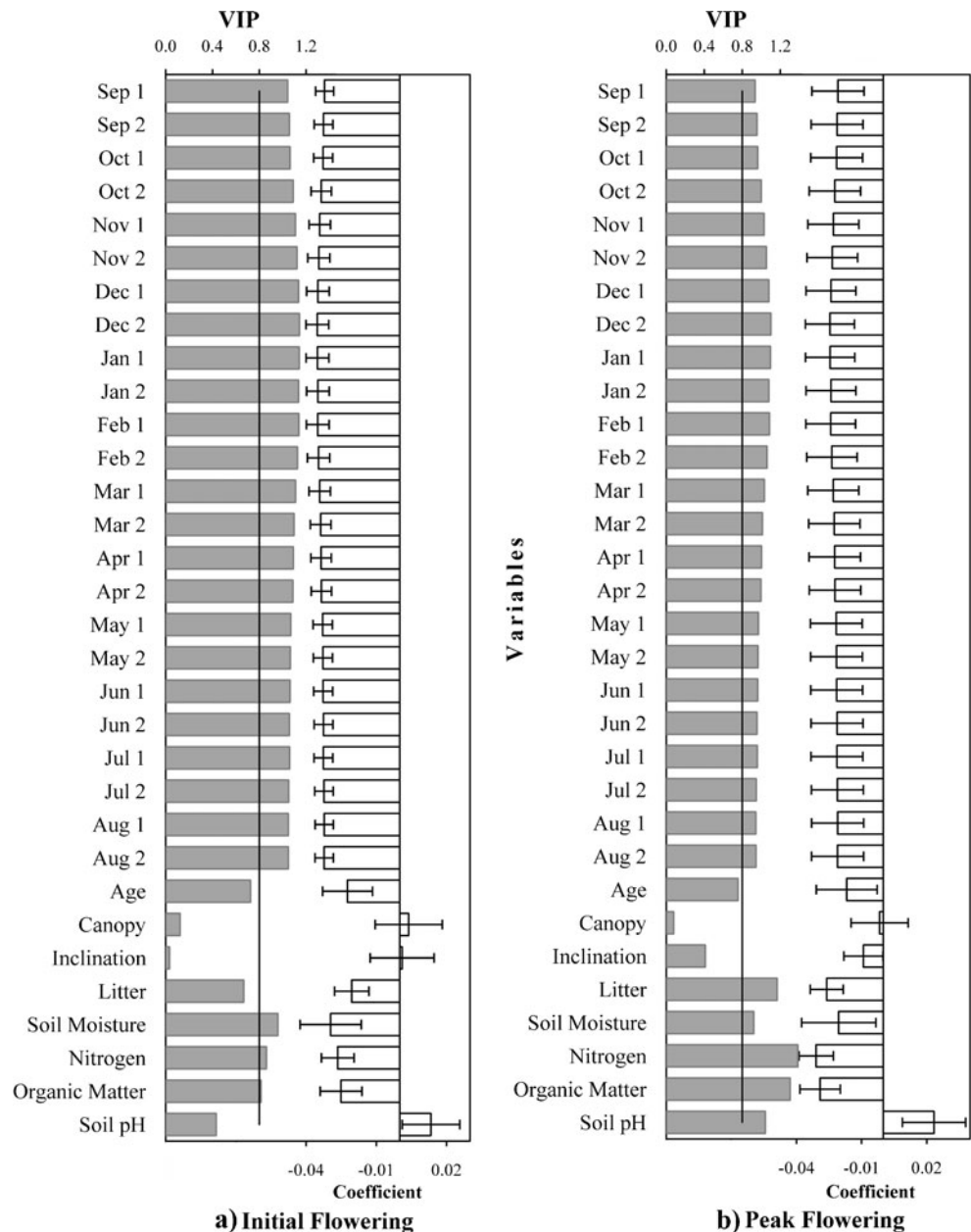
Flowering	Elevation											
	2976 m	3143 m	3169 m	3228 m	3250 m	3291 m	3301 m	3373 m	3409 m	3503 m	3546 m	3597 m
Initial	19-Mar	7-Apr	10-Apr	16-Apr	15-Apr	20-Apr	9-Apr	16-Apr	14-Apr	23-Apr	5-May	27-Apr
Peak	6-Apr	19-Apr	29-Apr	28-Apr	27-Apr	29-Apr	23-Apr	7-May	3-May	6-May	15-May	7-May
End	3-May	19-May	26-May	19-May	23-May	31-May	18-May	30-May	24-May	29-May	4-Jun	2-Jun

**Table 5** Flowering synchrony at the observation sites calculated for each plot and between plots

Parameter	Ele GNR plots (m)	Ave Syn in plot	Ave Syn btw plot	Ele GNR plots (m)	Ave Syn in plot	Ave Syn btw plot	Ele KCA plots (m)	Ave Syn in plot	Ave Syn btw plot	Ele KCA plots (m)	Ave Syn in plot	Ave Syn btw plot
Flowering synchrony	2150	0.931	0.916	2680	0.804	0.778	2976	0.771	0.531	3301	0.629	0.912
	2250	0.939	0.755	2700	0.890	0.920	3143	0.681	0.882	3373	0.670	0.912
	2350	0.780	0.891	2750	0.864	0.916	3169	0.717	0.882	3409	0.718	0.912
	2410	0.658	0.891	2830	0.649	0.779	3228	0.590	0.902	3503	0.731	0.924
	2500	0.974	0.886				3250	0.795	0.906	3546	0.697	0.729
						3291	0.668	0.779	3597	0.871	0.954	
Mean								0.859				0.852
SE								0.023				0.035

*Ele* elevation, *Ave* average, *Syn* synchrony, *in plot* refers to observed and calculated within each observation plot, *btw plot* values are calculated between observation plots based on averaging the flowering period in each plot and compared with remaining plots

**Fig. 4** Response of the initial flowering and peak flowering along elevation gradients in GNR according to PLS regression. **a** Standardized regression coefficients and variable importance in the projection (VIP) plotted against all variables used to explain initial flowering. **b** Same for peak flowering. Abbreviations of month names, followed by the numbers 1 and 2 indicate temperatures during the first and second half of the respective month



**Table 6** VIP and standardized coefficient values from PLS analysis for initial and peak flowering

Location	Variable	VIP (I)	Coefficient (I)	SD (I)	Lower (95 %)	Upper (95 %)	VIP (P)	Coefficient (P)	SD (P)	Lower (95 %)	Upper (95 %)
GNR	Sep 1–15 09	1.042	-0.032	0.004	-0.040	-0.025	0.936	-0.021	0.012	-0.044	0.003
	Sep 16–30 09	1.057	-0.033	0.004	-0.040	-0.025	0.955	-0.021	0.012	-0.045	0.002
	Oct 1–15 09	1.063	-0.033	0.004	-0.041	-0.025	0.963	-0.022	0.012	-0.045	0.002
	Oct 16–30 09	1.089	-0.034	0.004	-0.042	-0.025	0.999	-0.022	0.012	-0.046	0.001
	Oct 31-Nov 14 09	1.109	-0.034	0.005	-0.043	-0.025	1.031	-0.023	0.012	-0.046	0.000
	Nov 15–29 09	1.122	-0.035	0.005	-0.044	-0.025	1.053	-0.024	0.012	-0.046	-0.001
	Nov 30- Dec 14 09	1.135	-0.035	0.005	-0.044	-0.025	1.080	-0.024	0.011	-0.047	-0.002
	Dec 15–29 09	1.142	-0.035	0.005	-0.045	-0.026	1.101	-0.025	0.011	-0.047	-0.002
	Dec 30 09- Jan 13 10	1.141	-0.035	0.005	-0.045	-0.026	1.097	-0.025	0.011	-0.047	-0.002
	Jan 14–28 10	1.135	-0.035	0.005	-0.044	-0.026	1.080	-0.024	0.011	-0.047	-0.002
	Jan 29- Feb 12 10	1.138	-0.035	0.005	-0.045	-0.026	1.086	-0.024	0.011	-0.047	-0.002
	Feb 13–27 10	1.126	-0.035	0.005	-0.044	-0.025	1.061	-0.024	0.012	-0.046	-0.001
	Feb 28- Mar 14 10	1.110	-0.034	0.005	-0.043	-0.025	1.032	-0.023	0.012	-0.046	0.000
	Mar 15–29 10	1.097	-0.034	0.004	-0.042	-0.025	1.011	-0.023	0.012	-0.046	0.001
	Mar 30- Apr 13 10	1.091	-0.034	0.004	-0.042	-0.025	1.002	-0.022	0.012	-0.046	0.001
	Apr 14–28 10	1.087	-0.034	0.004	-0.042	-0.025	0.997	-0.022	0.012	-0.046	0.001
	Apr 29- May 13 10	1.068	-0.033	0.004	-0.041	-0.025	0.970	-0.022	0.012	-0.045	0.002
	May 14–28 10	1.065	-0.033	0.004	-0.041	-0.025	0.966	-0.022	0.012	-0.045	0.002
	May 29- Jun 12 10	1.062	-0.033	0.004	-0.041	-0.025	0.962	-0.022	0.012	-0.045	0.002
	Jun 13–27 10	1.057	-0.033	0.004	-0.040	-0.025	0.955	-0.021	0.012	-0.045	0.002
	Jun 28- Jul 12 10	1.059	-0.033	0.004	-0.041	-0.025	0.958	-0.021	0.012	-0.045	0.002
	Jul 13–27 10	1.051	-0.032	0.004	-0.040	-0.025	0.947	-0.021	0.012	-0.045	0.002
	Jul 28- Aug 11 10	1.048	-0.032	0.004	-0.040	-0.025	0.943	-0.021	0.012	-0.045	0.002
	Aug 12–26 10	1.048	-0.032	0.004	-0.040	-0.025	0.944	-0.021	0.012	-0.045	0.002
	Age	0.725	-0.022	0.011	-0.043	-0.001	0.756	-0.017	0.014	-0.044	0.011
	Canopy coverage	0.124	0.004	0.014	-0.024	0.032	0.077	-0.002	0.013	-0.028	0.024
	Inclination	0.032	0.001	0.014	-0.026	0.028	0.411	-0.009	0.009	-0.027	0.009
	Litter coverage	0.666	-0.021	0.007	-0.035	-0.006	1.168	-0.026	0.008	-0.041	-0.011
	Soil moisture	0.958	-0.030	0.013	-0.055	-0.004	0.920	-0.021	0.017	-0.054	0.013
	Soil nitrogen	0.860	-0.027	0.007	-0.040	-0.013	1.385	-0.031	0.008	-0.046	-0.015
Soil organic matter	0.814	-0.025	0.009	-0.043	-0.008	1.304	-0.029	0.009	-0.047	-0.011	
Soil pH	0.433	0.013	0.012	-0.011	0.037	1.044	0.023	0.015	-0.005	0.052	
KCA	Sep 1–15 09	0.839	-0.028	0.018	-0.063	0.007	0.686	-0.009	0.014	-0.037	0.020
	Sep 16–30 09	1.143	-0.040	0.011	-0.061	-0.019	1.051	-0.030	0.008	-0.045	-0.014
	Oct 1–15 09	1.282	-0.047	0.005	-0.057	-0.037	1.243	-0.043	0.004	-0.051	-0.036
	Oct 16–30 09	1.326	-0.050	0.004	-0.057	-0.043	1.331	-0.052	0.005	-0.063	-0.042
	Oct 31-Nov 14 09	1.305	-0.051	0.007	-0.064	-0.037	1.355	-0.059	0.009	-0.076	-0.041
	Nov 15–29 09	1.286	-0.051	0.009	-0.068	-0.034	1.350	-0.060	0.010	-0.080	-0.041
	Nov 30- Dec 14 09	1.310	-0.052	0.007	-0.066	-0.037	1.357	-0.059	0.009	-0.076	-0.042
	Dec 15–29 09	1.306	-0.052	0.008	-0.069	-0.036	1.357	-0.059	0.009	-0.077	-0.042
	Dec 30 09- Jan 13 10	1.303	-0.053	0.009	-0.071	-0.034	1.355	-0.060	0.009	-0.078	-0.042
	Jan 14–28 10	1.310	-0.052	0.008	-0.069	-0.036	1.358	-0.059	0.009	-0.076	-0.042
	Jan 29- Feb 12 10	1.300	-0.053	0.009	-0.071	-0.034	1.355	-0.060	0.009	-0.078	-0.042
	Feb 13–27 10	1.321	-0.052	0.007	-0.066	-0.039	1.358	-0.058	0.008	-0.073	-0.042
	Feb 28- Mar 14 10	1.326	-0.051	0.005	-0.060	-0.042	1.347	-0.055	0.007	-0.068	-0.042
	Mar 15–29 10	1.321	-0.050	0.004	-0.057	-0.043	1.309	-0.050	0.005	-0.058	-0.041
	Mar 30- Apr 13 10	1.301	-0.049	0.005	-0.059	-0.039	1.266	-0.045	0.005	-0.054	-0.036

**Table 6** (continued)

Location	Variable	VIP (I)	Coefficient (I)	SD (I)	Lower (95%)	Upper (95%)	VIP (P)	Coefficient (P)	SD (P)	Lower (95%)	Upper (95%)
	Apr 14–28 10	1.203	−0.043	0.009	−0.060	−0.026	1.130	−0.035	0.006	−0.047	−0.023
	Apr 29- May 13 10	1.221	−0.045	0.008	−0.060	−0.029	1.150	−0.036	0.006	−0.048	−0.024
	May 14–28 10	1.060	−0.035	0.015	−0.064	−0.007	0.954	−0.023	0.010	−0.043	−0.004
	May 29- Jun 12 10	0.802	−0.028	0.017	−0.061	0.005	0.636	−0.006	0.015	−0.035	0.023
	Jun 13–27 10	0.069	0.002	0.030	−0.056	0.060	0.140	0.030	0.023	−0.015	0.075
	Jun 28- Jul 12 10	0.433	−0.015	0.022	−0.057	0.028	0.230	0.014	0.019	−0.024	0.051
	Jul 13–27 10	0.092	0.001	0.029	−0.056	0.057	0.118	0.029	0.023	−0.015	0.073
	Jul 28- Aug 11 10	0.144	0.009	0.030	−0.049	0.067	0.357	0.038	0.022	−0.005	0.082
	Aug 12–26 10	0.459	−0.013	0.025	−0.062	0.037	0.268	0.012	0.021	−0.028	0.052
	Age	0.711	−0.101	0.041	−0.181	−0.021	0.631	−0.042	0.038	−0.117	0.032
	Canopy coverage	0.506	−0.036	0.047	−0.128	0.055	0.656	0.020	0.027	−0.033	0.073
	Inclination	0.175	0.101	0.101	−0.098	0.299	0.422	−0.008	0.070	−0.144	0.129
	Litter coverage	0.233	−0.099	0.047	−0.191	−0.007	0.084	−0.021	0.027	−0.073	0.031
	Soil moisture	0.860	−0.146	0.057	−0.257	−0.034	0.833	−0.070	0.049	−0.165	0.026
	Soil nitrogen	0.729	−0.070	0.048	−0.164	0.025	0.837	−0.061	0.032	−0.122	0.001
	Soil organic matter	0.700	−0.065	0.051	−0.164	0.034	0.819	−0.060	0.033	−0.124	0.004
	Soil pH	0.115	−0.016	0.100	−0.211	0.180	0.001	0.011	0.057	−0.102	0.123

VIP variable importance of the projection, SD standard deviation, I initial flowering, P peak flowering

not significantly different from zero, making interpretation of their influence difficult.

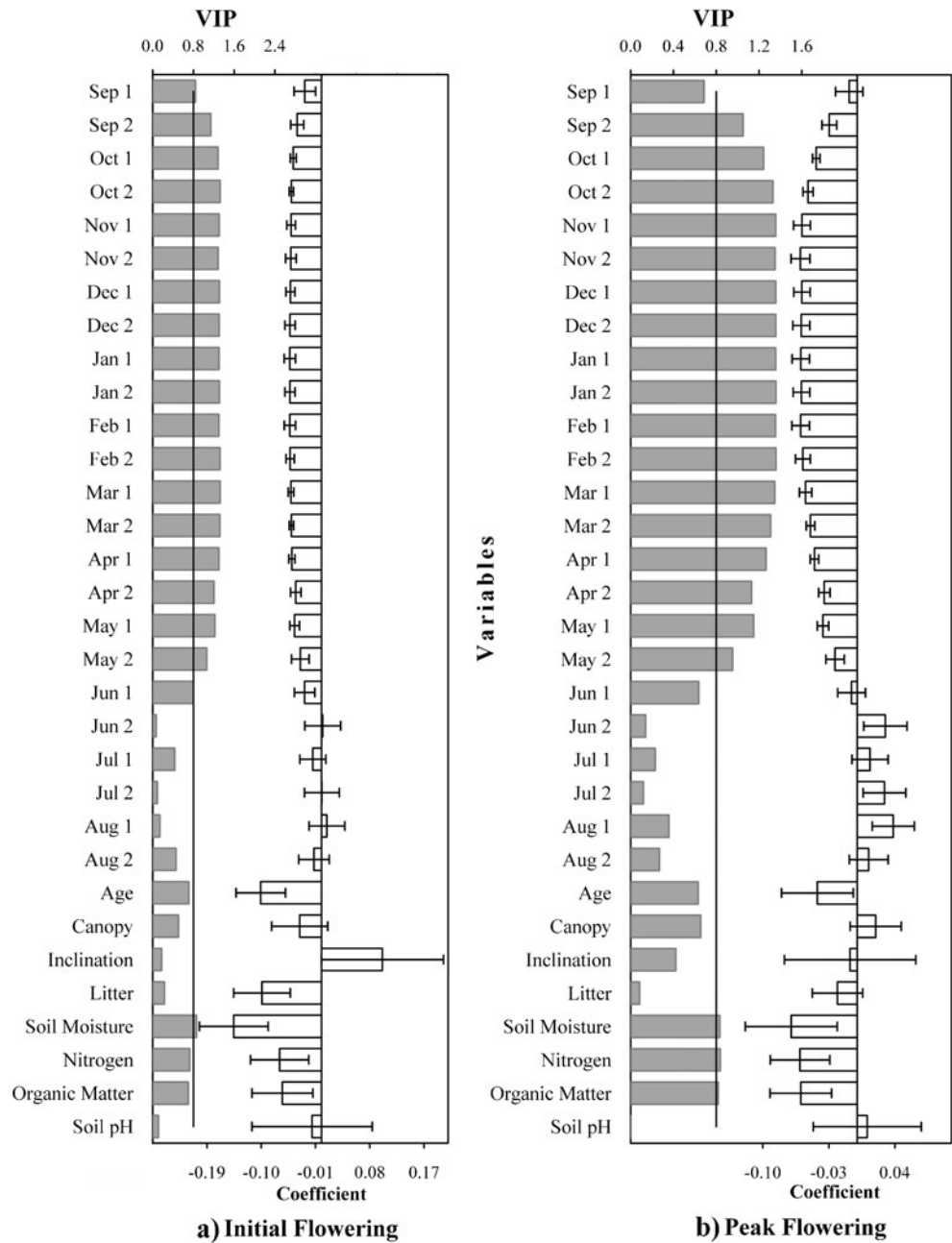
#### *Kanchenjunga Conservation Area (Nepal, KCA)*

At KCA, the variable importance plots (VIP) indicated that the most important variables for explaining initial flowering dates were temperatures between mid-autumn (Oct) and early spring (Mar). Soil moisture and temperatures in early-Autumn (Sept) and mid-late spring (April, May) were also important for explaining the response of flowering dates (Fig. 5a). For peak flowering, temperature during winter (Dec, Jan and Feb) was most important, along with autumn (late Sept, Oct and Nov) and spring (Mar, Apr and early May) temperatures, soil nitrogen, soil moisture and organic matter (Fig. 5b). Standardized PLS model coefficients revealed that high values for all the important variables had a negative (advancing) effect. Coefficients were significantly different from zero for soil moisture and temperature for initial flowering and for temperature for peak flowering (Fig. 5a and b and Table 6). Even though VIP values for soil nitrogen, soil moisture and organic matter were greater than 0.8, standardized coefficient confidence intervals included zero (Table 6 and Fig. 5), so that the effects of these parameters on bloom dates were not clear. Overall, our results indicated that winter temperature was the most important control on flowering events in both study areas.

#### **Discussion and conclusions**

Our field observations showed earlier bloom at lower elevations in both study sites, and shorter flowering periods with increasing altitude. These results are in line with earlier studies describing delayed flowering and contractions in bloom duration with elevation for different species (Crimmins et al. 2009; Rusch 1993). Occasional deviations from this pattern along our elevation gradients may have been caused by variations in micro-environmental factors (Giménez-Benavides et al. 2007). In spite of differences in the timing of first and peak bloom dates, flowering synchrony among trees within each of the study sites was high. This was probably due to longer flowering periods by individuals at lower elevations compared to those at higher altitudes, which ensured overlap even with late-blooming trees elsewhere. High synchrony among a high number of individuals within a given region favors genetic variation by enabling high levels of cross-pollination. This in turn should promote genetic diversity and thereby raise the capacity of a species to adapt to the harsh conditions of the sub-alpine regions as revealed by Stinson (2004) for *Potentilla pulcherrima*. Besides the need of trees at high elevations to complete their seed production process in a shorter time than trees of the same species at lower elevations, this evolutionary principle may be responsible for the observed flowering patterns. We suspect that flowering patterns in the study regions are particularly suited to genetically

**Fig. 5** Response of the initial flowering and peak flowering along elevation gradient in KCA according to PLS regression. **a** Standardized regression coefficients and variable importance in the projection (VIP) plotted against all variables used to explain initial flowering. **b** Same for peak flowering. Abbreviations of month names, followed by the numbers 1 and 2 indicate temperatures during the first and second half of the respective month



enrich the higher-elevation sites, because pollinator populations build up first at lower elevations and may be forced to move to higher elevations as availability of pollen at the lower locations decreases. The opposite process seems less likely, because at the end of the flowering phase at high elevations, there is little incentive for pollinators to move back downhill. Unlike bugs (Fielding et al. 1999) and flies (Kudo et al. 2004), however, some main pollinators of rhododendron, such as honey bees and bumble bees, do not appear synchronously with the flowering of host plants at different levels of an elevation gradient. A single hive of them can forage across a wide range (c. 1 to several kilometers) and over a long period of time (c. 5 months) (Dornhaus and Chittka 2004; Macdonald 2003; Osborne et al.

1999). Nevertheless, it seems likely that the capacity of high elevation-populations to adapt to environmental changes is higher than that of populations at lower elevations.

Flowering duration was shorter at plots in Nepal than in Yunnan, probably due to the longer prevalence of cold temperatures or even snow cover at KCA, which is at substantially higher elevation than the GNR plots. While much of the variation in flowering dates can be explained by temperature, not all plots along the elevation gradient behaved as expected, leaving variation in micro-climates to explain some of the variation (Gao et al. 2009; Whittaker and Niering 1975). Generally, soil temperatures in our study plots decreased with increasing elevation, except for

temperatures between June and September at KCA, which were higher than at lower elevations. This pattern, which may have been caused by stronger insolation at higher sites, may have helped advance peak flowering dates at high locations, promoting flowering synchrony.

Soil temperature showed a significant correlation with flowering phenology, confirming results by Dahlgren et al. (2007), who worked on *Actaea spicata*. This probably reflected the strong correlation between soil temperature and air temperature (Chudinova et al. 2006), which has been identified as the strongest driver of phenology. Late-autumn, winter and early-spring temperatures were the most influential variables for initial flowering phenology in the present study. This finding is consistent with previous studies reporting temperature as the major driver of spring phases (Menzel et al. 2005; Miller-Rushing and Primack 2008; Parmesan and Yohe 2003; Root et al. 2003). The primary advancing factor of rhododendron flowering onset at GNR seemed to be high temperatures during winter. These results show that unlike most other perennial plants of the temperate and cold climates (Yu et al. 2010), rhododendron is responsive to heat during all months of the winter. For temperate trees (Luedeling and Gassner 2012) or alpine grasslands (Yu et al. 2010), winter warming has been shown to delay spring phases, possibly caused by delayed fulfillment of plants' chilling requirements. Because rhododendron does not fall dormant and does not have a chilling requirement, it does not experience this effect, so that this species should not be affected by changes in winter chill due to climate change (Luedeling et al. 2011). Sharp et al. (2009) reported premature anthesis in fully-formed floral buds of *Rhododendron* cultivars under water deficit treatments without the need for a winter chilling treatment. Similar phenomena may also occur in nature.

In our work soil moisture along with soil nitrogen and organic matter also seemed to influence first flowering dates in both study sites, with high values for all parameters advancing the onset of flowering. This is in line with many previous findings for other species (Joiner and Gruis 1959; Blake and Harris 1960; Jackson and Bliss 1984; Ma et al. 1997; Wielgolaski 2001; Seghieri et al. 2009; Nord and Lynch 2009). Changes in soil moisture affect the uptake of soil nutrients (Nord and Lynch 2009), which is necessary for growth as well as for flowering.

Surprisingly, soil parameters (nitrogen, organic matter and litter coverage) were the most important influencing factors for peak flowering in the GNR plots, with winter temperatures being less important. The advancing effects of soil nitrogen, organic matter and litter may be related to nutrient availability. High amounts of both may also improve soil structure and water infiltration, and litter has been shown to keep the soil warm during the winter (Putman and Wratten 1984). At the Kanchenjunga plots, soil parameters did not seem to influence bloom dates, indicating that at the

high elevations in this area, temperature effects dominate plant responses.

Elevation likely serves as a proxy for mean ambient temperature, confirming the strong correlation between temperature and phenology in the KCA site. Temperatures in early spring, late autumn and winter were most important. For peak flowering, winter temperature was most important. Autumn and spring temperature, as well as soil moisture, nitrogen and organic matter content were also found to influence peak flowering.

PLS analysis revealed that effects of all variables on initial flowering dates worked in the same direction in both study areas. However, the order of importance and the strength of the effects differed between sites. Yet some variables were found to be significant only at one of the sites. This was true for the amount of plant litter on the soil surface, high amounts of which advanced bloom dates at GNR, probably via effects on soil moisture. At KCA, this effect was not found important, but this was most likely caused by human disturbance rather than ecological relationships. Inhabitants of the KCA region regularly collect leaf litter from most sites, leading to generally low litter cover, which may not be sufficient for exerting strong effects on bloom dates. In addition to temperature and other variables, solar radiation intensity (sunny vs. shady sites; Table 1) may contribute to the fluctuation of flowering activity.

Flowering phenology is a vital ecological phenomenon, which is under tight environmental control. Temperature is the strongest driver of phenology, making it highly likely that the timing of plant phases will be affected by climate change. Most studies have found an advancing trend with warming, but some recent studies (Luedeling and Gassner 2012; Yu et al. 2010) have indicated that many plants that evolved in cold-winter climates may also experience delayed phenology due to later fulfillment of chilling requirements. Our study indicates that the latter does not apply for rhododendron, an evergreen plant that does not experience winter dormancy. Instead, leaves of this species are receptive to warming during all winter months, leading to advances in spring phases in response to warming. It is thus quite possible that rhododendron will be better able than many other species to exploit additional thermal resources available due to climate change. Where winter-dormant species may struggle to adjust to new thermal regimes, rhododendron may simply grow faster and reproduce more vigorously. This may lead to range expansions in rhododendron in response to global warming, possibly at the expense of other species. The widespread occurrence of rhododendron in the Himalayas may be evidence of similar processes in the past. We suggest that the study of differential responses among plant types to climate change deserves more attention, to enhance our ability to project the effects of global warming on ecosystem composition.

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