

Demography of the giant monocarpic herb *Rheum nobile* in the Himalayas and the effect of disturbances by grazing

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- **Background** Perennity of giant rosette species in combination with a single ‘big bang’ reproduction followed by death of the genetic individual is relatively rare among plants. Such long-lived monocarpic plants are usually slow growing and can be found in deserts, bogs or in alpine regions of the tropics or sub-tropics. Due to their longevity, monocarpic perennials risk losing everything before reproduction, which make them particularly susceptible to disturbances. Because of the inherent difficulties in assessing whether long-lived populations are growing or declining, usually neither their demography nor the consequences of increasing grazing pressure are known.
- **Methods** We used integral projection modelling (IPM) to measure the growth rate and passage time to flowering of *Rheum nobile*, a monocarpic perennial, and one of the most striking alpine plants from the high Himalayas. Rosettes which were no longer found due to disturbances or grazing by yaks were either treated as missing or as dead in two series of analysis, thereby simulating demography with and without the impact of grazing cattle. Data were collected from plants at 4500 m a.s.l. in Shangri-la County, Yunnan Province, south-west China. In four consecutive years (2011–2014) and in two populations, 372 and 369 individuals were measured, respectively, and size-dependent growth, survival and fecundity parameters were estimated. In addition, germination percentage, seedling survival and establishment probability were assessed.
- **Key results** The probability of survival, flowering and fecundity were strongly size dependent. Time to reach flowering size was 33.5 years [95 % confidence interval (CI) 21.9–43.3, stochastic estimate from pooled transitions and populations]. The stochastic population growth rate (λ_s) of *Rheum nobile* was 1.013 (95 % CI 1.010–1.017). When disturbance by grazing cattle (yaks) was accounted for in the model, λ_s dropped to values <1 (0.940, 95 % CI 0.938–0.943).
- **Conclusion** We conclude that natural populations of this unique species are viable, but that conservation efforts should be made to minimize disturbances by grazing and to protect this slow-growing flagship plant from the high Himalayas.

Key Words: Flowering size, integral projection model (IPM), semelparity, seed-consuming pollination mutualism, selection, yak grazing.

INTRODUCTION

Rheum nobile was discovered and first described to western science in 1855 by J. D. Hooker, the contemporary and friend of Darwin and the later director of the Royal Botanical Gardens in Kew. Hooker noted: ‘the present is certainly the most striking of the many fine alpine plants of Sikkim’ (Hooker and Fitch, 1855). He was probably not aware then that he had discovered, at an elevation above 4000 m a.s.l., one of the very few giant and most charismatic monocarpic perennials from above the tree line in the Himalayas. Alpine plants usually are dwarfed, slow growing and long-lived perennials with repeated flowering and seed production, thereby saving resources for future growth and reproduction. In contrast, monocarpic perennials have an extended juvenile phase, saving resources for a single and fatal act of reproduction during which all available resources are consumed

(Schaffer, 1974). In alpine regions, such plants are mostly giant herbs, with a single large inflorescence growing from a rosette, and reproducing in a single reproductive event, which has been called ‘big bang’ seed production (Young and Augsburger, 1991). This distinct life form is relatively rare among plants and occurs sometimes in nutrient-poor habitats such as bogs, and more frequently as a unique life form of tropical high mountains. Well-known examples are *Puya raimondii* in the high Andes in Peru (Sgorbati *et al.*, 2004), *Argyroxiphium sandwicense* (silversword) of volcanoes on Hawaii (Krushekbysjy *et al.*, 2013), the giant *Lobelia* plants of tropical mountains in Africa (Young, 1990), *Lupinus alopecuroides* from the Paramo of Ecuador (Vasquez *et al.*, 2016) or *Echium wildpretii* from the Teyde volcano of Tenerife (Stöcklin, 2011).

The selective forces shaping such an unusual life form are poorly understood. Theory suggests that monocarpic perennials

should evolve when reproductive success is increasing with increasing reproductive effort (Schaffer and Schaffer, 1977, 1979). This might be favoured by pollinator preferences for large inflorescences, increasing pollination efficiency with size, and pollinator satiation (Young and Augsburger, 1991). Typically, giant monocarpic plants have a rosette growth form and produce an unbranched, indeterminate inflorescence allowing for an exponentially increasing seed and fruit number with size (Hart, 1977; Silvertown, 1983). The slow growth and the many years it takes until reproduction make individuals of such plants highly vulnerable, particularly when habitat conditions are unpredictable or when disturbance is high. As an example, the endemic Mauna Kea silversword from Hawaii experienced a severe population decline because of predation by alien ungulates and had to be saved by an out-planting programme (Robichaux et al., 1997).

Rheum nobile from the Himalayas is unique, due to its unusual life form and giant growth at an elevation between 4000 to 6000 m a.s.l. (Li and Gao, 1998; Chowdhery and Agrawala, 2009; Xu et al., 2013). At flowering, the large translucent bracts form a large, tower-like inflorescence of >1 m in height protecting the reproductive organs (Iwashina et al., 2004; Song et al., 2013b). Pollination occurs by a seed-consuming fungus gnat, which is attracted by a specific floral scent (Song et al., 2014). Pollination occurs while female flies stay overnight under the bracts and lay their eggs in flowers and developing fruits, which are then consumed by the larvae. The mutualism is clearly beneficial for the plant (Song et al., 2013b, 2014).

North-western Yunnan, China, where the present study was carried out, is part of Diqing Tibetan Autonomous Region, which is largely Tibetan in ethnicity, language and culture, and with a traditional agropastoral transhumance with yaks (*Bos grunniens*) across elevations (Litzinger, 2004). Yaks are highly relevant in Tibetan culture, especially regarding their function as a food source, i.e. for meat and milk (Haynes et al., 2013). Grazing areas visited by yaks may include *R. nobile* habitats, though this plant occurs in very remote areas. Chinese government policy to increase economic growth is in conflict with traditional land use and led to a greater yak and cattle population and an increase in grazing pressure (Bao and Wu, 2003). When collecting demographic data for this study, we therefore considered disturbances and grazing by yaks in the study sites, to assess their impact on demography and the long-term survival of the study populations.

Many studies have documented negative impacts of herbivory on plants; however, as most studies are short term or focus on only a particular aspect of the life cycle, the population-level consequences of grazing are poorly understood (Maron and Crone, 2006, and references therein). These authors conclude that large mammalian grazers usually affect population growth negatively, but may under particular conditions even have positive effects, i.e. when recruitment is enhanced by the creation of gaps in closed grassland. Clearly, herbivory effects on plants are context dependent (Maron et al., 2014). In the case of long-lived, monocarpic rosette plants, population persistence may be questioned under heavy grazing pressure of large herbivores, as in the above-mentioned silversword from Hawaii (Robichaux et al., 1997), or in one of the monocarpic *Echium* species from the Canary Islands, where reproductive structures

in recent years were heavily damaged by feral goats (Jaca et al., 2019). In long-lived monocarpic perennials, survival and growth have by far the largest effect on population growth, as has been demonstrated by Kuss et al. (2008), explaining the negative consequences of damage and heavy grazing on such species.

As in most other long-lived monocarpic herbs, nothing is known about the longevity of *R. nobile*, i.e. the passage time of individuals to flowering and reproduction. However, when to flower and at what size or age is crucial for the long-term survival of plant populations (Charnov and Schaffer, 1973). Plants tend to optimize the timing of reproduction by balancing current reproduction with expected future reproduction, and this is largely determined by a size-specific pattern of growth and survival. The cost of reproducing too early is reduced fecundity, and an evolutionarily stable strategy is expected to balance fecundity at a particular age or size with expected future fecundity (Stearns, 1992; Kuss et al., 2008). For monocarpic plants, their evolutionary demography was summarized by Metcalf et al. (2003). These authors showed that the relevant demographic functions (growth, survival and fecundity) in monocarps show a similar pattern and are largely size specific. The relative growth rate is a decreasing function of plant size, and survival, flowering probability and fecundity are increasing functions of size. Due to this simplicity and because reproductive costs and life time fecundity can be measured easily in plants which die after having flowered only once, monocarps have been frequently used to test evolutionary hypotheses. Their single reproduction is thought to occur at a size that maximizes fitness, and their passage time to flowering is considered as a key determinant of Darwinian fitness. These ideas were initially tested mostly in short-lived monocarpic plants, because of the difficulties in following the fate of long-lived individuals over their entire life. Kuss et al. (2008) demonstrated that the evolution of long-lived monocarps seems to follow similar general rules to that of shorter-lived monocarps. However, demographic studies of long-lived monocarpic plants are scarce, and for monocarpic giant herbs from tropical mountains neither important demographic functions or constants for population persistence, nor the evolutionarily relevant passage time to flowering are known.

Here, we use an integral projection model (IPM) to calculate demographic functions and to assess survival, the passage time to flowering and the population growth rate in two populations of *R. nobile* in north-west Yunnan, China. IPMs have been developed to overcome the simplifying and restrictive assumptions of more classical matrix models (e.g. Caswell, 2001) which classify individuals of plant populations into a limited number of discrete classes. This may be especially problematic for small demographic data sets (Ramula et al., 2009). In contrast, IPMs (Easterling et al., 2000; Ellner and Rees, 2006) use the parameters of regression equations to project changes in continuously size-structured populations in discrete time. Thus, demographic rates are modelled as continuous functions of an individual's size rather than dividing individuals into discrete classes. IPMs have been shown to be more reliable and less biased than matrix models because they require fewer parameters to be estimated and, for those that are estimated, they are taken from the complete data set, rather than by dividing the data into classes (Ramula et al., 2009). In general terms

(Rees *et al.*, 2014), the fate of individuals within a population is determined by a continuously varying measure of body size (x) strongly linked to survival, growth and reproduction.

We had the following specific aims with this study. (1) We use demographic monitoring and integral projection modelling to identify the most important size-dependent functions and constants for continuous population persistence in a long-lived monocarpic perennial from the high Himalayas. (2) We estimate the necessary passage time for individuals to become flowering and reproductive and thereby their longevity. (3) We estimate the population growth rate in the absence and presence of disturbances and grazing by yaks.

MATERIALS AND METHODS

Study species and sites

Rheum nobile J.D. Hooker and Thompson (Polygonaceae) is a rare perennial monocarpic herb, endemic to the Himalayas, and occurring from north-east Afghanistan, Pakistan, India, Nepal, Bhutan, Tibet, Myanmar to the Hengduan Mountains in south-west China at elevations from 4000 to 6000 m a.s.l., mostly on open scree in remote areas (Li and Gao, 1998; Chowdhery and Agrawala, 2009; Song *et al.*, 2013a). The plant grows vegetatively over many years, with basal leaves forming a giant rosette. In the year of flowering, a single stem several centimetres in diameter and of 1–1.5 m height is formed, with thousands of flowers covered by large translucent, yellow-whitish bracts forming a conspicuous tower-like inflorescence, attractive and visible from far away. The translucent bracts create a glasshouse effect and protect the reproductive organs from rain, mist, high UV radiation and low temperature (Song *et al.*, 2013b). Flowering occurs from early June to early July. The small flowers have green sepals, no nectar, one ovule, and six stamens, and last for 3–4 d; the entire inflorescence lasts for 7–10 d. Autonomous selfing is possible, but *R. nobile* depends largely on insects for successful pollination and high seed set (Song *et al.*, 2014). During anthesis, females of a fungus gnat, *Bradysia* sp. (Sciaridae), are attracted by a specific floral compound. The flies serve as the main pollinators, even though these insects deposit their eggs in the ovary and their larvae feed on a sub-set of the developing seeds. The net outcome of this pollinating seed-consuming mutualism is beneficial for both partners (Song *et al.*, 2013b, 2014). After seed ripening, the entire monocarpic individual dies; regeneration occurs exclusively from seeds that are non-dormant (Song *et al.*, 2013a).

Data for this study were collected from 2011 to 2014 at two scree sites where the plant occurs naturally, and which are representative for the climatic conditions under which the species occurs in the eastern Himalayas: Huluhai (28°31'N, 99°57'E, 4450 m a.s.l.) and Yongjiongnyi (28°24'N, 99°55'E, 4490 m a.s.l.), in Shangri-la County, Yunnan Province, south-west China. Mean annual precipitation at the nearest meteorological station (28°23'N, 99°01'E, 4290 m a.s.l.) 95 km away was 680–790 mm. Mean annual air temperature is –1.0 °C, with a difference in the mean monthly temperature between the coldest and the warmest month of approx. 15 °C (Wang, 2006). At the two study sites, the vegetation adjacent to the scree includes alpine meadows and *Rhododendron* shrub.

Demographic data of Rheum nobile

In summer 2011, in two populations at Huluhai and Yongjiongnyi, 372 and 369 individuals (rosettes), respectively, were sampled randomly in the entire scree area where the population occurred, including rosettes of all sizes from <3 cm to >90 cm in diameter. This large number of individuals was selected initially to ensure that in the three consecutive years of the census there would still be sufficient individuals of all sizes to calculate continuous demographic functions. The selected individuals were marked with wooden stakes with iron labels. In 2011 and three consecutive years (2012–2014), the number of leaves, the diameter of rosettes and the size of the largest leaf of all rosettes that survived (length and width) were measured. Rosettes which did not survive (only dead biomass left) were considered as dead in the analyses (IPM) described below. Rosettes which showed marks of disturbances and grazing by yaks and were dead or no longer found in the following year were considered either as missing or as dead, once in a series of analysis without these rosettes and once in a series of analyses with these rosettes included as dead, thereby simulating demography with and without disturbance and grazing by yaks. We consider a beneficial effect of yak presence from nutrients in the form of dung as negligible due to the low population density of *R. nobile* on scree. When individuals reproduced, the number of flowers, fruit set, percentage of predated fruits and ripe seeds were counted. From our observations across several years and from a number of sites, *R. nobile* seeds are not dormant.

Integral projection model (IPM)

The central assumption of an IPM is that individuals with identical sizes have the same odds of different future fates. The state of the population at time t is described by a distribution function, $n(x, t)$, where $n(x, t)dx$ is the number of individuals with size in the range $[x, x + dx]$. The population dynamics are then

$$\begin{aligned} n(y, t+1) &= \int_L^U [P(y, x) + F(y, x)]n(x, t)dx \\ &= \int_L^U K(y, x)n(x, t)dx \end{aligned}$$

The kernel $K(y, x)$ describes all possible transitions from size x to y , including births, and $[L, U]$ is the set of all possible sizes. The kernel comprising the survival and growth function is composed of two parts describing the production of size y offspring by size x parents, $F(y, x)$, and the movement of individuals from size x to y , $P(y, x)$. The kernel K plays the role of the projection matrix in a matrix projection model (Rees *et al.*, 2014). In particular, the finite rate of population increase (λ) can be derived as the dominant eigenvalue of K , and passage times to reach any given size can be derived from the survival–growth part, $P(y, x)$, of K (Caswell, 2001; Metcalf *et al.*, 2009).

The model (Easterling *et al.*, 2000; Ellner and Rees, 2006) as described above was applied to the demographic data of *R. nobile* by specifying the dependence of survival, growth and fecundity on size. This was achieved by writing the survival–growth function as

$$P(y, x) = s(x)[1 - p_f(x)]g(y, x)$$

where $g(y, x)$ is the probability of an individual of size 'x' growing to size 'y'. The probability of flowering, $p_f(x)$, enters the survival–growth function because reproduction is fatal in monocarpic species. The fecundity function is given by

$$F(y, x) = p_e s(x) p_f(x) f_n(x) f_d(y)$$

where p_e is the probability of seedling establishment, i.e. the product of germination rate and seedling survival (see below), $s(x)$ and $p_f(x)$ describe the probability that an individual of size 'x' survives or flowers, respectively, $f_n(x)$ is the number of seeds it produces and $f_d(y)$ is the probability density of seedling size 'y'.

The model was solved numerically using the midpoint rule (Ellner and Rees, 2006) by defining meshpoints x_i such that the interval from minimum to maximum size [$L = \text{minSize} = 0.1$, $U = \text{maxSize} = 12$, respectively] was evenly divided into m ($= 100$) size classes and setting x_i at the midpoint of the i th class. In practice, this was done using the appropriate functions `makeIPMPmatrix` and `makeIPMFmatrix` of the R library `IPMpack` (Metcalfe et al., 2013). Finally, K is obtained by assembling the two component matrices (P and F) to form the kernel, K .

Potential eviction was checked using the function `evictionMeasuresFC.Iter` (Williams et al., 2012). This function estimates differences ($d\lambda$) between estimates of λ with and without eviction. When $d\lambda$ is small, the effect of eviction on the predicted population growth rate is small even if a large proportion of individuals is evicted (Williams et al., 2012, p. 2010). In our case, we found only two out of 12 (2 populations \times 3 years \times 2 missings excluded/dead = 12) $d\lambda > 0$ and only 1 > 0.01 (population YJY, year 3). Therefore, potential eviction should have very small effects on our estimates of λ , and no eviction corrections were applied.

Size-dependent growth, survival and fecundity parameters

We used the log-transformed product of number of leaves and length and width of the largest leaf as our measure of plant size. The statistical models were fitted to the combined data from both populations (Huluhai and Yongjiongnyi) and three transitions (2011–2012, 2012–2013 and 2013–2014), including population and year effects when they were significant.

To parameterize the growth part of the survival–growth function, linear regressions of size_{*t*} vs. size_{*t+1*} were tested using different models. The model with population- and year-specific size and quadratic size terms fit best [lowest corrected Akaike information criterion (AICc)] and was selected (model m.8 in Supplementary data Appendix A.1; Table 1). Quadratic size terms differed slightly for the first transitions and were negative for the third transition (2013–2014) for both populations (Fig. 1). There was some indication that the variance decreased with increasing size for the first two transitions. However, since estimates of growth rates (λ) and passage time to flowering size (see below) using parameter estimates of growth models with decreasing variance were always within the 95 % confidence intervals (CIs) of bootstrapped estimates with constant variance, we only report results from IPMs with constant variances.

This is further supported by the fact that fits of models with decreasing and constant variances were actually very similar. For the survival part of the survival–growth function, general linear models (GLMs) with binomial errors and population- and year-specific size and quadratic size terms fitted best (m.8 in Supplementary data Appendix A.2; Table 1).

Flowering probability, fitted with logistic regression, was best described with a single intercept and size term (i.e. there were no differences in flowering probabilities between populations or years).

Finally, the number of seeds produced by plants was fit using GLMs with Poisson errors and population- and year-specific size and quadratic size terms. However, because the quadratic size term led to unsatisfactory fits (first decreasing then increasing seed production with plant size) in one of the two populations (Huluhai), we decided to omit the quadratic term from the fecundity functions.

To estimate the time it takes an individual to reach flowering size, we used the average size of flowering individuals (size as defined above, i.e. the log-transformed product of number of leaves and length and width of the largest leaf) in the two populations (Table 2). There was very little variation between populations and years, so we used ten as the threshold size to be reached by an individual in order to flower.

To assess effects of uncertainty in parameter estimates of the regressions on the estimates of finite rate of increase (λ) and passage time to reach flowering size, 99 random samples from the multinomial distribution of parameter estimates given by the original regressions (as given in Table 1) were drawn, IPMs parameterized and λ and passage time estimated. The same bootstrap samples were used to obtain 95 % CIs by taking the 2.5 and 97.5 percentiles of the bootstrapped samples.

In addition to the estimates of growth rates (λ) and passage times to flowering per transition year and the two sites, we also ran stochastic simulations to obtain single estimates for growth rate (λ_s) and passage time across the three years and two populations. We used the function `stoch.growth.rate` in package `popbio` (2.4.4.) to estimate stochastic population growth rate (λ_s). Note that the function `stoch.growth.rate` in package `popbio` estimates $\log(\lambda_s)$ more efficiently and with more useful output (e.g. CI) than the function `stochGrowthRateSampleList` in package `IPMpack`. We used functions `sampleIPM` and `sampleIPMOoutput` in package `IPMpack` (2.1) to estimate stochastic passage time and 95 % CIs based on the sequence of environmental conditions across the two populations and three years.

Size-independent constants

Size-independent constants to include in the demographic model, i.e. the germination rate, seedling survival rate and establishment probability, were assessed independently of the census data. For the germination rate, the number of seedlings around all the eight and nine plants reproducing in 2013 in Huluhai and Yongjiongnyi, respectively, were counted in 2014 and divided by the number of seeds produced by their mother plants. By including the locations of all plants reproducing in the previous year, we accounted for a maximum of environmental variation at the study sites. For seedling survival, five

TABLE 1. *Statistical models and parameter estimates describing demographic processes of Rheum nobile in two populations over three annual transitions each*

Demographic process	Population	Transition	<i>n</i>	Parameter estimates (s.e.)
Growth dependent: \hat{y}	HLH	1	319	$0.95 (0.13) + 0.85 (0.04) x + 0.01 (0.004) x^2$
		2	270	$1.14 (0.20) + 0.77 (0.06) x + 0.01 (0.005) x^2$
		3	230	$-1.17 (0.42) + 1.51 (0.12) x - 0.04 (0.008) x^2$
	YJY	1	303	$0.83 (0.22) + 0.88 (0.07) x + 0.01 (0.005) x^2$
		2	258	$-0.06 (0.24) + 1.10 (0.07) x - 0.01 (0.005) x^2$
		3	209	$-1.67 (0.42) + 1.57 (0.12) x - 0.04 (0.008) x^2$
Survival probability dependent: $\text{logit}(s)$	HLH	1	28/347	$-3.34 (1.21) + 1.76 (0.58) x - 0.09 (0.06) x^2$
		2	17/287	$-4.30 (1.73) + 2.32 (0.64) x - 0.17 (0.05) x^2$
		3	13/243	$-9.25 (2.85) + 3.69 (0.94) x - 0.25 (0.07) x^2$
	YJY	1	17/320	$-2.62 (1.86) + 1.20 (0.70) x - 0.05 (0.06) x^2$
		2	11/269	$3.09 (6.15) + 0.47 (1.63) x - 0.06 (0.10) x^2$
		3	24/233	$1.16 (3.08) + 0.05 (0.90) x + 0.01 (0.06) x^2$
Flowering probability dependent: $\text{logit}(p_f)$	Both	All	51/1699	$-27.1 (3.1) + 2.6 (0.3) x$
Fecundity (seeds/plant) dependent: f_n	HLH	1	5/347	$\exp[0.94 (0.18) + 0.80 (0.018) x]$
		2	5/287	$\exp[5.84 (0.22) + 0.30 (0.022) x]$
		3	12/243	$\exp[3.18 (0.09) + 0.54 (0.009) x]$
	YJY	1	7/320	$\exp[4.65 (0.10) + 0.42 (0.010) x]$
		2	6/269	$\exp[4.41 (0.10) + 0.45 (0.010) x]$
		3	16/233	$\exp[0.48 (0.09) + 0.80 (0.008) x]$
Establishment (p_e) Seedling size	Both	All	477	Size independent: 0.035 Mean = 1.09; s.d. = 0.71

The models are functions of $x = \log$ size, i.e. number of leaves \times (width \times length) of longest leaf. Quadratic size terms (x^2) were included if indicated by model selection criteria (i.e. Akaike information criteria; details are given in Supplementary data Appendix A). The predicted values are the conditional mean \hat{y} of log size next year given the current size and current size² for growth and survival; s , survival probability; p_f , flowering probability; f_n , fecundity; p_e , establishment rate (i.e. the product of germination rate, 0.072, and first-year seedling survival, 0.480). Populations, Huluhai (HLH), Yongjiongnyi (YJY); Transitions, 1 (2011–2012), 2 (2012–2013), 3 (2013–2014); n , number of individuals. For survival and flowering probability as well as fecundity, the first number gives the number of surviving and flowering individuals, respectively.

(Huluhai) and six plots (Yongjiongnyi) of size 80 \times 80 cm were established early in 2011 close to all plants which had reproduced in the preceding year. Emerging seedlings until the end of season 2011 in these plots were counted, and the size (diameter) of the surviving seedlings was measured in the following year. Seedling survival was calculated by dividing the number of seedlings surviving in 2012 by the number of seedlings counted in 2011. Germination rate and seedling survival were then multiplied to calculate the establishment probability p_e as a model parameter.

Statistics

All analyses were performed with R (version 3.1.1, [R Development Core Team, 2014](#)) and in particular package IPMpack (version 2.1, [Metcalf et al., 2013](#)) using the midpoint integration type without correction and 100 meshpoints with minimum and maximum size set to 0.1 and 12, respectively.

RESULTS

Natural mortality and losses due to yaks

From 2011 to 2014, 58 (15.5 %) of the initially marked rosettes in Huluhai, and 52 (14.1 %) in Yongjiongnyi died prior to flowering (not including those missing due to disturbances or grazing). A much larger number of rosettes were lost in the

three years due to disturbances and herbivory by yaks: 25, 32 and 25 (22.0 % in total) in Huluhai, and 47, 34 and 21 (37.9 % in total) in Yongjiongnyi.

Germination rate, seedling survival and establishment probability

The number of seedlings counted in 2014 around plants that had flowered in the preceding year did not differ between the two populations (Wilcoxon rank sum test, $W = 49$, $P = 0.24$). Moreover, there was no difference in the number of seeds produced by individual plants in the two populations (Wilcoxon rank sum test, $W = 17$, $P = 0.79$). Thus, the germination rate for both populations calculated from the available data was 0.072. Mean seedling survival in Huluhai was 44 % ($n = 5$ plots) and in Yongjiongnyi it was 52 % ($n = 6$ plots). Because the two populations did not differ in first-year seedling survival (Wilcoxon rank sum test, $W = 9$, $P = 0.33$) we used the average = 0.48 across populations to calculate the establishment probability $p_e = 0.072 \times 0.48 = 0.035$.

Survival, flowering and fecundity

Survival first increased with size in both populations ([Fig. 2](#)) and then either remained close to 1.0 (2011–2012) or decreased slightly at very large sizes (2012–2013 and 2013–2014). Flowering probability ([Fig. 3](#)) sharply increased when rosettes reached a threshold size corresponding to a rosette diameter of approx. 70–110 cm.

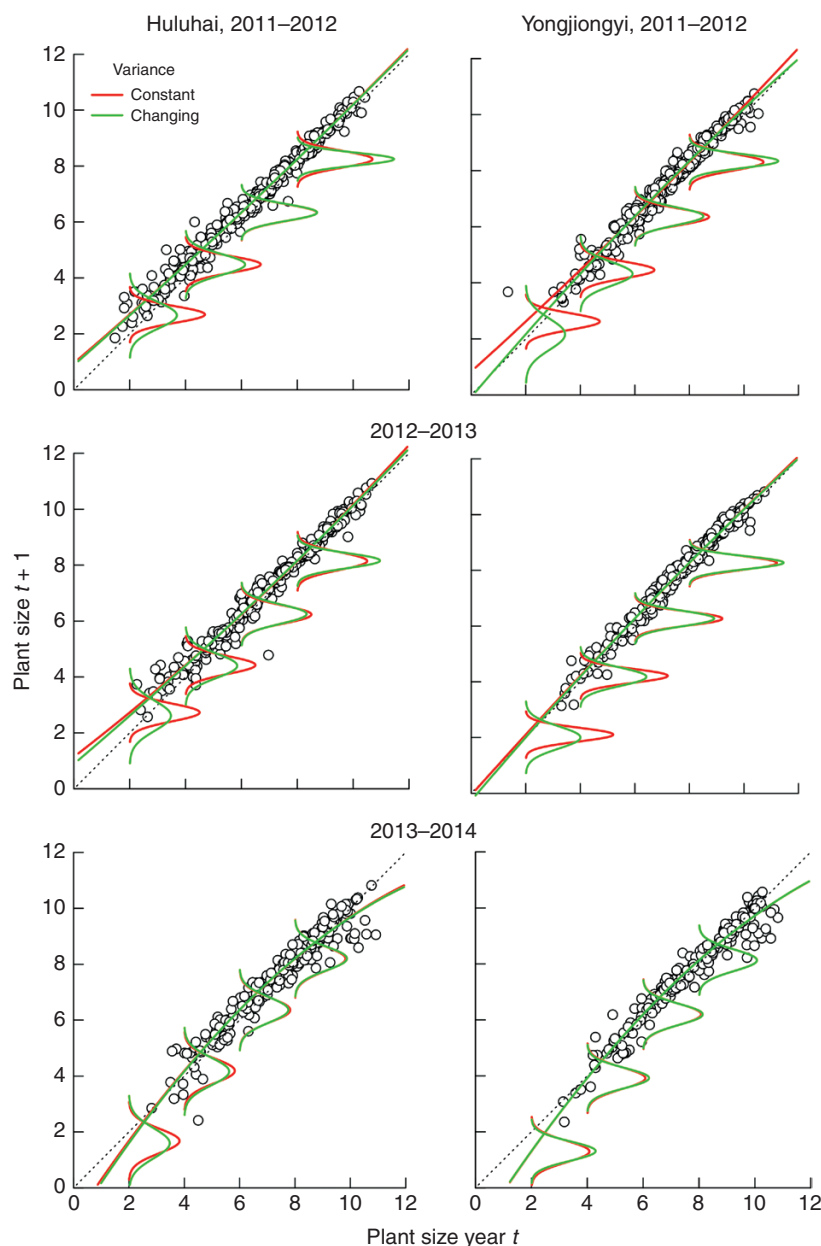


FIG. 1. Growth relationships of two populations (Huluhai and Yongjiongyi) in successive years in the monocarpic plant *Rheum nobile*. Plant size represents rosette size: $\log[\text{number of leaves} \times (\text{length} \times \text{width}) \text{ of the longest leaf}]$. See Table 1 for parameters of the fitted relationships.

The number of flowering plants among the initially marked rosettes in the three years was 22 (5.9 %) in Huluhai and 29 (7.9 %) in Yongjiongyi; among populations and year, the number of flowering individuals varied between five and 16 (Table 2).

Flowering individuals on average produced $10\,279 \pm 525$ (\pm s.e.) flowers, of which 96 % set fruits, of which on average 15.4 ± 4.7 % aborted during ripening. Loss due to predation by larvae of the pollinating fly was 25.2 ± 4.7 %, yielding finally 6323 ± 366 viable seeds per reproducing individual of *R. nobile*. Neither population nor year affected the number of flowers, the number of fruits or the number of viable seeds significantly; however, in 2014, the abortion rate was much higher than in previous years ($P < 0.001$), and the predation rate in 2014 was

lower than in previous years ($P < 0.05$), yielding in sum fewer viable seeds in both populations in 2014 (n.s., Table 3).

Population growth rate

Bootstrapped values of finite rates of increase, λ , were close to 1.0 for both populations and all three transitions (Fig. 4). The stochastic population growth rate (λ_s) estimated from pooled transitions and populations was 1.013 (95 % CI 1.010–1.017) and dropped to 0.940 (95 % CI 0.938–0.943) if missing individuals were treated as dead and thereby considered as consumed by yaks. As expected, treating missing individuals as

dead yielded lower λ values compared with estimates based on excluding these missing individuals from the analyses. Over the three transitions (2011–2014), λ values of population Huluhai decreased considerably from values above to values below 1.0. Similar to λ values in Huluhai, λ values for the first two transitions (2011–2012 and 2012–2013) for population Yongjiongnyi were >1.0 . However, 1.0 was included in their 95 % CIs, which were considerably larger than those for Huluhai. As in Huluhai, λ values for the 2013–2014 transition were considerably smaller than 1.0, indicating a decline in population growth in this year in both populations.

Time to reach flowering

Passage times to reach average flowering sizes was 33.5 years (95 % CI 21.9–43.3, stochastic estimate from pooled transitions and populations) if missing individuals due to disturbance and grazing by yaks were excluded from the analyses. As for the λ values, there was some variability in the bootstrapped passage times between the two populations

and among years (Fig. 5). Passage times estimated from individuals at Yongjiongnyi for the transition from 2012 to 2013 showed the most conspicuous deviation (approx. 46 years) from the average passage time of around 30 years to reach flowering size.

Elasticities

Elasticities for the growth–survival functions were very high (>95 %), and for fecundities (flowering and seed production) they were very low (<5 %) independently of year, population or of how missing rosettes were treated. Consequently, the effect of seed predation on population growth rate λ is negligible. Even when seed production was set to the level observed for self-pollination (roughly 25 % of that actually observed), λ values were not much smaller compared with those reported above and still close to one.

DISCUSSION

The IPM predicted remarkably similar values of the population growth rate λ at the two sites and only slight differences among the three years (Fig. 4). Taken together, the stochastic growth rate λ_s across populations and years was slightly larger than one when the impact of disturbance and grazing is neglected, indicating persistence of *Rheum nobile* populations in the future, or even a moderate population growth under natural conditions. In two of the three years (transitions), population growth λ was clearly above one at both sites, while it was below one in the third year, probably as a consequence of a more than doubled abortion rate of developing seeds in this year, reducing viable seeds considerably (Table 3). The stochastic passage time to reach flowering was 33.5 years; there was little variation among sites and years, with a single outlier year at one site (Fig. 5). As expected for a monocarpic perennial, the probability of survival (Fig. 2) and the

TABLE 2. Mean size and ranges of flowering individuals in two populations (Huluhai and Yongjiongnyi) of *Rheum nobile*, a perennial, semelparous (monocarpic) plant of the high Himalayas. Size was used to parameterize an IPM and is defined as $\log[\text{number of leaves} \times (\text{width} \times \text{length}) \text{ of longest leaf}]$

Population	Year	n	Size of flowering individuals		
			Minimum	Mean	Maximum
Huluhai	2012	5	9.5	9.9	10.3
	2013	5	9.6	9.9	10.2
	2014	12	9.3	10.1	10.9
Yongjiongnyi	2012	7	8.7	9.9	10.5
	2013	6	8.8	9.7	10.2
	2014	16	8.3	10.0	10.8

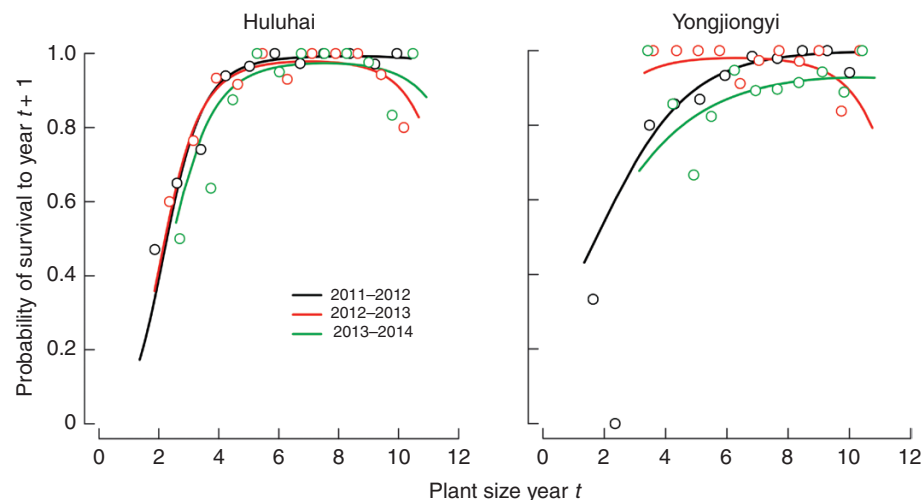


FIG. 2. Survival probability of two populations (Huluhai and Yongjiongnyi) in successive years in the monocarpic plant *Rheum nobile*. Data points are binned survival probabilities in 11 classes for graphical display. Lines represent fits of logistic regressions for separate transitions. Plant size represents rosette size: $\log[\text{number of leaves} \times (\text{length} \times \text{width}) \text{ of the longest leaf}]$. See Table 1 for parameters of the fitted relationships.

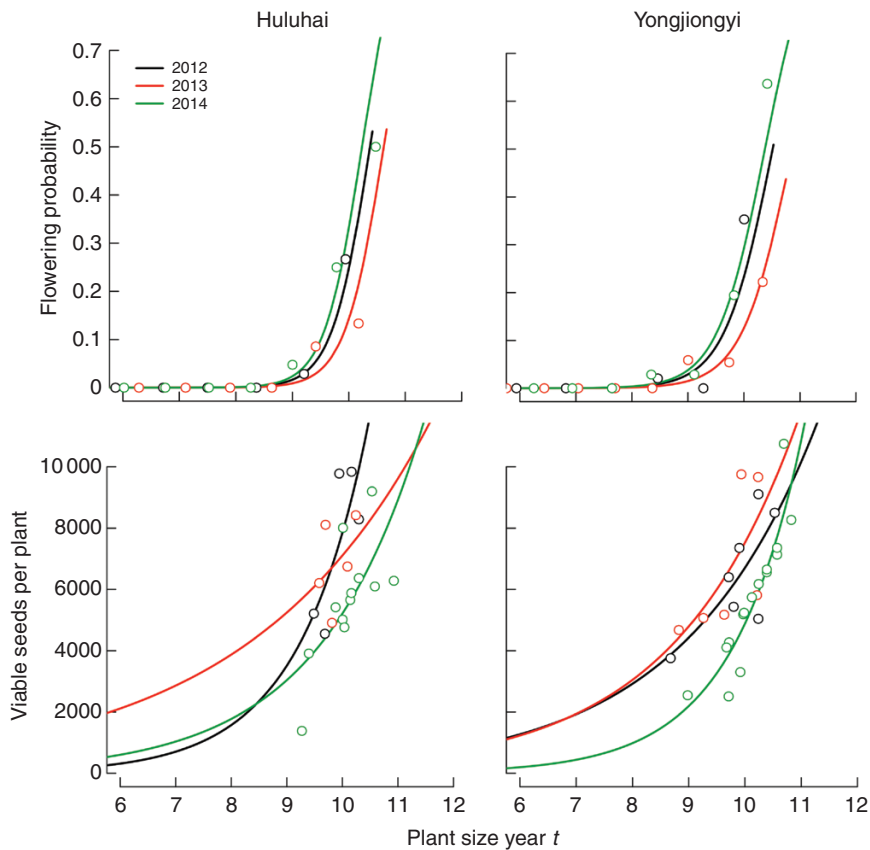


FIG. 3. Flowering probability (top panels) and fecundity (viable seeds per plant, bottom panels) of two populations (Huluhai and Yongjiongyi) in successive years in the monocarpic plant *Rheum nobile*. Data points for flowering probability are binned in 11 classes for graphical display. Lines represent fits of logistic regressions for flowering probability and GLMs with Poisson errors and log-link for fecundity, respectively, for separate transitions. Plant size represents rosette size: $\log[\text{number of leaves} \times (\text{length} \times \text{width}) \text{ of the longest leaf}]$. See Table 1 for parameters of the fitted relationships. Note that the x -axis starts at 6 (not 0) and that for flowering probability, different regression lines have been drawn although model selection statistics (Supplementary data Appendix A) indicate that there are no significant differences between populations or among years.

TABLE 3. Abortion rate of developing seeds, predation rate by larvae of a seed-consuming pollination fly and number of viable seeds in two populations (Huluhai and Yongjiongyi) in three consecutive years (2012–2014) of *Rheum nobile*, a perennial, semelparous (monocarpic) plant of the high Himalayas

	Year	n	Abortion rate (%) (mean \pm s.e.)	Predation rate (%) (mean \pm s.e.)	Viable seeds (mean \pm s.e.)
Huluhai	2012	5	7.9 \pm 2.9	26.5 \pm 2.0	7534 \pm 1045
	2013	5	9.9 \pm 2.9	26.6 \pm 2.0	6879 \pm 1045
	2014	12	22.1 \pm 2.0	23.7 \pm 1.4	5574 \pm 739
Yongjiongyi	2012	7	9.0 \pm 2.6	27.6 \pm 1.8	6532 \pm 1045
	2013	6	8.8 \pm 2.6	26.8 \pm 1.8	6691 \pm 953
	2014	16	26.6 \pm 2.4	21.8 \pm 1.7	5636 \pm 883

probability of flowering and fecundity (Fig. 3) were strongly size dependent, with a threshold size for flowering which varied only little (Metcalf *et al.*, 2003).

Germination and establishment

The observed establishment rate of >3 % after 1 year is rather high if compared with reports from other alpine species in open

habitats (Chambers, 1995; Stöcklin and Bäumler, 1996; Forbis, 2003; Wepler *et al.*, 2006). Seeds of *R. nobile* are relatively large (20–25 mg), and so are the emerging seedlings, which may explain the high seedling establishment and survival rate in this species. As our estimate is based on only a single year, we cannot exclude that the high values were an overestimate due to particularly beneficial conditions in the specific year. Dispersal distances in *R. nobile* are low (mostly within 0.5 m distance of the mother plant, B. Song, pers. obs.) because reproductive organs are covered by bracts and because of the high seed weight. Recruitment in this species is limited by microsite availability on scree and negatively affected by shading as soon as there is some vegetation present in suitable sites (Song *et al.*, 2013a). Microsite availability is probably the most important factor limiting recruitment, and many seeds are lost because they fall on substrate unsuitable for germination. Loss due to drought, on the other hand, is unlikely in the eastern Himalayas, as soils at this elevation remain constantly moist due to frequent precipitation and foggy conditions (Zhang *et al.*, 2014). We found no indication that recruitment conditions differed among sites. The results of our demographic modelling are not affected by variable recruitment conditions among years, as we have recruitment data from only one year, what may be considered as a weakness. However, we do not consider this as problematic, as temporal variation in demographic studies is usually not much

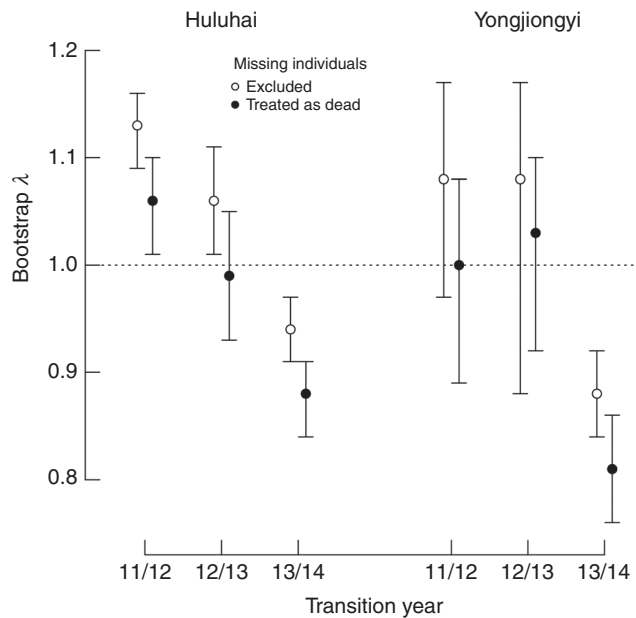


FIG. 4. Growth rates (finite rate of increase, λ) of two populations (Huluhai and Yongjiogongyi) of *Rheum nobile*, a perennial, semelparous (monocarpic) plant of the high Himalayas. Integrated projection models (IPM, Pmatrix + Fmatrix) were parameterized using estimates of growth (linear regression), survival (logistic regression) and fecundity functions separately in each of three transition years. Dominant eigenvalues of the matrices were bootstrapped by drawing 99 random samples from the multinomial distribution of parameter estimates given by the original regressions (as given in Table 1). Error bars represent the 95 % confidence intervals. Because some individually marked plants were missing in each year, estimates of growth rates were calculated by excluding these missing individuals or treating them as dead.

affected by recruitment, but much more by variation in post-seedling survival (Buckley *et al.*, 2010).

Demographic pattern

As expected, the relevant demographic functions growth, survival, probability of flowering and fecundity were all strongly size dependent. Growth was linearly related to size and deviated only little from a constant relative growth; the quadratic size term of the function was very low and not always negative (Fig. 1; Table 1). Hence, we did not observe a consistently decreasing relative growth rate with size as in most perennial plant species. A decreasing growth rate in plants with size has been explained by self-shading, declining nitrogen content, accumulation of non-photosynthetic tissue over time or other unknown factors (Metcalf *et al.*, 2003; Kuss *et al.*, 2008). The constancy in relative growth of *R. nobile* is probably best explained by the fact that as long as plants are not flowering, there is no readjustment in allocation, morphology or leaf physiology of rosettes, which in this species regrow from storage tissue (i.e. root) each year.

The mortality of established plants was very low and restricted to smaller rosettes. As a consequence, survival reached almost 100 % for plants having attained a certain size (Fig. 2), and mortality of larger plants occurred only after reproduction. Such a high survival probability is most probably a consequence of no inter- and only low intraspecific competition in the scree

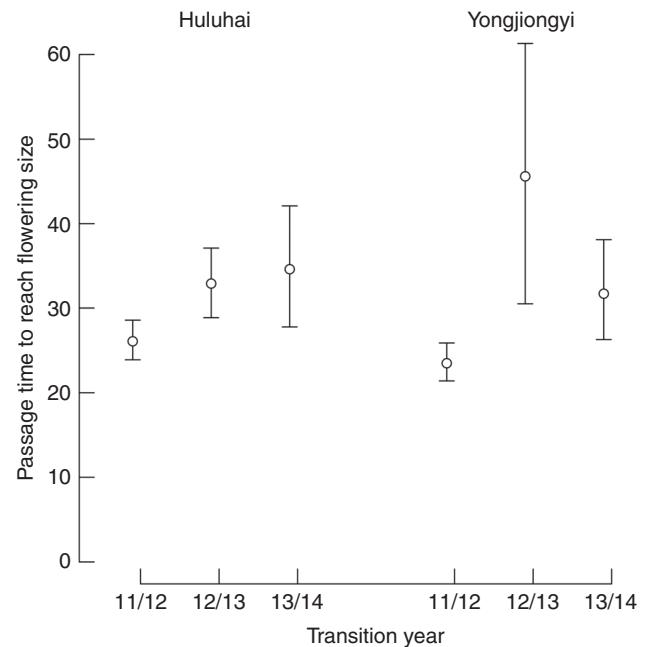


FIG. 5. Passage time to reach flowering size in two populations (Huluhai and Yongjiogongyi) of *Rheum nobile*, a perennial, semelparous (monocarpic) plant of the high Himalayas. Integrated projection models (IPM, Pmatrix) were parameterized using estimates of growth (linear regression) and survival (logistic regression) functions separately in each of three transition years. Passage time to reach flowering size [i.e. $\log(\text{number of leaves} \times \text{length} \times \text{width of longest leaves}) = 10$] was bootstrapped by drawing 99 random samples from the multinomial distribution of parameter estimates given by the original regressions (as given in Table 1). Error bars represent the 95 % confidence intervals. Because some individually marked plants were missing in each year, estimates of passage time to reach flowering size were calculated by excluding these missing individuals.

habitat at elevation >4000 m a.s.l. The few other co-occurring plant species are very small, while *R. nobile* is a very robust plant. The survival function included a population- and year-specific term indicating some environmental impact on mortality, most probably related to weather conditions, which may of course differ between locations, even when we consider the climatic conditions of the study locations as representative for the species range in the Eastern Himalayas. Herbivory by wild animals or insects at this elevation is not relevant (B. Song, pers. obs.), with the exception of yaks. In contrast to the low observed natural mortality, mortality resulting from disturbances and grazing by yaks was disproportionally larger (see below). That survival probability is increasing with rosette size is no surprise and is the case in most rosette plants (Werner, 1975; Werner and Caswell, 1977). Mortality in perennial plants is either density dependent, a result of senescence, or a consequence of reproductive cost in iteroparous perennials (Stearns, 1989). Rosettes of *R. nobile* represent an extended juvenile life stage, and none of the above factors causing mortality appears relevant when a rosette has reached a certain size.

Threshold size of flowering and time to reach it

Flowering probability was almost zero until a threshold size close to the maximum size of rosettes was reached. At this size,

flowering probability sharply increased (Fig. 3). The threshold size of flowering, usually defined as the size at which 50 % of the plants are flowering, is likely to represent the necessary amount of stored resources required for reproduction (Young and Augsburger, 1991). For short- as well as for long-lived monocarpic perennials, such a threshold size is common (Tissue and Nobel, 1990; Wesselingh and de Jong, 1995). As the probability of flowering in *R. nobile* was best described as a simple function of plant size (Table 1), the threshold size for flowering is largely a biological constant in this species not related to site or yearly variation. In monocarpic perennial plants, the threshold size of flowering is considered as an evolutionarily stable strategy (ESS), representing the size at which reproductive fitness is maximized (Metcalf et al., 2003). There is good experimental evidence from short-lived monocarpic species that flowering is genetically controlled and may differ among habitats or due to constraints by herbivores affecting survival (Wesselingh and de Jong, 1995; Wesselingh et al., 1997). As we found no difference in the threshold size among sites and years, we have no clues for genetic variation in this trait between the populations included in our study; however, such variation may exist in other populations of *R. nobile* experiencing environmental conditions different from those present at our locations. Also the steep increase of flowering probability with plant size in this species is an indication of low genetic variation in this trait. A more gradual passage to flowering with size is expected when genetic or environmental variation acting on this trait is high. This has been observed in the short-lived monocarp *Cynoglossum officinale* (Wesselingh et al., 1993). A steep passage to flowering similar to that in *R. nobile* has been observed in the monocarpic *Campanula thyrsoidea* from the European Alps and seems to be characteristic for long-lived perennials, thereby confirming this theory (Kuss et al., 2008).

The passage time to reach the threshold size of flowering was more variable than the threshold size itself (Fig. 5). This is not surprising because the time to reach the threshold size may depend strongly on variation in growth rate, itself related to environmental conditions such as temperature, drought, length of the vegetation period or soil conditions. One year at one site (transition 2012–2013 in Yongjiogngyi) showed a distinctly longer passage time to flowering with larger CIs; the particular reason for this was unclear. Size but not age is a good predictor of the onset of flowering, and particularly so in short- and long-lived monocarpic plants (Lacey, 1986, and references therein). Nevertheless, the longevity of giant monocarpic herbs from alpine vegetation has always been the subject of curiosity, but we know of only few published longevity data for monocarpic perennials of tropical high elevation habitats, and those that exist are guesses and, with one exception, not based on accurate demographic modelling. For *Puya raymondii*, Sgorbati et al. (2004) report estimates of 80–100 years until flowering, for the Silversword of Hawaiian volcanoes the estimate is 20–80 years (Krushelnicky et al., 2013), and demographic modelling of *Lobelia telekii* yielded a passage time to flowering of 40–70 years (Young, 1985). Our stochastic passage time to flowering for *R. nobile* of 33.5 years is well in line with these estimates. Such a long delay of flowering is only affordable when the risk of mortality is low relative to the increase in seed production through further vegetative growth,

and thus is a necessary pre-condition for the selection of perennial monocarpy (Metcalf et al., 2003, and references therein).

Fecundity

Flowering plants of *R. nobile* produced on average >10 000 flowers and >6000 viable seeds. Despite year- and site-specific variability indicating some environmental effects on seed crop, we observed no significant differences in flower production per inflorescence across years and sites. The reason for the much higher abortion rate in 2014 is not known, but it might result from lower pollinator visits in this year, as seed production in *R. nobile* depends largely on pollination by *Bradysia* flies (Song et al., 2013b, 2014). This interpretation is supported by the fact that in the particular year with a high abortion rate there was also a lower seed predation caused by the larvae of the pollinating flies which lay their eggs in developing fruits (Table 3). Thus, pollen limitation might be an explanation for the lower population growth rate in this year (Fig. 4), despite the low elasticity of seed production. This is interesting in itself, as there are only few studies on the effect of and conditions under which pollen limitation affects population growth rate in plants (Baer and Maron, 2018, and references therein). For long-lived plants which are able to reproduce only once in their life time, a negative effect of low pollinator visits in a particular year is no surprise, as plant species with this strategy are expected to maximize fecundity and to minimize costs with increasing reproductive investment (Schaffer, 1974). The selection regimes favouring perennial monocarpy are much debated, and open to speculation in a particular case, because selection may have operated in the past. Clearly an increasing reproductive benefit with increasing reproductive effort will favour perennial monocarpy (Schaffer, 1974; Schaffer and Schaffer, 1977; Young, 1990). Increased pollinator attraction and pollination efficiency when pollinators preferentially visit large inflorescences is likely to have also favoured perennial monocarpy in *R. nobile*. It has been experimentally demonstrated that the spectacular tower of translucent bracts that protect the large inflorescence of *R. nobile* are indeed enhancing pollinator visits and pollination success, and the visual cue for attracting the pollinating fly is the better the larger it is (Song et al., 2013b). Because of the usually small number of reproducing plants in a population, the size of this visual display, which is enhanced by UV absorbance of the translucent bracts (Omori et al., 2000), is an important factor for the detection of reproducing plants by insects. As we found elasticities for the growth–survival function to be very high (>95 %), and for fecundity, including seed production, to be very low (<5 %), the high predation loss of developing seeds by larvae of the pollinating fly as well as their yearly variation is affordable for the plant, also because autonomous selfing in this self-compatible plant is low (Song et al., 2014).

Population growth rate and the impact of grazing yaks

Our model estimated a stochastic population growth rate (λ_s) for *R. nobile* slightly larger than one, indicating a moderate

population growth over time. The stochastic growth rate dropped clearly below one when missing plants were treated as dead instead of being excluded. As missing plants mostly disappeared either due to grazing yaks or by disturbances through these heavy animals, our results indicate that agricultural land use even at such high elevation may cause problems for the long-term survival of these rare and long-lived plants. We cannot completely exclude that other unknown factors may have contributed to missing rosettes, but at the remote sites of our study natural disturbances are unlikely. Local Tibetan people sometimes collect *Rheum* roots for medicinal uses, but as this was never observed, it was probably rare in our study sites. Relative to variation among years, the decrease in the stochastic growth rate due to missing rosettes was relatively small; nevertheless, our study demonstrates that in this species grazing by yaks has a negative impact on population growth rate. Grazing in the high Trans-Himalaya has a long history of several millennia. In traditional Tibetan regions, grazing pressure by yaks has dramatically increased in recent decades, causing conflicts between pastoralism, wildlife and conservation efforts to protect biodiversity (Haynes *et al.*, 2013). Grazing pressure is highest in grassland and close to villages, and mostly during winter and spring, but above the upper limit of forests where *R. nobile* occurs there is a vast pastureland for yaks in summer and autumn (Yang and Du, 1990). Even in these remote sites, a balance between traditional land use and conservation needs is important. Conservation policies should consider that at remote sites in the Himalayas above 4000 m elevation, even moderate grazing by yaks is likely to pose a threat to the rare *R. nobile*, and this flagship species could be endangered by intensified traditional pastoralism.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of Appendix A: model selection statistics.

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