



Annual mowing has the potential to reduce the invasion of herbaceous *Lupinus polyphyllus*

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Received: 9 March 2020 / Accepted: 9 July 2020 / Published online: 17 July 2020
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Abstract In order to manage invasive plant species efficiently, it is necessary to have a thorough understanding of different strategies of population control, including the underlying mechanisms of action and the consequences for target populations. Here, I explored the effectiveness of biomass removal as a method of control for the invasive perennial herb *Lupinus polyphyllus*. More specifically, using seed material from 11 populations, I assessed among-population variation (if any) in plant compensatory growth as a response to annual biomass removal under standardised growing conditions over two consecutive years, and quantified the demographic effects of a single biomass-removal event. In all study populations, annual biomass removal reduced plant size, flowering probability, and shoot and root biomass. Biomass removal also reduced plant survival and the number of flowering shoots, but these effects were pronounced at certain time points only. A population-level demographic analysis revealed that a single biomass-removal event considerably decreased the long-term population growth rate (λ); this decline in λ was due to a reduction in plant fecundity followed by survival and growth. These findings suggest that annual mowing has the potential to curb invasions of *L. polyphyllus*

because plants are not able to fully compensate for drastic biomass loss.

Keywords Compensatory growth · Demography · Invasive species · Mechanical weed management · Population growth rate · Vital rates

Introduction

Across all taxa, the number of invasive species is increasing worldwide, with vascular plants representing a considerable proportion of all invaders (Seebens et al. 2017). Such an increase in invasive plant numbers is largely due to intensified global trade (Seebens et al. 2015), which is unlikely to change; this suggests that the monetary costs associated with the control of invasive species will probably continue to increase. Therefore, in order to use resources efficiently and maximise the probability of success of management plans for invasive species, it is necessary to first understand the underlying mechanisms of individual control actions targeted at invasive plants (Kettenring and Reinhardt Adams 2011).

Biomass removal by mowing or cutting shoots is a popular method of control for invasive plant species (Kettenring and Reinhardt Adams 2011). Ideally, this control method depletes the resources of individual plants and, consequently, reduces growth and survival

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(Stoll et al. 1998). However, (over)compensatory responses to damage are common in a wide range of both wild and cultivated plant species (reviewed in Garcia and Eubanks 2019). That is, control actions may to some extent promote plant growth, resulting in either equal or greater biomass or reproductive output compared to undamaged plants. Indeed, many invasive plant species are able to regrow rapidly after biomass removal (e.g., Broughton 2003; Averill et al. 2008; Jia et al. 2009; Rouified et al. 2011). Invaders also tend to show greater phenotypic plasticity than their non-invasive congeners (reviewed in Davidson et al. 2011, but see Palacio-López and Gianoli 2011), which may enable them to either partially or fully recover from damage. For example, a single clipping event at a height of 2 cm had no effect after 7 weeks on the aboveground biomass of the herbaceous perennial Japanese knotweed (*Fallopia japonica*) due to its high compensatory growth (Rouified et al. 2011).

Different populations of the same invasive plant species may respond differently to control methods (Shea et al. 2005; Evans et al. 2012). This intraspecific variation in responses could be due to species-environment interactions (Shea et al. 2005; Evans et al. 2012; Pichancourt et al. 2019) or differences in tolerance to damage. For non-invasive perennial and biennial herbs, among-population variation in tolerance to damage is associated with damage history or damage frequency (Lennartsson et al. 1997; Boalt et al. 2010; König et al. 2014), with populations that experience higher levels of herbivore damage being more tolerant to it (Boalt et al. 2010). Such intraspecific variation in response to damage may also be present in invasive plant species, potentially complicating control efforts. In order to disentangle genetic factors from environmental factors that may lead to population-specific responses to a control method, it is necessary to analyse demographic data from multiple populations of invasive plants grown under standardised conditions.

Because it reduces photosynthesis (Schwachtje and Baldwin 2008), biomass removal has the capacity to alter plant resource allocation patterns, measured as carbon storage (e.g., Holland et al. 1996). As an example, for the clonal alligator weed (*Alternanthera philoxeroides*), repeated shoot mowing reduced aboveground biomass but increased belowground biomass (Jia et al. 2009). If such an increase in

allocation to roots following shoot damage is common in invasive plants, control methods such as mowing may not necessarily curb invasive populations but may actually enhance invasion potential (Jia et al. 2009). However, changes in individuals' vital rates or plant traits following control actions do not automatically serve as a proxy for population-level consequences (e.g., Shea and Kelly 1998; Ramula et al. 2008; Knight et al. 2011). For example, Ramula et al. (2008) demonstrated that a large reduction (60–80%) in plant growth or seed production was required to reduce the long-term population growth rate of short-lived invaders, while an even more drastic reduction in vital rates was necessary for long-lived invaders. Therefore, to quantify the overall effect of management on plant populations, it is necessary to use a measure that integrates different vital rates into a single population growth rate. A demographic model, which is based on multiple vital rates, provides a tool for such a population-level assessment (Caswell 2001).

Lupinus polyphyllus Lindl. (Fabaceae) is an herbaceous, perennial invader with a broad habitat preference (Söber and Ramula 2013; Ramula 2014). It is able to regrow after shoot damage (personal observation) and reproduces mainly from seed, but vegetative propagation by rhizomes is also possible to some extent (Li et al. 2016). For this species, regular mowing to remove aboveground biomass prior to seed maturation is recommended as an environmentally friendly management strategy (e.g., Fremstad 2010), although its efficiency has been questioned in practice (Wissman et al. 2015, p. 19). In a part of its introduced range, Finland, different populations of *L. polyphyllus* originate from repeated introductions from multiple sources and show moderate levels of genetic differentiation (Li et al. 2016), which might affect population responses to control actions. Using seeds from multiple populations of *L. polyphyllus* in southwestern Finland, I explored plant performance and resource allocation in response to annual biomass removal under standardised growth conditions over two consecutive years. I asked the following three questions: (1) How does annual biomass removal affect plant vital rates (survival, growth, flowering probability), biomass, and root:shoot allocation? (2) Do populations respond differentially to annual biomass removal, i.e. do they differ in tolerance to damage? (3) What is the overall effect of a single biomass

removal event on the long-term population growth rate? I predicted that plants would be able to at least partially compensate for biomass loss during the growing season, but that these responses would differ among populations due to phenotypic plasticity and different genetic backgrounds. I also hypothesised that annual biomass removal would lead to a reduction in the long-term population growth rate due to a drastic reduction in vital rates.

Methods

Study species

Lupinus polyphyllus (garden lupin) is a perennial herb, 50–100 cm high, that is native to North America and invasive in Europe, southern Australia, New Zealand, and Chile (Fremstad 2010; Meier et al. 2013). Due to its showy inflorescences and rhizomatous root system that stabilises the soil, the species has been used in horticulture and landscaping (Fremstad 2010). In Finland, *L. polyphyllus* can flower in its second year in natural populations (Jauni and Ramula 2017), but many individuals may flower even during their first summer under common garden conditions (personal observation). An individual plant is able to produce hundreds of seeds (Aniszewski et al. 2001; Ramula 2014), which are dispersed ballistically up to a few metres from the mother plant (Jantunen et al. 2005). Seeds may remain viable in the soil for decades (Fremstad 2010). In Finland, the species is associated with a decline in vascular plant diversity (Valtonen et al. 2006; Ramula and Pihlaja 2012) and arthropod abundance (Valtonen et al. 2006; Ramula and Sorvari 2017).

Annual biomass removal and plant performance

Seeds were hand-collected from 11 populations of *L. polyphyllus* in southwestern Finland (a minimum of 20 plants per population) at the end of July in 2016. The populations were located mostly on road verges and wastelands about 2–30 km apart, and varied in the amount of genetic diversity (Li et al. 2016). The seeds were cleaned and stored in paper bags at room temperature for later use. In December 2016, several hundred seeds per population were sown into plastic pots (100 seeds per pot) filled with a commercial

potting mix. To break seed dormancy, the pots were kept at a low temperature (15 °C daytime, 12 °C night) with a photoperiod of 16 h light and 8 h dark in the greenhouse at the Ruissalo Botanical Garden of the University of Turku for 2 months, after which the temperature was gradually increased to 20 °C in the daytime and 17 °C at night. After the germination peak, which occurred in February–March of 2017, seedlings were individually planted into 8 × 8 cm plastic pots (80 seedlings per population, 880 plants in total). The plants were watered when necessary, but no fertiliser was added.

In early June 2017, when all the plants were still at the vegetative stage, they were replanted into larger pots (volume of 1.2 L, filled with a commercial potting mix) and their height was recorded. To simulate biomass loss by mowing, half of the plants were randomly assigned to be clipped (cut to a height of 5 cm) or not clipped (undamaged control). Due to some mortality in the greenhouse, there were 422 cut and 418 undamaged plants at the beginning of the experiment. The plants were then moved to a common garden, in which they were randomly placed in two blocks separated with a corridor of about 1 m, and were grown until August 2018. No fertiliser was added during the experiment, but the plants were watered regularly.

In addition to the initial size measurement in June 2017, the plants were measured three times during the experiment (August 2017, June 2018, and August 2018); each time measurements were recorded of survival, leaf height, base diameter, and the number of flowering shoots. The biomass removal treatment was repeated in the second year after measurements were taken in early June 2018 (i.e. the leaves of the treated plants were again cut to 5 cm). Due to a warm spring in 2018, many individuals were already flowering at that time. In this, the treatment mimicked control actions in natural populations, because vegetation on road verges is typically mown at the main flowering peak of *L. polyphyllus* in Finland. To avoid the spread of *L. polyphyllus* in the common garden, flowering shoots were regularly removed before seeds ripened (3–4 times during the growing season) and the number of flowering shoots per individual was recorded each time. At the end of the experiment (August 2018), about half of the plants per treatment were chosen haphazardly and harvested to obtain dry biomass. Leaves and shoots were cut at the level of the soil

surface and the roots were washed before drying; the shoots and roots were dried separately at 65 °C for 48 h.

Statistical analyses

To explore the effect of annual biomass removal on plant size during the experiment, I constructed a linear mixed effect model (LME) with the response variable of log (plant size), determined as leaf height \times base diameter, and the fixed, categorical explanatory variables of treatment (biomass removal, control), time (August 2017, June 2018, August 2018), and their interaction (using lme4::lmer; Bates et al. 2015) in R software (R3.5.3; R Development Core Team 2019). Plant size (log-transformed), measured at the beginning of the experiment before the first biomass removal took place, was included as a covariate. Population and plant ID were included as random factors to account for the repeated measurements taken from the same plants during the experiment. I investigated the effect of annual biomass removal on survival and fecundity in a similar way. For survival and flowering probability, I used a binomial, logit-link generalised linear mixed effect model (GLMM), while for the number of flowering shoots (based on the plants that flowered during the experiment), I used a Poisson, log-link GLMM (lme4::glmer; Bates et al. 2015) with the same model structure as described above. For GLMMs, potential overdispersion was checked from the residuals and none was found (dispersion factor ranging from 0.59 to 0.99). Finally, I tested for differences in biomass and root:shoot allocation between the damaged and undamaged control plants using LMEs, with population as a random factor and plant size at the beginning of the experiment as a covariate. Root:shoot ratio was calculated as the proportion of root biomass of the total biomass. For all statistical models, I used the common slope for treatment across populations because population-specific slopes were not supported in any of the cases (model AICs were larger with different slopes than with the common slope, $\Delta\text{AIC} > 2$ in all cases). The significance of the fixed variables was tested with a Wald Chi square test (using car::Anova; Fox and Weisberg 2019). Pairwise comparisons for significant interactions between fixed explanatory variables were conducted using contrasts (lsmeans::contrast; Lenth 2016).

Population growth rate and LTRE analysis

To assess the overall fitness effect of annual biomass removal on population growth, I constructed an integral projection model (IPM) based on the clipped and control plants, respectively, and calculated the long-term population growth rate (λ). The integral projection model predicts vital rates (survival, growth, and fecundity) at year $t + 1$ as a continuous function of an individual's size in year t , resulting in a large matrix after discretisation (Easterling et al. 2000). Population dynamics of *L. polyphyllus* can be described with an IPM consisting of the following two equations.

$$S(t + 1) = s_s(1 - e)S(t) + \int_L^U p(x)f_1(x)seed(1 - e)n(x, t)dx \quad (1)$$

$$n(y, t + 1) = ef_d(y)S(t) + \int_L^U [s(x)g(y, x) + p(x)f_1(x)seedef_d(y)]n(x, t)dx \quad (2)$$

The first equation describes the total number of seeds in the seed bank at year $t + 1$. Seeds come from two sources: seeds that survive in the seed bank from the previous year (s_s) and do not establish, e (the first portion of the equation), and new seeds that enter the seed bank as a result of reproduction (the second portion of the equation), in which $p(x)$ denotes the flowering probability of individuals of size x , $f_1(x)$ is the number of flower shoots produced of individuals of size x , and $seed$ is the average number of seeds per flowering shoot. The second equation describes the number of herbaceous individuals and their sizes (y) present in the population at year $t + 1$. Herbaceous individuals come from two sources: germination from the seed bank (the first portion of eq. 2) and direct germination of seeds that never enter the seed bank (the second portion of eq. 2). In Eq. 2, $f_d(y)$ is the probability distribution of seedling size, $s(x)$ is survival of individuals of size x , and $g(y, x)$ is growth of individuals of size x (see Ramula 2014 for model details). As the present dataset from the common garden study does not capture the entire life-cycle of the species (it lacks information on seed bank transitions and seed production), I used previously published data on the seed bank and seedlings (Ramula

2014) as well as unpublished data on seed production to complete the life-cycle. All these data come from the 11 study populations (see Table 1 for model parameters and data sources).

To estimate vital rates as a function of plant size (leaf height \times base diameter in cm), I used mixed effect models with population as a random factor. I modelled plant growth for year $t + 1$ (June 2018) in relation to plant size from year t (June 2017) with a linear mixed effect model. To model survival and flowering probabilities at year $t + 1$ as a function of plant size from year t , I used a binomial logit-link GLMM, while for the number of flowering shoots at year $t + 1$, I used a Poisson log-link GLMM. For all models, plant size was log-transformed and a quadratic size term was fitted; the model with the lowest AIC was chosen (linear or quadratic). To calculate seed production for each plant, I multiplied the number of flowering shoots (from the GLMM) by the average number of seeds per inflorescence estimated from the field populations in the summer of 2017 (see Table 1 for data on seed production).

To describe population dynamics, the IPM was discretised into a 50×50 matrix, in which the first class consisted of the persistent seed bank, as in Ramula (2014). The lower size limit in the model (L) was defined as $0.9 \times$ the minimum observed plant size in June 2017, and the upper size limit (U) was defined as $1.1 \times$ the maximum observed plant size in June 2017. The models were corrected for eviction in survival for large individuals (log size about > 4.5) using the ceiling approach (Williams et al. 2012). The long-term population growth rate (λ) was calculated as the leading positive eigenvalue of the discretised matrix using the package *popbio* in R (Stubben and Milligan 2007), and the 95% confidence intervals of λ were calculated based on 1000 bootstrap replicates. As the IPM is based on two consecutive time points (June 2017 and June 2018), it quantifies the effect on population dynamics of a single biomass removal event (June 2017) when all plants were at the vegetative stage.

To assess the contributions of changes in vital rates following biomass removal to λ , I used a life

Table 1 Summary of demographic parameters and data sources used to construct integral projection models for *Lupinus polyphyllus* in control and annual biomass removal treatments

Vital rate	Parameter (SE)	Source	n
<i>Control treatment</i>			
Survival probability (s)	$\text{logit}(s) = -9.17(2.81) + 2.82(0.68)x$	This study	418
Growth (g), variance	$y = 4.12(0.38) + 0.26(0.09)x, \sigma^2 = 0.54$	This study	391
Flowering probability (p)	$\text{logit}(p) = 1.76(2.09) + 0.04(0.47)x$	This study	392
No. flowering shoots (f_1)	$f_1 = \exp(-0.32(0.43) + 0.32(0.10)x)$	This study	341
Seeds per inflorescence ($seed$)	$seed = 101$	Unpubl. field data from 2018	275 plants from 11 populations
Plant establishment (e)	$e = 0.12$	Ramula (2014)	11 populations
Seedling size distribution (f_d)	$f_d: \mu = 1.92, \sigma^2 = 0.17$, normal distribution	Ramula (2014)	124
<i>Biomass removal treatment</i>			
Survival probability (s)	$\text{logit}(s) = -9.68(2.21) + 2.65(0.53)x$	This study	422
Growth (g), variance	$y = 3.49(0.58) + 0.37(0.13)x, \sigma^2 = 0.69$	This study	343
Flowering probability (p)	$\text{logit}(p) = -3.92(2.13) + 1.17(0.49)x$	This study	343
No. flowering shoots (f_1)	$f_1 = \exp(-1.09(0.68) + 0.41(0.16)x)$	This study	258
Seeds per inflorescence ($seed$)	$seed = 101$	Unpubl. field data from 2018	275 plants from 11 populations
Plant establishment (e)	$e = 0.12$	Ramula (2014)	11 populations
Seedling size distribution (f_d)	$f_d: \mu = 1.92, \sigma^2 = 0.18$, normal distribution	Ramula (2014)	124

The models are functions of log plant size x

table response experiment, LTRE. The LTRE analysis considers the absolute differences in vital rates between the two treatments (biomass removal and control), multiplied by the sensitivity of λ to those vital rates (Caswell 2001). Due to different sensitivities of vital rates, the LTRE contributions do not necessarily equal the absolute differences in vital rates (Caswell 2001). I calculated vital rate sensitivities for the additive sub-matrices of survival-growth and fecundity (Griffith 2017) based on the IPM constructed for the control treatment (sensitivity::popbio; Stubben and Milligan 2007).

Results

Annual biomass removal and plant performance

Biomass removal in each growing season affected all plant traits considered, except for root:shoot ratio at harvest (Table 2). However, the effect of annual biomass removal on survival, plant size, and the number of flowering shoots varied over time

(Table 2). Biomass removal had no effect on plant survival during the first growing season, while it considerably reduced survival in the second year, both in early and late summer (Fig. 1a). The clipped plants were smaller than the control plants particularly at the end of the first growing season (i.e. after the first biomass removal event; Fig. 1b). Moreover, annual biomass removal reduced flowering probability at all three censuses (Fig. 1c) and the number of flowering shoots in the year following the treatment (Fig. 1d). The plants that experienced annual biomass removal over two consecutive years had smaller shoot and root biomass than the control plants at harvest (Table 2, Fig. 2). Plant responses to biomass removal did not differ among populations, as indicated by a common slope across 11 study populations for different response variables (Table 2).

Population growth rate and vital rate contributions

The demographic model constructed based on the control plants predicted that without management the population would increase by about 42% per year

Table 2 Results from linear mixed effects models and generalised linear mixed models used to examine the effects of annual biomass removal on the perennial herb *Lupinus polyphyllus* over two consecutive years

Response variable	Explanatory variable	χ^2	df	p
Plant size	Initial plant size (covariate)	61.63	1	< 0.001
	Treatment (biomass removal, control)	93.17	1	< 0.001
	Time (3 levels)	133.73	2	< 0.001
	Treatment \times Time	37.79	2	< 0.001
Survival	Initial plant size (covariate)	2.24	1	0.135
	Treatment	0.20	1	0.658
	Time	153.77	2	< 0.001
	Treatment \times Time	24.04	2	< 0.001
Flowering prob.	Initial plant size (covariate)	7.45	1	0.006
	Treatment	18.55	1	< 0.001
	Time	279.07	2	< 0.001
	Treatment \times Time	3.17	2	0.205
No. flowering shoots	Initial plant size (covariate)	15.46	1	< 0.001
	Treatment	45.12	1	< 0.001
	Time	150.03	2	< 0.001
	Treatment \times Time	7.04	2	0.030
Shoot biomass	Initial plant size (covariate)	0.19	1	0.661
	Treatment	28.18	1	< 0.001
Root biomass	Initial plant size (covariate)	2.21	1	0.137
	Treatment	97.63	1	< 0.001
Root:shoot ratio	Initial plant size (covariate)	0.54	1	0.462
	Treatment	1.55	1	0.213

Population and plant ID were used as random factors, population was fitted with a common slope

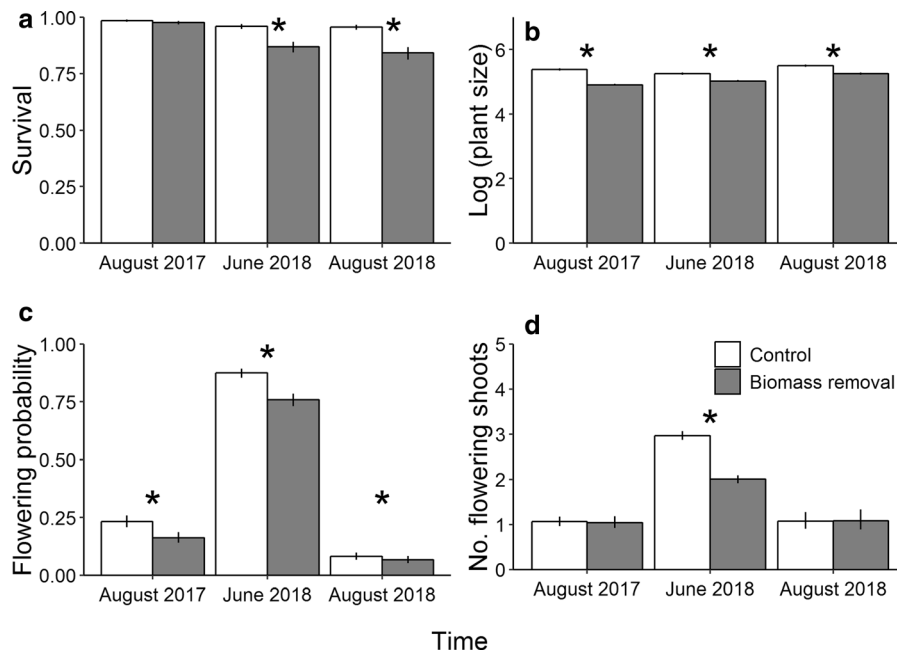


Fig. 1 The effects of annual biomass removal events, conducted in early June 2017 and 2018, on the performance of the perennial herb *Lupinus polyphyllus* (least square mean \pm SE).

Asterisks (*) indicate differences between control and damaged plants ($p < 0.05$, contrasts)

under the common garden conditions ($\lambda = 1.423$ [95% CL 1.412–1.434]). A single biomass removal event at the vegetative stage considerably decreased population growth rate; in this group the population was predicted to grow by about 9% per year ($\lambda = 1.093$ [95% CL 1.090–1.096]). The LTRE analysis revealed that this decline in λ after annual biomass removal was about equally due to a reduction in plant fecundity and survival-growth (summed LTRE contributions: -0.179 and -0.144 , respectively; Fig. 3).

Discussion

Annual biomass removal in two consecutive years reduced plant vital rates (survival, growth, fecundity) and biomass in all 11 study populations of *L. polyphyllus* grown under common garden conditions. This result suggests that among-population variation in tolerance to biomass removal in the study species is minor, and that the underlying responses to this management action might not be population-specific per se. This finding is in contrast to previous studies on native herbs that have reported among-population variation in tolerance to herbivore damage

(Lennartsson et al. 1997; Boalt et al. 2010; König et al. 2014; Lehndal and Ågren 2015). The lack of among-population variation in tolerance to biomass removal in the present study could be due to the intensity of the damage applied (i.e. cutting all aboveground biomass), and it is possible that populations might show more diverse responses to milder damage caused by, e.g., herbivores. Another contributing factor could be the relatively similar management history of the populations, as most of them were unmanaged and the seeds were collected from undamaged plants only. Finally, the study populations originated from the same geographic region (SW Finland) and represented only a subsample of populations in a part of the species' introduced range, which might also explain the similarity in responses to annual biomass removal.

To date, most assessments of attempts to control invasive species are based on a single control event and a follow-up period of a year or less (reviewed in Kettenring and Reinhardt Adams 2011). The present study revealed that longer-term studies covering multiple growing seasons may be necessary to reveal the overall effects of control actions on perennial plants. For *L. polyphyllus*, biomass removal in the first

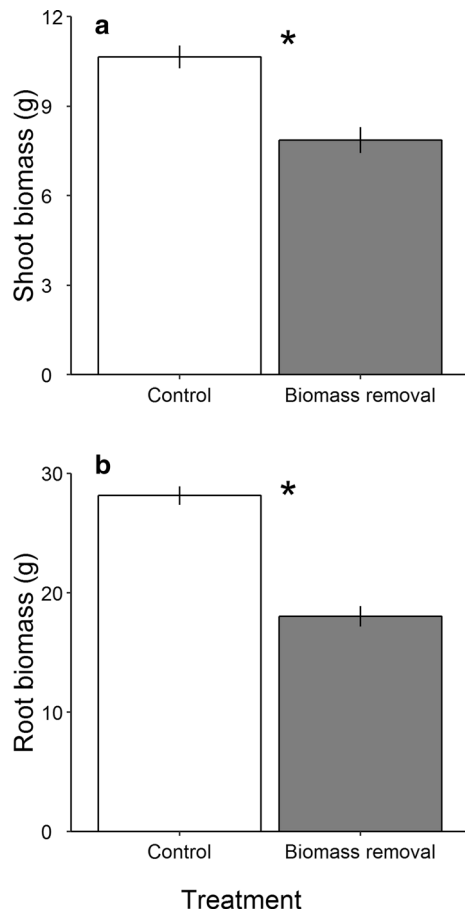


Fig. 2 The effects of annual biomass removal events, conducted in early June 2017 and 2018, on the biomass of the perennial herb *Lupinus polyphyllus* (least square mean \pm SE). Asterisks (*) indicate differences between control and damaged plants ($p < 0.05$, LME)

year had no effect on plant survival later in the same season, but it considerably reduced survival the next year. In other words, biomass removal incurred costs in the year following the damage; it depleted the plants' available resources, which was detrimental for some individuals. Such delayed costs for plant performance can only be detected in longer-term studies. In addition to delayed costs, biomass removal reduced the growth and flowering probability of *L. polyphyllus* in the same growing season, indicating that the plants were not able to fully compensate for biomass loss under common garden conditions. This finding is not surprising, given the severity of the damage applied. In general, plant (over)compensatory responses to shoot damage occur at low-to-moderate

damage levels (e.g., Huhta et al. 2003). In addition to damage level, a plant's ability to compensate for biomass loss depends on the amount of resources available, with compensatory growth often increasing with increasing resource availability (Belsky 1986; Maschinski and Whitham 1989; Ramula et al. 2019). As the growing conditions in the common garden (without competitors) were probably more favourable than those in natural populations, this study might have overestimated plants' compensatory ability. On the other hand, the effect of biomass removal was examined using potted plants, which ignores intraspecific competition and, consequently, density dependence. Ignoring density dependence might have underestimated plant compensatory responses: in dense weed populations, mowing can result in stronger (over)compensatory growth because it relaxes density dependence in vital rates (Buckley et al. 2001; Pardini et al. 2009). Indeed, He and Ding Ji (2015) observed that in the perennial invasive plant *Alternanthera philoxeroides*, the compensatory response to herbivore damage was greater in dense monoculture than in sparse stands. Overall, in natural weed populations, interactions with local environmental conditions may greatly affect plant demography and, consequently, population responses to control actions (Shea et al. 2005; Evans et al. 2012; Pichancourt et al. 2019).

A population-level assessment revealed that a single biomass removal event, applied when the plants were at the vegetative stage, greatly reduced the long-term population growth rate (λ), and that this reduction was about equally due to reductions in both plant fecundity and survival-growth. This finding is in line with previous demographic studies, which have reported that the population dynamics of short-lived, rapidly growing perennial herbs (e.g., Silvertown et al. 1993; Ramula et al. 2008) are sensitive to relative changes in fecundity and growth. However, the relative importance of different vital rates to population dynamics partially depends on the magnitude of population growth rate, with the importance of fecundity diminishing with declining λ (Silvertown et al. 1993; Ramula et al. 2008). Consequently, the contributions of vital rates to λ are likely to differ between rapidly growing and more stable weed populations. Although a single biomass removal event considerably reduced λ in the present study, repeated control actions in consecutive years are probably required to curb invasions of *L. polyphyllus* in the long

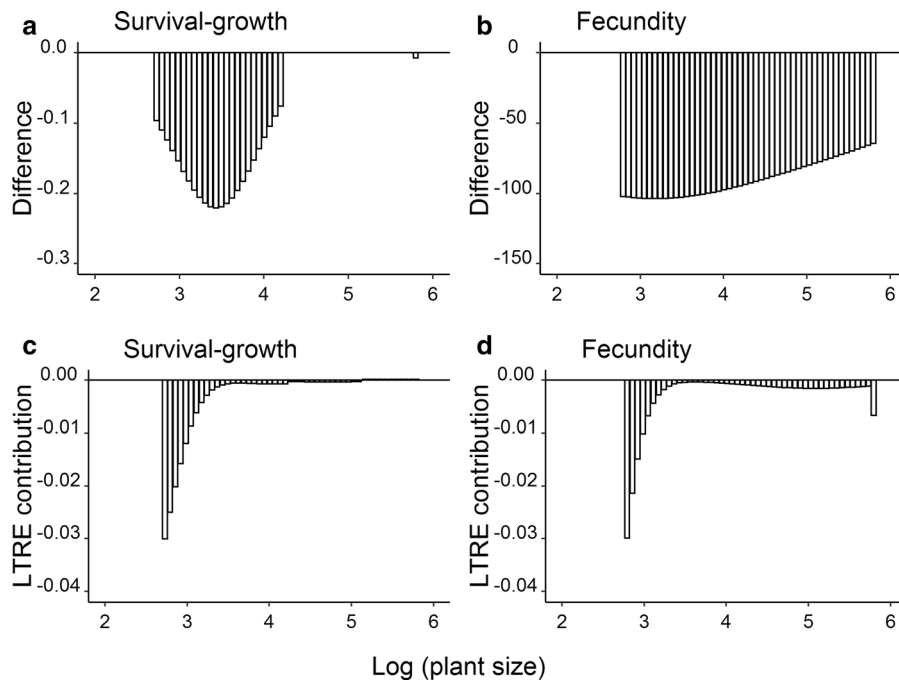


Fig. 3 Contributions of the vital rates of the perennial herb *Lupinus polyphyllus* to the reduction in the long-term population growth rate (λ) after an annual biomass removal event,

measured as a-b) absolute changes in vital rates compared to control plants of a given size and c-d) contribution from a life table response experiment (LTR)

run. Rather small (but significant) differences in vital rates between the damaged and control plants observed here (Figs. 1, 2) indicate that the species does demonstrate some compensatory growth even after drastic biomass removal. Therefore, a single biomass removal event is likely to only temporarily reduce population growth. Due to the lack of empirical data on seed bank parameters, germination, and seed production per flower shoot, these demographic parameters in the population model were assumed to be constant between the two treatments. Constant seed bank parameters are likely to have a minor effect on the results because a previous study based on 37 populations of this species suggests that its population growth rate is not sensitive to variation in the seed bank parameters in increasing populations (Ramula 2017). However, biomass removal on its own may affect some of these fecundity parameters either quantitatively or qualitatively through changes in seed quality. As an example, in the annual plant *Raphanus raphanistrum*, herbivory on maternal plants reduced seed mass in some cases but increased it in others, which then affected offspring performance (Agrawal 2001). If such transgenerational effects occur also in *L.*

polyphyllus, the present study might have misestimated (either over or under) the total effects of mowing on populations. Moreover, the removal of flowering shoots (although necessary to prevent the spread of this invasive species) might have induced compensatory growth. If so, the current study might have overestimated λ for the control plants and, consequently, the overall effect of clipping on the population.

Although results from common garden conditions cannot be directly translated into field populations, the present study suggests that annual biomass removal by mowing over multiple consecutive years has the potential to curb invasions of *L. polyphyllus*. This finding indicates that annual mowing may indeed represent an environmentally friendly method for the control of this perennial invader.

Acknowledgements Open access funding provided by University of Turku (UTU) including Turku University Central Hospital. I am grateful to the staff and trainees of the Ruissalo Botanical Garden who took care of the plants in the common garden, and to two anonymous reviewers for their constructive comments on the manuscript. This work was supported by the Academy of Finland (#285746).

Authors' contributions SR designed and conducted the study.

Funding This work was supported by the Academy of Finland (#285746).

Compliance with ethical standards

Conflict of interest The author declares that she has no conflict of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Availability of data and material All relevant data and related metadata underlying reported findings are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cfxpnvx37>.

Code availability An annotated computer code for the population model is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cfxpnvx37>.

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