Potential impacts of tolerance to herbivory on population dynamics of a monocarpic herb[1]

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PREMISE OF THE STUDY: Mammalian herbivores, particularly white-tailed deer, can have a major impact on plant abundance and distribution. However, plants can tolerate herbivory by increasing seed production or seed quality. We used the monocarpic perennial *Prenanthes roanensis* to examine tolerance to mammalian herbivory through seed quality and modeled the effects of tolerance on population growth rate.

METHODS: We examined seed quality (proportion of viable seeds, seed mass, germination, and seedling size) on damaged and undamaged plants to determine the extent to which plants tolerate herbivory. We then varied seed quality parameters over a range of values in population models to compare population growth rates under "no-tolerance" conditions (herbivory, but no tolerance) to those under "tolerance" conditions.

KEY RESULTS: In most populations, plants damaged by herbivores had a greater proportion of viable seeds per plant or a greater probability of seed germination. Incorporating observed tolerance into population models did not significantly increase population growth rate. However, at low germination rates, increased germination of seeds from damaged plants has the potential to significantly increase population growth rate.

CONCLUSIONS: Damaged plants can compensate for loss of reproductive heads by increasing seed viability and germination rates in the remaining seeds. This study is one of the first to demonstrate that tolerance through seed quality has the potential to affect population growth rate. Our results suggest that incorporating tolerance into population models may help elucidate mechanisms by which plant populations persist despite herbivory.

KEY WORDS Asteraceae; compensation; fecundity; germination; monocarp; population growth rate (λ); population variability; *Prenanthes roanensis*; seed quality; seed viability; tolerance

Herbivores are a key component of ecosystems and can influence the distribution and abundance of plants (Maron and Crone, 2006). Herbivory has been shown to negatively impact individual plant fitness through reductions in plant growth, survival, and reproduction (Strauss and Zangerl, 2002), which can result in reduced population growth rates (Russell et al., 2001; Maron and Crone, 2006). Many studies have shown that herbivory can reduce plant population growth rates below sustainable levels (i.e., λ < 1) and, therefore, can limit where populations persist (Bastrenta et al., 1995; Ehrlén, 1995; Louda and Rodman, 1996; Knight, 2004; McGraw and Furedi, 2005; Knight et al., 2009; Eckberg et al., 2014).

Mammalian herbivores that consume bolting stems affect the fecundity of plants. Not only do they directly decrease flower number

and, thus, seed output, but also a diminished floral display can reduce pollinator attraction (Juenger and Bergelson, 1997; McCall and Irwin, 2006). In species that have low selfing rates, herbivory can therefore lead to a reduction in the number of viable seeds per plant (Lohman et al., 1996). Additionally, loss of photosynthetic tissue can modify resource allocation, which can decrease seed size (Lee and Bazzaz, 1980), leading to lower germination rates and smaller seedling sizes (Mueller et al., 2005). Herbivores that affect reproductive output may have a particularly negative impact on populations of monocarpic plants, especially those that lack a seed bank, as regeneration depends upon current seed rain (Louda and Potvin, 1995). Population growth rates of monocarpic species tend to be sensitive to changes in fecundity (Silvertown et al., 1993), so small reductions in either the number of seeds or the quality of seeds produced can have large negative consequences for population growth rate.

However, in general, many plant species have evolved mechanisms to tolerate herbivory (Strauss and Agrawal, 1999; Stowe et al., 2000; Tiffin, 2000). Tolerance implies that plants are able to regrow and reproduce after experiencing herbivory (Strauss and Agrawal,

1999). This mitigation of the detrimental effects of herbivory can range from incomplete compensation to overcompensation (Maschinski and Whitham, 1989; Stowe et al., 2000). Compensating lost fecundity due to grazing can be achieved by increasing the number of flowers on the damaged plant or increasing the number or quality of seeds in undamaged flowers. For example, damage to the apical meristem of a plant can cause an increase in branching and subsequent flower production, resulting in a similar or greater number of flowers compared with an undamaged plant (Paige and Whitham, 1987; Benner, 1988; Maschinski and Whitham, 1989; Huhta et al., 2000; Rautio et al., 2005). Alternatively, plants may redirect resources to increase the maternal investment in the remaining flowers. This change in investment can occur by directly increasing the number of seeds per flower (Lehtilä and Syrjänen, 1995), increasing the number of seeds per plant through alterations to floral sex expression that increase the proportion of female or hermaphroditic flowers (Hendrix and Trapp, 1981; Krupnick and Weis, 1998; Wise and Cummins, 2006), or decreasing the number of aborted flowers, fruits, or seeds (e.g., Ruiz et al., 2002; Wise and Cummins, 2006). Resource reallocation may also increase seed size in undamaged flowers as a compensatory response to flower loss (Pilson and Decker, 2002; Gruntman and Novoplansky, 2011), and large seed sizes can subsequently increase germination rates and seedling survival and growth (Gómez, 2004).

The extent to which monocarpic plants mitigate reduced fecundity through tolerance may be important for their population persistence. It is presently unclear what effects plant tolerance might have at the population-level (Juenger and Lennartsson, 2000), though the few studies that have explicitly incorporated tolerance into population models suggest it may be important. A study on an iteroparous perennial found that tolerance through increased clonal reproduction had the potential to buffer population growth rate from the negative effects of herbivory on plant growth (Evju et al., 2011). Moreover, another study found that incorporating fecundity compensation was important to understanding complex population dynamics in an annual plant (Buckley et al., 2005). While tolerance has the potential to positively influence population persistence, we know little about the impact of tolerance on population growth rate. Such studies are important for understanding the mechanisms by which plant populations are able to persist despite high levels of herbivory.

We explored the effects of tolerance to mammalian herbivory on population growth rate (λ) in populations of the monocarpic perennial *Prenanthes roanensis* Chickering (Chickering) (Asteraceae). Reproductive individuals of *P. roanensis* begin bolting in the spring, flower in the late summer, and disperse seed in the fall. During this time, they experience significant herbivory from white-tailed deer (*Odocoileus virginianus*). Additionally, in one of the populations, wild ponies and cattle contribute to herbivore pressure and may be contributing to its decline (λ < 1; Aikens and Roach, 2014). Unlike other plant species, *P. roanensis* does not increase its branching after being grazed. Rather, reproductive individuals grow one branch off the grazed, main stem that will develop inflorescences. Therefore, we examined the ability of populations to tolerate herbivory through increased seed viability, seed mass, seed germination, and subsequent seedling size, which we collectively term seed quality, in damaged plants.

We conducted two experiments: a seed quality experiment and a population growth rate modeling experiment. Specifically, we asked (1) how does herbivory affect seed quality and (2) how do changes in seed quality from herbivory affect population growth rate? For each of four populations, we measured seed quality traits from plants that were damaged by herbivores and from plants that were undamaged to determine the extent to which individuals tolerate herbivory in each population. To answer the second question, we modeled population growth rate, using demographic data from a previous study (Aikens and Roach, 2014), but in this study we focused on seed quality estimates to compare two different scenarios: a "no-tolerance" scenario in which plants do not demonstrate tolerance to herbivory and a "tolerance" scenario in which tolerance is included. Additionally, we explored the parameter space of the seed quality variables found to differ between undamaged and damaged plants to determine how variation in these variables might influence population growth rate.

MATERIALS AND METHODS

Study species—*Prenanthes roanensis* is a short-lived, monocarpic, perennial plant endemic to high elevations in the Southern Appalachians. It has two distinct life stages: a nonreproductive stage characterized by a rosette and a reproductive stage in which the rosette is replaced by a bolting stem. Reproductive plants generally begin bolting by late May and flower in late August to early September. Each reproductive head, or capitulum, produces 5–13 ligulate florets. The florets are composed of stamens, which are fused by their anthers to form a tube, from which the style emerges with pollen. The style splits and curls back on itself, presumably for self-fertilization, though selfing rates in this species are low (M. Aikens, unpublished data). Bumblebees (*Bombus* spp.) appear to be one of the primary pollinators, though other insects have been observed foraging in florets. Seeds germinate in the spring, after a requisite cold stratification, and there is little evidence of a seed bank (M. Aikens, personal observation). Transitioning from the nonreproductive to the reproductive stage also requires vernalization, though plants may overwinter several times before becoming reproductive. Because the plant has a thickened taproot, damage to the aboveground vegetation does not necessarily result in the death of the plant. Instead, following damage, the plant may remain dormant for the year, and leaves may reappear the following year. Additionally, while largely monocarpic, *P. roanensis* is not a strict monocarp. The taproot can break apart and give rise to new nonreproductive individuals asexually through fragmentation. Therefore, the ramet is monocarpic, but the genet has potential to reproduce again.

Study populations—We conducted this study in four natural populations of *P. roanensis*: Big Bald, Roan, Mt. Rogers, and Whitetop. Big Bald and Roan are located in the center of the range along the Tennessee–North Carolina border. Mt. Rogers and Whitetop are located at the northern edge of the range in southwest Virginia. The populations are located in grassy, open habitat between 1580 and 1710 m in elevation. Deer herbivory was common at all sites, and at Mt. Rogers, wild ponies and cattle were also present. Site characteristics are presented in Appendix S1 (see Supplemental Data with the online version of this article).

Experiment 1: Seed quality—In October 2011, we haphazardly collected seeds across each of the four populations from individuals damaged by herbivores and individuals that were undamaged, including from some plants protected by deer netting (see below). The

number of individuals sampled varied by site, but we sampled a minimum of 26 individuals per damaged/undamaged treatment per site.

We assessed seed quality by measuring seed viability, seed mass, seed germination, and seedling size. In general, seed viability was measured on all plants from which seed was collected. However, we only sampled a subset of damaged individuals from Big Bald (see Appendix S2 for sample sizes with online Supplemental Data). Seed viability was tested by randomly selecting 20 seeds per plant and using tweezers to determine whether seeds were filled or not. If less than 20 seeds were collected from a plant, we tested viability on all seeds collected. For individuals that contained viable seed, we randomly selected 2–4 filled seeds per plant to be weighed to 0.0001 mg precision on a microbalance. After weighing, the seeds were planted in individual cells in 9 × 18 cell flats in an incomplete random block design as we could not include a seed from every individual plant in each flat. Seeds were placed on the surface of moistened MetroMix soil (Sunshine Professional Growing Mix, Sun Gro Horticulture, Bellevue, Washington, USA) and covered with a layer of sand. Flats were cold stratified at 4°C for 16 wk, then transferred to a mist bench in the greenhouse on 5 April 2012. Beginning 6 d after cold stratification, germination was recorded every other day. After 40 d on the mist bench, we stopped recording germination because no new germination had been recorded in the previous 8 d. The length of the largest leaf on each seedling was measured, using digital calipers to 0.01 mm precision, 24 d after the seedling emerged. The number of individuals used for measurements on seed viability, seed mass, germination, and seedling size are given in Appendix S2.

To determine whether herbivory affected seed quality, we compared seed viability and, in filled seeds, seed mass, seed germination, and seedling size between damaged and undamaged plants at each of the four sites. Statistical analyses for seed quality were conducted in SAS (version 9.3; SAS Institute, Cary, North Carolina, USA). In each analysis, herbivory treatment (damaged vs. undamaged), population, and herbivory × population interaction effects were included as fixed effects. Seed viability, measured as the proportion of filled seeds per plant, was arcsine-transformed to meet the assumption of normality of residuals and analyzed by ANOVA (PROC GLM). For seed mass, seed germination, and seedling size, we nested individual plants within the herbivory × population interaction term because each individual plant had multiple seeds that were measured. We also included flat as a random block effect for seed germination and seedling size. Seed germination was analyzed using a generalized linear mixed model (PROC GLIMMIX), and seed mass and seedling size were analyzed with a mixed-effects ANOVA using Satterthwaite's approximation (PROC MIXED) for the degrees of freedom due to the unbalanced design. In all analyses, when the herbivory × population effect was significant, we conducted contrasts to determine which populations had significant herbivory effects.

Experiment 2: Population growth rate (λ) models—The population growth rate models combined the seed quality data described above with demographic data from a previous study conducted in these populations from 2009 to 2012 (Aikens and Roach, 2014). Briefly, tagged plants in each population were censused annually. Size of nonreproductive plants was measured as length of the longest leaf; size of reproductive plants was measured as the basal stem diameter. On each reproductive plant, the number of reproductive heads was counted. Additionally, 19–22 reproductive heads were collected from each of the four populations each year, and the seeds in

each head were counted to determine an average number of seeds per head for each site in each year. Fecundity, measured as the number of seeds per plant, was calculated by multiplying the number of heads on the reproductive plant by the site- and year-specific average number of seeds per head (online Appendix S3). Reproductive plants with cut stems were noted as evidence of damage by herbivores.

During the first 2 years of the demographic study, the majority of reproductive plants in these populations were damaged by herbivores (75%), so we experimentally protected plants to ensure we would be able to accurately estimate the fecundity of undamaged plants. This protection also ensured we captured variance in plant size of undamaged plants to better understand the relationship between reproductive plant size and fecundity. We protected reproductive individuals by individually surrounding them with deer netting in two populations in early June 2011. The mesh of the deer netting was large enough to let pollinators through, and furthermore, the tops of the plants were not covered, allowing pollinators access to the florets. These experimental manipulations were done at only two populations because permitting issues in the National Forest prevented us from protecting plants at the other locations. At Mt. Rogers, one 20-m transect and two 10-m transects were established. We tagged and protected the closest plant to each half meter mark along the 20-m transect and the closest plant to each meter mark along the 10-m transects (61 total plants). At Roan, we established four transects: two 10-m transects and two 20-m transects. On all four transects, we tagged and protected the closest individual to each meter mark (60 total plants). In late August 2011, we measured stem diameter at the base of the plant to 0.01 mm precision with digital calipers and counted the number of reproductive heads on each protected plant.

We used integral projection models (IPMs) to calculate population growth rates (λ) based on the life cycle of *P. roanensis* (Fig. 1), which includes two continuous stages and one discrete stage
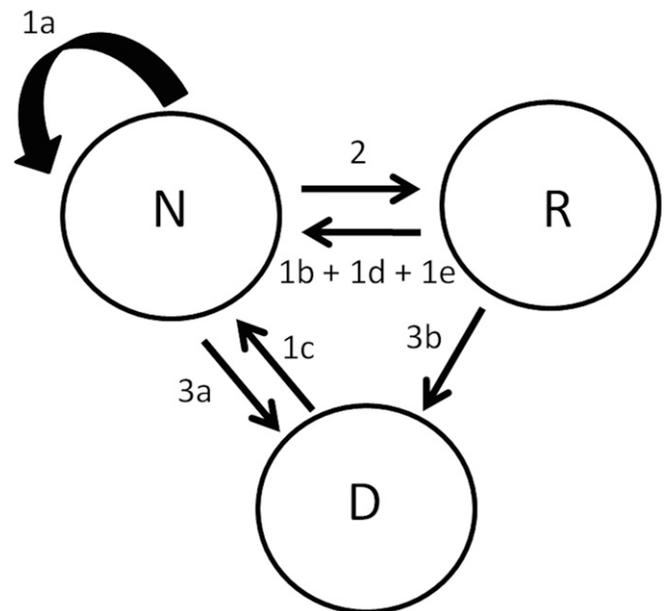

FIGURE 1 Life-cycle diagram showing the three life-stages of *P. roanensis*: nonreproductive (N), reproductive (R), and dormant (D). The arrows indicate annual transitions and the numbers correspond to the equations in the text.

(Aikens and Roach, 2014). Nonreproductive and reproductive stages are continuous and size-based; nonreproductive size was measured as length of the longest leaf and reproductive size was measured as basal stem diameter. Plants present in a year, missing the next year, but present once again the following year were characterized as dormant. Due to the short length of the study, plants missing for more than 1 year were assumed to be dead. To include fragmentation in the model, we made the assumption that a nonreproductive individual within 2 cm of a previously reproductive individual was derived from fragmentation. Note that although we did include fragmentation in the model, removing it (i.e., modeling the life cycle of *P. roanensis* as strictly monocarpic) did not change population growth rates. This lack of change is likely because only about 34% of reproductive individuals throughout the demographic study survived through fragmentation, and they often reappeared as very small nonreproductive individuals, so they were less likely to survive to the next year. Thus, compared with other life-history transitions, fragmentation was not an important contributor to population growth rates.

We modeled population growth rate (λ) using three equations that estimate the number of nonreproductive, reproductive, and dormant plants following Jacquemyn et al. (2010). The number of nonreproductive plants of size x_2 in year $t + 1$ depends on the number of nonreproductive plants of size x_1 that remain nonreproductive (Eq. 1a), the number of reproductive plants of size z_1 that transition back to nonreproductive through fragmentation (Eq. 1b), the number of dormant plants that become nonreproductive (Eq. 1c), the fecundity of reproductive plants of size z_1 damaged by herbivores (Eq. 1d), and the fecundity of reproductive plants of size z_1 undamaged by herbivores (Eq. 1e):

$$n(x_2, t+1)$$
$$= \int_x \sigma_N(x_1)[1 - \mu_N(x_1)][1 - \beta_N(x_1)]\gamma_{NN}(x_2, x_1)n(x_1, t)dx \quad \text{Eq. 1a}$$

$$+ \int_z \sigma_R(z_1)[1 - \mu_R(z_1)]\gamma_{NR}(x_2, z_1)r(z_1, t)dz \quad \text{Eq. 1b}$$

$$+ \gamma_{ND}(x_2)D(t) \quad \text{Eq. 1c}$$

$$+ \int_z \varphi_E(z_1)v_E\delta_E\gamma_{SR,E}(x_2)\rho r(z_1, t)dz \quad \text{Eq. 1d}$$

$$+ \int_z \varphi_U(z_1)v_U\delta_U\gamma_{SR,U}(x_2)(1 - \rho)r(z_1, t)dz, \quad \text{Eq. 1e}$$

where the parameters are defined in Table 1 and the equation numbers refer to life-cycle transitions in Fig. 1. The number of reproductive plants of size z_2 in year $t + 1$ depends on the number of nonreproductive plants of size x_1 that become reproductive and survive to time of flowering in late summer (Eq. 2):

$$r(z_2, t+1)$$
$$= \int_x \sigma_N(x_1)[1 - \mu_N(x_1)]\beta_N(x_1)\gamma_{RN}(z_2, x_1)\tau n(x_1, t)dx. \quad \text{Eq. 2}$$

The number of dormant plants in year $t + 1$ depends on the number of nonreproductive plants of size x_1 (Eq. 3a) and the number of reproductive plants of size z_1 that become dormant (Eq. 3b):

$$D(t+1) = \int_x \sigma_N(x_1)\mu_N(x_1)n(x_1, t)dx \quad \text{Eq. 3a}$$

TABLE 1. Abbreviations for vital rate parameters in Eqs. 1–3.

Abbreviation	Parameter
σ_N	probability of survival of a nonreproductive plant [a]
σ_R	probability of survival of a reproductive plant [a]
μ_N	probability of a nonreproductive plant going dormant [a]
μ_R	probability of a reproductive plant going dormant [a]
β_N	probability of a nonreproductive plant flowering [a]
γ_{NN}	growth distribution of nonreproductive plant sizes [a]
γ_{NR}	distribution of nonreproductive plant sizes after transitioning from a reproductive state [a]
γ_{ND}	distribution of nonreproductive plant sizes after transitioning from a dormant state [a]
γ_{RN}	distribution of reproductive plant sizes after transitioning from a nonreproductive state [a]
$\gamma_{SR,E}$	distribution of nonreproductive seedling sizes arising from damaged reproductive plants [a]
$\gamma_{SR,U}$	distribution of nonreproductive seedling sizes arising from undamaged reproductive plants [a]
φ_E	number of seeds produced by damaged reproductive plant [b]
φ_U	number of seeds produced by undamaged reproductive plant [b]
v_E	probability of seed viability from a damaged plant [b]
v_U	probability of seed viability from an undamaged plant [b]
δ_E	probability of germination of viable seed from a damaged plant [b]
δ_U	probability of germination of viable seed from an undamaged plant [b]
ρ	proportion of reproductive plants damaged by herbivores [b]
τ	probability of a reproductive plant surviving the summer to flowering [a]

[a] Parameter estimated by Aikens and Roach (2014).
[b] Parameter estimated in this study.

$$+ \int_z \sigma_R(z_1)\mu_R(z_1)r(z_1, t)dz. \quad \text{Eq. 3b}$$

Site-specific parameter estimates for survival, dormancy, flowering, and growth were obtained from Aikens and Roach (2014) (online Appendix S4). Generalized linear mixed effects models with the binomial family and a log link function were used to model survival parameters [$\sigma_N(x)$; τ; $\sigma_R(z)$], dormancy parameters [$\mu_N(x)$; $\mu_R(z)$], and flowering of nonreproductive plants [$\beta_N(x)$]. Linear mixed models using a Gaussian error structure were used to model growth [$\gamma_{NN}(x_2, x_1)$; $\gamma_{RN}(z_2, x_1)$], the transition, due to fragmentation, of reproductive plants to nonreproductive plants [$\gamma_{NR}(x_2, z_1)$], and the transition of dormant plants to nonreproductive plants [$\gamma_{ND}(x_2)$]. For all models, we included site and year as random effects and tested a full model with random slopes and intercepts for site and year against more restricted models using log-likelihood ratio tests ($P < 0.05$) (Bolker et al., 2009). We also tested whether plant size was a significant predictor of each vital rate by using AIC (Akaike's information criterion) values to compare a model with and without plant size as a fixed effect (Burnham and Anderson, 2002; Bolker et al., 2009). Plant size was an important predictor of nonreproductive survival [$\sigma_N(x)$], the probability of a nonreproductive plant going dormant [$\mu_N(x)$], the probability of a nonreproductive plant flowering [$\beta_N(x)$], growth within the nonreproductive stage [$\gamma_{NN}(x_2, x_1)$], and growth from a nonreproductive plant into a reproductive plant [$\gamma_{RN}(z_2, x_1)$] and thus included as a fixed effect in these models.

We used the fecundity data collected from the field in 2009–2011 and from the protected plants in 2011 to estimate the relationship

between basal plant diameter and the number of seeds per plant for damaged and undamaged plants. Most reproductive plants in the 2009–2011 field data were damaged. We used these plants to model fecundity as a function of size for damaged plants $[\varphi_E(z_1); n = 328]$. We combined the undamaged plants from the field with the protected plant data to model fecundity as a function of size for undamaged plants $[\varphi_U(z_1); n = 266]$. For both models, we included basal diameter as a fixed effect and used a negative binomial model (glmmADMB using the nbinom option in R; Skaug et al., 2012). We tested whether to include site and year as random effects by comparing AIC values among models (Burnham and Anderson, 2002). The models ranged from a full model that included random slopes and intercepts for both site and year to the simplest model in which neither site nor year were included as random effects. We also tested whether basal diameter was a significant predictor of the number of seeds per plant by comparing AIC values between a model that included basal diameter and one that did not include basal diameter. If ΔAIC was > 2, the model with the lowest AIC was used; if ΔAIC was < 2, the models were considered equally parsimonious, and we used the simpler model (Burnham and Anderson, 2002).

Site-specific parameter estimates for seed viability and germination were obtained from the seed quality data. We used the average proportion of viable seeds per plant at a site as an estimate of the probability a seed is viable, calculating separate averages for damaged (v_E) and undamaged plants (v_U). Similarly, we used the average proportion of viable seeds that germinated per plant from a site as an estimate of the probability of a viable seed germinating, calculating separate averages for damaged (δ_E) and undamaged plants (δ_U).

The proportion of plants damaged per site (ρ) was an average of the proportion of reproductive plants observed with damage across the three years fecundity was measured in the field study (2009–2011) (Appendix S3). Herbivores have been found to selectively graze larger plants (e.g., Lin and Galloway, 2010). We used logistic regression to determine whether basal plant diameter predicted the probability of being damaged by an herbivore. Size was significant at only one of the four sites, Whitetop ($z = 3.57$, $P < 0.001$). We investigated the effect of size-dependent herbivory on population growth rate at Whitetop compared to using the average proportion of plants eaten and found population growth rate (λ) changed by only 0.01. Therefore, we did not incorporate size-dependent herbivory into the model.

Although we measured the size of seedlings resulting from seeds of damaged and undamaged plants, size did not differ significantly between damaged and undamaged plants (see Results). Therefore, we used seedling size estimates from the field study in Aikens and Roach (2014), using the same seedling size for damaged $[\gamma_{SR,E}(x_2)]$ and undamaged $[\gamma_{SR,U}(x_2)]$ plants. We assumed that seedling size was independent of the size of the maternal plant. We used the smallest 10% of nonreproductive individuals from each site to estimate a mean and variance for seedling size using a linear mixed effects model and then modeled seedling size for each site using a normal distribution.

All nonreproductive functions were fit using the natural logarithm of length of the largest leaf to meet the assumption of homogeneity of variance. All reproductive functions were fit using the square root of basal stem diameter to meet normality and homogeneity of variance assumptions.

We estimated the numerical solution to the IPM following the midpoint rule (Easterling et al., 2000; Ellner and Rees, 2006). We used 50 mesh points for nonreproductive size and 50 mesh points for reproductive size; increasing and decreasing the number of mesh points did not alter the population growth rate. Integrals were taken over a range corresponding to 1.1 times the maximum plant size across all four populations and 0.9 times the minimum plant size across the populations.

Two types of population growth models were run per site: a "no-tolerance" scenario and a "tolerance" scenario in which ambient levels of tolerance were included. In the no-tolerance scenario, we allowed seed production to be affected by herbivory, but not seed quality. We accomplished this by modeling the average proportion of plants damaged by herbivores at a site with the damaged fecundity function and the rest of the plants at the site with the undamaged fecundity function. However, we used seed viability and seed germination estimates from undamaged plants to ensure tolerance was not included in the model. In the tolerance scenario, we modeled seed production as affected by herbivory, as in the no-tolerance scenario, but we also included seed viability and seed germination estimates for damaged and undamaged plants. In both scenarios, we assumed that seeds are not microsite-limited in this species (Turnbull et al., 2000). It is unclear whether recruitment in *P. roanensis* is seed-limited or microsite-limited because we did not estimate the number of natural recruits in the field.

Greenhouse estimates of germination are likely overestimates of field germination, and these overestimates may influence population growth rates calculated from the integral projection models. For example, the sensitivity of population growth rate to germination may vary over the range of germination rates. If population growth rate is more sensitive to lower germination rates, then using greenhouse germination rates in our population models may underestimate the effect of tolerance on population growth rate. To explore this possibility, for sites with significant germination differences between damaged and undamaged plants, we varied the germination rates over a range of values that more closely mimicked field conditions, but kept the difference in the proportion of seeds that germinated between damaged and undamaged plants constant. In a previous study, we found that the proportion of seedlings that emerged in the field ranged from approximately 0.01 to 0.20 (Aikens and Roach, 2014). These values were calculated by recording germination of seeds in plots, which included both viable and unviable seeds. Therefore, the proportion of seedlings that emerge represents the proportion of viable seeds × the proportion of viable seeds that germinate. We used the proportion of viable seeds from undamaged plants from our data in Experiment 1 and calculated a range of germination values for seeds from undamaged plants based on obtaining the following emergence values that cover the range observed in the field: 0.01, 0.05, 0.10, 0.15, and 0.20. For each seedling emergence value, we calculated population growth rate in a no-tolerance scenario and a tolerance scenario. For the no-tolerance scenario, the proportion of seeds that germinated from damaged plants was the same as the proportion of seeds that germinated from undamaged plants. For the tolerance scenario, we calculated the proportion of seeds that germinated from damaged plants for each of the emergence values by using the percentage difference in germination observed between damaged and undamaged plants at the site. This simulation allowed us to compare "no-tolerance" and "tolerance" population growth rates among a variety of more realistic germination rates. Seed viability and germination values used in this simulation are presented in online Appendix S5.

We also explored the extent to which the proportion of viable seeds and the proportion of seeds that germinate would need to increase in damaged plants to increase population growth rate in

the tolerance scenario above that of the no-tolerance scenario. In other words, what proportion of viable seeds or proportion of seeds that germinate is necessary for tolerance to significantly increase population growth rate? We explored this question only at the sites in which these seed quality characteristics significantly differed between damaged and undamaged plants. To keep germination values more realistic (i.e., lower than the greenhouse germination values obtained in Experiment 1), we used the proportion of viable seeds from undamaged plants in Experiment 1 to calculate seed germination for undamaged plants for emergence values of 0.01, 0.10, and 0.20. To determine how increases in seed viability in damaged plants would affect population growth rate, we varied seed viability for damaged plants between 0.50 and 1 and included one case where seed viability for damaged plants was equal to seed viability for undamaged plants (i.e., no tolerance). To determine how increases in germination of seeds from damaged plants would affect population growth rate, we varied seed germination for damaged plants between 0.10 and 1 and included one case where seed germination for damaged plants was equal to seed germination for undamaged plants (i.e., no tolerance). The seed viability and germination values used in these simulations are presented in Appendix S5. This analysis allowed us to determine whether any increase in viable seeds or germination of seeds of damaged plants would be enough to increase population growth rate above that of the no-tolerance scenario, and it allowed us to examine this from three realistic undamaged plant emergence rates.

We calculated 95% confidence intervals for all population growth rate (λ) estimates by bootstrapping the data 2000 times. We randomly sampled observations with replacement within each population and year, keeping the total number of observations for each population–year combination the same as the original data set. We then refit the size-dependent vital rate models to obtain new parameter estimates and used these new estimates to calculate population growth rate. All model parameterization and population growth rate modeling was conducted in R version 3.1.0 (R Core Team, 2014).

RESULTS

***Experiment 1: Seed quality*—**Seed viability was significantly affected by herbivory, but the effects depended on the population as indicated by the significant herbivory × population effect (Table 2). Contrasts between damaged and undamaged plants within a site demonstrated that seed viability was significantly positively affected by herbivory at Big Bald, but was significantly negatively affected by herbivory at Mt. Rogers, where it decreased the average proportion of viable seeds per plant by 15% compared to undamaged plants (Table 3). At Roan and Whitetop, there were no differences in seed viability between damaged and undamaged plants.

Neither herbivory nor the herbivory × population interaction affected seed mass or seedling size, but there was a significant herbivory × population effect on germination (Table 2). Whitetop and Roan had significantly greater germination of seeds from damaged plants, and Mt. Rogers had lower germination of seeds from damaged plants that approached significance (Table 3).

***Experiment 2: Population growth rate models*—**Site-specific parameter estimates for all demographic functions are provided in Appendix S4. Because seed viability and seed germination varied by

TABLE 2. The effects of herbivory, population, and herbivory × population interaction on seed quality characteristics of *Prenanthes roanensis*.

Variable	$F_{num\ df, den\ df}$	P
A) Seed viability		
Herbivory	$0.81_{1,298}$	0.37
Population	$14.08_{3,298}$	<0.001
Herbivory × population	$5.71_{3,298}$	<0.001
B) Seed mass		
Herbivory	$0.08_{1,283}$	0.77
Population	$5.92_{3,283}$	<0.001
Herbivory × population	$2.12_{3,283}$	0.10
C) Germination		
Herbivory	$2.01_{1,282}$	0.16
Population	$12.02_{3,282}$	<0.001
Herbivory × population	$3.05_{3,282}$	0.03
D) Seedling size		
Herbivory	$0.72_{1,258}$	0.40
Population	$7.96_{3,254}$	<0.001
Herbivory × population	$2.09_{3,251}$	0.10

site, the effects of tolerance on population growth rate also differed by site.

In a comparison of the populations between the no-tolerance and tolerance scenarios, three of the four populations showed a small increase in population growth rate (λ) when tolerance was included in the model, but this difference was not significant based on the overlapping 95% confidence intervals (Fig. 2). Plants at Mt. Rogers did not demonstrate tolerance to herbivory through seed quality. Rather, the reduced probability of seed viability and germination from damaged plants compared with undamaged plants caused a reduction in population growth rate when seed quality characteristics from damaged plants were included in the "tolerance" model.

Germination of seeds from damaged plants was 23% greater than for seeds from undamaged plants at Roan and 43% greater than for seeds from undamaged plants at Whitetop. When we examined more realistic germination rates, preserving these percentage differences between germination of seeds from damaged and undamaged plants, we found no significant differences between the no-tolerance and tolerance models at either site (Fig. 3). Therefore, the observed difference in seed germination of seeds from damaged and undamaged plants was not enough to increase population growth rate above the no tolerance scenario, even at germination rates which more closely mimic field conditions.

TABLE 3. Mean seed viability (proportion of filled seeds) and germination of filled seeds (±SE) for herbivore-damaged and -undamaged plants of *Prenanthes roanensis* in each of the four populations. Significance levels denote contrast results for differences between damaged and undamaged plants for each population.

Population	Damaged mean	Undamaged mean	$F_{num\ df, den\ df}$
A) Seed viability			
Big Bald	0.64 (0.05)	0.42 (0.05)	$7.94_{1,298}$***
Roan	0.46 (0.04)	0.46 (0.04)	$0.04_{1,298}$
Rogers	0.22 (0.03)	0.36 (0.04)	$8.36_{1,298}$***
Whitetop	0.55 (0.05)	0.47 (0.05)	$0.81_{1,298}$
B) Germination			
Big Bald	0.84 (0.04)	0.79 (0.05)	$0.75_{1,282}$
Roan	0.80 (0.03)	0.65 (0.05)	$4.48_{1,282}$**
Rogers	0.76 (0.05)	0.86 (0.05)	$3.08_{1,282}$*
Whitetop	0.63 (0.05)	0.44 (0.06)	$4.57_{1,282}$**

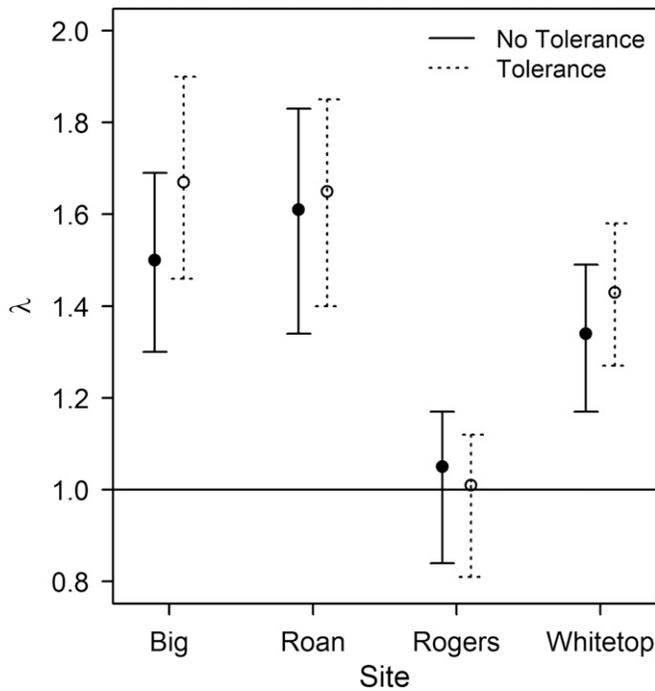*Note:* *$P < 0.10$; **$P < 0.05$; ***$P < 0.01$.

FIGURE 2 Population growth rates for the "no-tolerance" and "tolerance" scenarios. The solid line at $\lambda = 1$ represents a stable population. Error bars represent 95% confidence intervals from bootstrapping.

FIGURE 3 Population growth rates for the "no-tolerance" and "tolerance" scenarios at (A) Roan and (B) Whitetop for a variety of seedling emergence rates that mimic those observed in the field. The *x*-axis represents the proportion of seedlings that emerge from seeds of undamaged plants. Lowering values of seedling emergence to field estimates was done by reducing the germination rate. However, the difference in the germination rates of seeds from undamaged and damaged plants was held constant across all values of undamaged seedling emergence (23% for Roan; 43% for Whitetop). The solid line at $\lambda = 1$ represents a stable population. Error bars represent 95% confidence intervals from bootstrapping.

Based on the results of the seed quality analyses in Experiment 1, we examined how varying the difference in seed viability between damaged and undamaged plants at Big Bald and varying the difference in seed germination between damaged and undamaged plants at Roan and Whitetop would affect population growth rate (Fig. 4). In all analyses, we examined how varying differences in seed quality would affect population growth rate when the proportion of seedlings that emerged was 0.01, 0.10, and 0.20. At Big Bald, 42% of seeds from undamaged plants were viable. Increasing the percentage of viable seeds in damaged plants to 50–100% did not significantly increase population growth rate above that found under the no-tolerance scenario for any of the emergence rates (Fig. 4A–C). At Roan and Whitetop, when the proportion of undamaged seeds that germinated was high (e.g., 0.43; emergence = 0.20), it was not possible to increase germination enough such that tolerance could cause population growth rate to be significantly greater than a no-tolerance scenario. However, when the proportion of seeds that germinated from undamaged plants was low (e.g., 0.02; seedling emergence = 0.01), increasing germination of damaged seeds by 900% to 0.20 at Roan (Fig. 4D) and by 400% to 0.10 at Whitetop (Fig. 4G) caused population growth rate to be significantly greater than in the no-tolerance model. Additionally, at Whitetop, when the proportion of seeds that germinated from undamaged plants was moderate (e.g., 0.21; seedling emergence = 0.10), increasing the germination rate by 280% to 0.80 resulted in a population growth rate significantly greater than the no-tolerance model (Fig. 4H).

In summary, tolerance to herbivory was realized through increased seed viability in damaged plants at Big Bald and through increased germination of seeds from damaged plants at Roan and Whitetop. However, incorporating tolerance into population growth models did not increase population growth rate above that of a no-tolerance scenario using either greenhouse germination
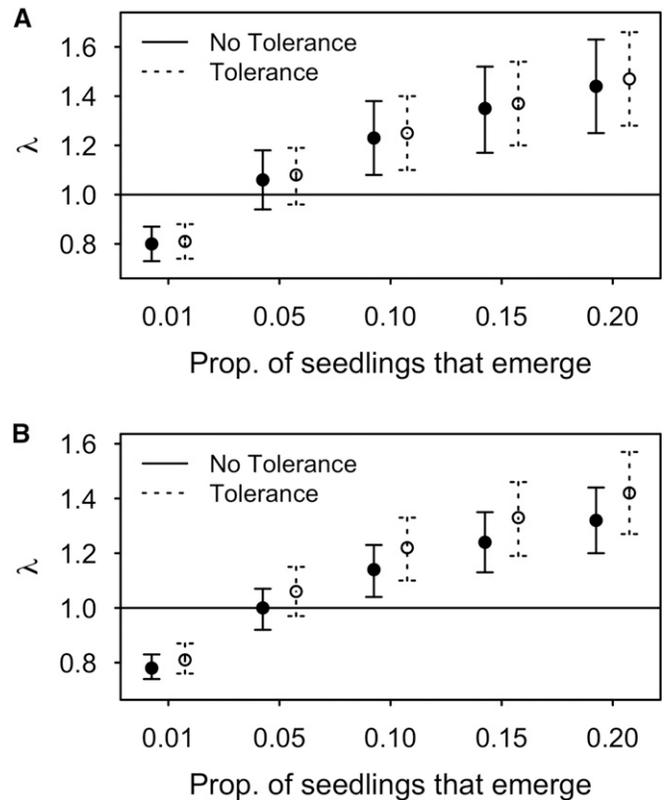
rates or a series of lower germination rates that more closely mirror those of the field. Only by increasing the difference in germination of seeds from damaged and undamaged plants at low undamaged seed germination rates were we able to see an effect of tolerance on population growth rate.

DISCUSSION

Herbivores can have a negative effect on individual fitness, which can translate into reduced population growth rates. Our results demonstrate that the negative effects of herbivory on individual plants can be ameliorated through increased seed quality in some plant populations, but this tolerance had a limited impact on population growth rate. We did not find that the observed tolerance was enough to significantly increase population growth rate above that of a no-tolerance scenario, but we did find that increasing germination rates of seeds from damaged plants has the potential to significantly increase population growth rate. This increase in germination could help to offset the effects of a reduction in seed production due
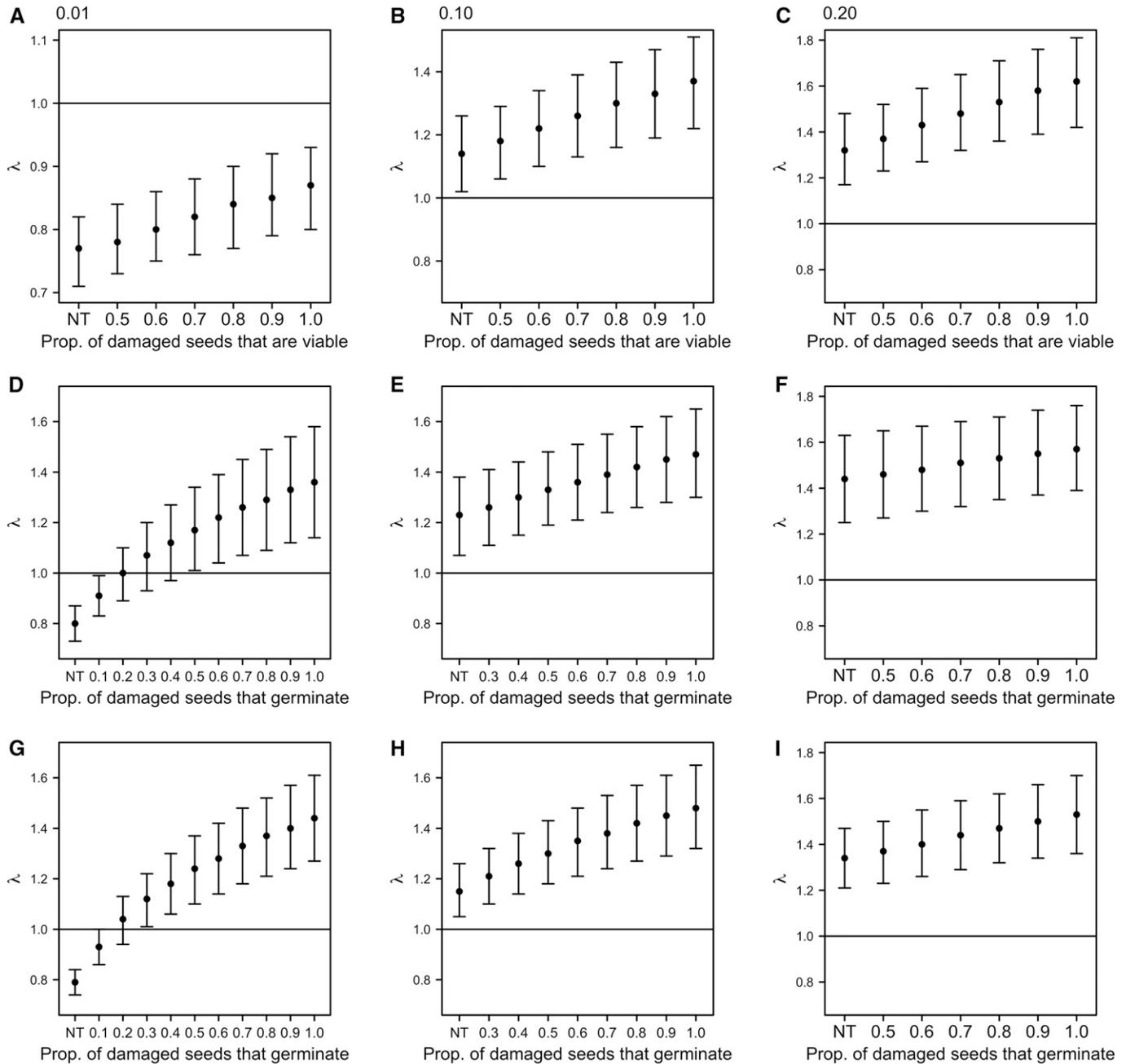
FIGURE 4 Population growth rates for a range of seed viability values of damaged plants at Big Bald (panels A–C), germination values of seeds from damaged plants at Roan (panels D–F), and germination values of seeds from damaged plants at Whitetop (panels G–I). For each site, simulations were done with undamaged seedling emergence values of 0.01 (panels A, D, and G), 0.10 (panels B, E, and H), and 0.20 (panels C, F, and I). Lowering values of seedling emergence to field estimates was done by reducing the germination rate of seeds from undamaged plants. NT = no tolerance: damaged viability or germination is equal to undamaged viability or germination. The solid line at $\lambda = 1$ represents a stable population. Error bars represent 95% confidence intervals from bootstrapping.

to herbivory on population growth rate. To our knowledge, this study is the first to explore the effects of tolerance to herbivory through seed quality on population growth rate (but see Buckley et al. [2005] for a general model incorporating fecundity compensation on plant population dynamics).

In *Prenanthes roanensis*, tolerance occurred through increased seed viability and increased germination. Utilization of stored reserves from underground storage organs has been implicated in some plants' abilities to tolerate herbivory (Tiffin, 2000), and thus, the tuber of *P. roanensis* may enable reallocation of its resources to seeds. Provisioning through seeds has been found to be a common mechanism by which plants tolerate herbivory (Agrawal, 2001; Pilson and Decker, 2002; Marshall et al., 2005). Plants damaged by herbivores have been found to have greater seed mass (Agrawal,

2001; Pilson and Decker, 2002), and larger seeds are correlated with increased germination rates and seedling sizes (Gómez, 2004; Mueller et al., 2005). However, we did not find seed mass to be significantly different between seeds from damaged and undamaged plants. Another mechanism by which plants use seeds to compensate for flower loss is by increasing the number of seeds per flower (Ehrlén, 1992; Lehtilä and Syrjänen, 1995; Pilson and Decker, 2002; Fang et al., 2006). It seems unlikely that this type of compensation occurs in *P. roanensis* given that the number of seeds per reproductive head shows minimal variation within a population and year (Appendix S3). However, one avenue of further research would be to compare the number of viable seeds per reproductive head between damaged and undamaged plants, as viable seed set per reproductive head may be affected by herbivory (e.g., Marshall et al., 2005).

The variation in seed viability and germination observed in damaged plants among the four populations demonstrates spatial variation in the ability of plants to compensate. There are many factors that influence the ability of a plant to tolerate herbivory through compensation, including the timing and severity of damage (Maschinski and Whitham, 1989; Lowenberg, 1994; Gruntman and Novoplansky, 2011) and resource availability (e.g., Hawkes and Sullivan, 2001; Wise and Abrahamson, 2007). These factors may explain the inability of plants to compensate at Mt. Rogers. In particular, high intensity grazing, such as grazing from wild ponies and cattle at this site, may cause severe damage and reduce the ability of the plant to tolerate herbivory (Lowenberg, 1994). Additionally, Mt. Rogers contains a different suite of plant species than the other three sites (Aikens and Roach, 2014), suggesting fundamental abiotic differences between this site and the others. Therefore, we cannot rule out the possibility that resource availability may affect tolerance to herbivory at this site. Alternatively, the significantly lower seed viability of damaged plants compared with undamaged plants at Mt. Rogers may be due to an alteration or a reduction in the size of the floral display (Juenger and Bergelson, 1997; McCall and Irwin, 2006), thus reducing pollinator visitation in this species, which depends on pollinators for seed set. Regardless, the impact of herbivory and the lack of tolerance in this population are likely reasons why the natural population growth rate of Mt. Rogers was found to be below 1 (Aikens and Roach, 2014).

Using natural damage to estimate tolerance has been criticized because it can produce biased estimates of tolerance due to confounding factors (Tiffin and Inouye, 2000; Lehtilä, 2003). Compensation or overcompensation in damaged plants could be a result of systematic differences between the abiotic or biotic environment of damaged and undamaged plants. For example, greater seed quality observed in damaged plants may occur if they inhabit higher quality habitat. While we cannot rule out this possibility, damaged and undamaged individuals from whom we collected seed were interspersed in our populations, mitigating the possibility of large-scale environmental differences. Experiments in which artificial damage is imposed on individuals may provide more support for our results. However, plants may not respond the same way to artificial damage (Karban and Baldwin, 1997), and it may be difficult to use artificial damage to accurately mimic the natural timing and intensity of herbivory, both of which affect tolerance (Maschinski and Whitham, 1989; Lowenberg, 1994; Gruntman and Novoplansky, 2011). Since there are drawbacks to both natural and artificial damage, combining both approaches in an experiment would allow one to take advantage of the strengths of each approach (Lehtilä, 2003).

Due to this limitation in our study, we explored the potential for tolerance to influence population growth rate through simulations that varied differences in seed viability and germination between damaged and undamaged plants.

The effect of tolerance on population growth rate depends both on the sensitivity of population growth rate to the life-history trait through which tolerance is realized and the magnitude of tolerance. In monocarpic plants, population growth rate is sensitive to fecundity parameters (Silvertown et al., 1993), such as seed germination (Tenhumberg et al., 2008; Aikens and Roach, 2014). Our results demonstrated that population growth rate was particularly sensitive to changes in seed germination only when germination rates were low (Fig. 4D, G). When the proportion of seeds from undamaged plants that germinated was low (i.e., emergence = 0.01), we found a nonlinear relationship between seed germination from damaged plants and population growth rate; increasing the germination rate of seeds from damaged plants from 10 to 20% resulted in a larger increase in population growth rate than increasing this germination rate from 90 to 100%. It was only at these low germination rates that we saw tolerance significantly increase population growth rate. Furthermore, the germination rate of seeds from damaged plants must increase by a magnitude greater than that observed in our study. A higher germination rate may be possible if stressful field conditions impact poorer quality seeds (i.e., from undamaged plants) more than they impact higher quality seeds (i.e., from damaged plants). Whether the right conditions for tolerance to impact population growth, namely, low germination rates of seeds from undamaged plants and a substantial increase in the germination rates of seeds from damaged plants, is possible under natural conditions warrants further testing.

In modeling population dynamics, we made several assumptions. First, we assumed that germination was seed-limited rather than microsite-limited. If *P. roanensis* was microsite-limited, tolerance in the form of increased seed viability or germination would have less of an effect on population growth rate because the number of germinants would be limited by the number of microsites available, not the germination rate of the seeds. Thus, the "no-tolerance" and "tolerance" population growth rates would be more comparable. Second, we did not include density-dependence in our model, which similarly may affect population dynamics. Density does vary among the four populations, ranging from 26.37 per m^2 at Mt. Rogers to 92.69 per m^2 at Roan (Aikens and Roach, 2014). Increasing or decreasing plant density can change survival, growth, and reproduction parameters. High plant density has been shown to negatively impact survival and growth (e.g., Silva Matos et al., 1999), whereas low-density populations can reduce the reproductive output of plants (e.g., Bosch and Waser, 1999). Moreover, plant density can interact with herbivory to affect plant population dynamics (Buckley et al., 2005). For example, herbivores can influence whether demographic transitions are density-dependent (Underwood and Halpern, 2012). Future studies should be designed to elucidate how density-dependence interacts with both herbivory and tolerance to affect plant population dynamics.

White-tailed deer (*Odocoileus virginianus*), which are largely responsible for the herbivory experienced by *P. roanensis*, have become overabundant in the eastern United States, which has consequences for plant population persistence (Russell et al., 2001; Côté et al., 2004). Our study is one of the first to model the impact of tolerance, through enhanced seed quality, on population growth rate. Although we did not find that observed differences in seed

viability or germination between undamaged and damaged plants significantly affected population growth rate, our simulations demonstrate that tolerance has the potential to increase population growth rate under particular conditions. Explicitly incorporating tolerance into plant population models can help elucidate the degree to which individual-level tolerance translates into population-level effects. Furthermore, examining herbivory and tolerance in multiple populations can provide insight into the factors that affect the persistence of plant populations, despite herbivory, and the distribution of a plant species.

ACKNOWLEDGEMENTS

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