Population demographics and trade-offs to reproduction of an invasive and noninvasive species of *Rubus*

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Abstract

Do trade-offs between growth and reproduction differ between an invasive and noninvasive plant species and how do such trade-offs relate to population demographics? To help address these questions, we compared demographics for an invasive plant species, *Rubus discolor*, with a noninvasive congener, *R. ursinus*, in several populations of varying density. Removal of floral buds from reproductive canes increased the size of juvenile canes that arose from clonal sprouting in *R. ursinus*, suggesting a trade-off between current reproduction and growth. Removal of floral buds had no effect on growth of *R. discolor*. *R. ursinus* displayed trade-offs between reproduction (sexual and vegetative) and future growth based on negative correlations between leaf area production and both clonal sprouting and seedling production during the previous year. *R. discolor* did not exhibit these trade-offs. Both species had high population growth rates in low-density populations, but exhibited little or no growth in high-density populations. A life table response experiment was used to determine the underlying cause for the effect of density on population growth. For *R. ursinus*, lack of population growth in high-density populations was due primarily to increased mortality of clonally sprouting canes, while for *R. discolor*, it was due to decreased clonal cane production. Elasticity analysis revealed that clonal growth was more important than sexual reproduction for population growth of both species. However, elasticity values for sexual reproduction in *R. discolor* were greater in high- than low-density populations. This suggests an increased reliance on sexual reproduction in populations that had reached stable sizes, which could increase the capacity of *R. discolor* to disperse to new sites. Elasticity analyses were also used to simulate the efficacy of various control strategies for *R. discolor*. Control of this species could be attained by reducing clonal production within existing populations while reducing seed production to limit establishment of new populations.

Introduction

Invasiveness in plant species has been correlated with the ability to reproduce abundantly and grow rapidly. Reproductive traits, such as the capacity for both sexual and vegetative reproduc-

tion, an ability to self-fertilize, a lack of seed dormancy, and multi-seeded fruit, have been related to invasiveness because they confer the capacity to rapidly colonize a site, which is the first stage of the invasion process (Baker 1965; Bazzaz 1986; Reichard and Hamilton 1997; Daehler

1998; Sakai et al. 2001). Fast growth rates reflect rapid acquisition and allocation of resources, which enable a species to swiftly establish a population following colonization. While life-history theory predicts a trade-off between high reproduction and growth rates (Stearns 1992), research examining growth, competitive ability, and reproduction in purple loosestrife (*Lythrum salicaria*), a noxious wetland invader, suggests that not all invasive plant species are subject to such trade-offs (Keddy et al. 1994). There is relatively little direct experimental evidence or observational data examining the life-history trade-offs of reproduction in invasive plant species.

The trade-offs between reproduction and growth are due to competition for limited resources within an individual (Stearns 1992). The mechanisms underlying these trade-offs are physiological, where reproductive effort may be expressed as the amount of resources (e.g., carbon) allocated to reproduction at the expense of other functions (Geber 1990; Fox and Stevens 1991; Stearns 1992). The consequences of allocation to reproduction, along with the constraints imposed by resource availability, are expressed at the demographic level and are called the long-term or demographic costs of reproduction (Fox and Stevens 1991; Nicotra 1999). It is at this level that the costs of reproduction may be observed as a decrease of growth or increase of mortality associated with increased reproduction. The balance among these demographic trade-offs of reproduction ultimately determines the population growth rate for a species.

Theory predicts that high allocation of resources to reproduction confers a competitive advantage during site colonization, but that allocation of resources should shift to vegetative growth after colonization to facilitate population establishment (Sakai et al. 2001). Thus, density-dependent shifts in resource allocation between sexual reproduction and vegetative growth may be expected. However, relatively little is known about density effects on population growth rates of invasive plant species or how these effects compare with those found in native species (Parker 2000). Even less is known about the specific life-history factors that contribute to population growth at different densities as an invasion progresses.

Demographic matrix analysis can be used to assess population growth and the factors that contribute to it and may have valuable management applications. For example, they can be used to identify the most important life-history stage or process to the population growth of a species, information which can be used to guide decisions with the objective of sustaining or increasing the population size of rare species (e.g., Charron and Gagnon 1991; Maschinski et al. 1997; Kaye et al. 2001) or to target and decrease the population size of invasive species (e.g., Maxwell et al. 1988; Shea and Kelly 1998; McEvoy and Coombs 1999; Parker 2000). A further application of demographic analyses to invasive plant study is they can provide valuable, but often ignored, insights into the connection between theories of plant invasions and quantitative field data, such as determining whether population growth remains constant throughout the stages of invasion (Parker 2000).

The native, noninvasive *R. ursinus* Cham. and Schlecht. (trailing blackberry) and the invasive *R. discolor* Weihe and Nees (also *R. procerus*; Himalayan blackberry) are members of the same sub-genus (*Rubus*), share many life-history characteristics, and often grow together in the same sites in the Pacific Northwest United States (PNW). A recent study compared the reproductive effort between these species (McDowell and Turner 2002). Reproduction in the non-invasive species was associated with decreased leaf water status, causing early stomatal closure, and with decreased leaf nitrogen concentration, contributing to lower photosynthetic capacity. However, these physiological costs of reproduction were not observed in the invasive *Rubus*. The objective of the current study is to examine the implications of these physiological costs at the plant and population scales. We used stage-based demographic models and field experiments and observations to address the following questions: (1) What are the demographic trade-offs between reproduction and growth and how do they differ between an invasive species and a noninvasive congener? (2) How do these trade-offs affect the population demographics of these two species? and 3) How do population demographics influence invasiveness and potential control strategies of *R. discolor*, the invasive species?

Materials and methods

Study species

Rubus ursinus is native to the PNW. Its canes typically grow to about 3 m in length and produce approximately 25 fruit per cane in a year (McDowell and Turner 2002). *R. ursinus* is considered noninvasive in its native range, where this study took place. *R. discolor* was first introduced to the PNW from Europe via India for fruit production (Kent 1988) and is considered an invasive plant species outside of its native range because it can grow, reproduce, and proliferate following introduction. Canes of *R. discolor* can grow to 10 m in length and produce over 700 fruit in a year (McDowell and Turner 2002).

Rubus ursinus and *R. discolor* share several morphological and ecological characteristics. They grow together in open to moderately shady sites at low- (sea-level) to mid- (~2000 m) elevations in the PNW. Both species are described as biennial/perennial, indicating that roots are perennial while above-ground canes live for two years. However, canes arising from seeds actually develop for three years. Seeds germinate in the winter or early spring and plants remain in a seedling stage for approximately one year. In the following year, canes remain vegetative while nearly all elongation occurs. In the spring of the third season, the canes shed their leaves and develop lateral reproductive shoots. The entire cane senesces following reproduction. Both species have perennial rhizomes (below-ground stems) that can produce and simultaneously support several clonally sprouted canes that emerge and grow as vegetative canes for one year and reproduce in the following year. Therefore, in contrast to the canes that arise from seeds, the canes that arise clonally develop for only two years, but in both cases, the roots may be perennial. An additional form of clonal spread that may occur in both species, as in several other *Rubus* species, arises when the tip of a cane roots in the soil, forming a new perennial root crown (Heslop-Harrison 1959). As with other species of *Rubus*, clonal spread from above-ground and below-ground structures may be very important to the population growth of both of these species (Heslop-Harrison 1959; Baret et al. 2003)

Study site

All research was conducted within the McDonald-Dunn Research Forest near Corvallis, OR (44°40' N, 123°20' W, ~350 m elevation) which receives approximately 300 cm of rain annually, as measured at a nearby (~5 km) meteorological station (Oregon Climate Service). In 1999, plots were established around existing populations of each species in a recent clearcut for demographic monitoring. Populations were selected to represent either early population colonization (presumed based on low density of the target species) or established populations (high density of the target species). Therefore, low-density populations for both species were selected to have approximately 6–12 canes each while high-density populations had approximately 45–55 canes each. To control for the same number of individuals per population between the species, plot sizes for *R. discolor* were larger than for *R. ursinus* because *R. discolor* canes are approximately twice as large. Eight high- and low-density 5 × 5 m plots were established for *R. discolor* and six high- and low-density 2 × 2 m plots were established for *R. ursinus*. Fewer populations were selected for *R. ursinus* because there were fewer populations available of the appropriate densities. In 2001, six additional plots were established around populations of varying densities of each species to be used for an experiment manipulating sexual reproduction. All populations were located within 0.5 km of each other in a large clearcut, with similar levels of irradiance and potential access to equivalent resources.

Field and laboratory methods

We conducted one census of each population in fall 1999. Two censuses of each population were conducted per year in 2000 and 2001. At those times, one census was done in the spring, before growth of surrounding vegetation obscured the seedlings, and another was done in the fall, after most mortality of seedlings and canes occurred. In our initial census (1999), all canes were numbered and tagged, and their position within each plot was mapped. In subsequent censuses, we tagged and mapped new canes and recorded the mortality of previously identified canes.

During a census, canes were classified into one of four stages based on *Rubus* life-history. These stages were seedling, cane_s, cane_v, or reproductive canes (Figure 1). In this study, cane_s were defined as vegetative canes that had developed from seedlings, while cane_v were vegetative canes that arose from either rhizome sprouting or tip-rooting of reproductive canes. Reproductive canes developed from both cane_s and cane_v and had the potential to produce both fruit and vegetative sprouts (cane_v). In the first census, cane_s and cane_v were distinguished by their position relative to living or senesced reproductive canes. Our ability to make this distinction was validated by examining root connections in neighboring populations not used in the study. In all subsequent censuses, cane_s and cane_v were easily distinguished because all seedlings were identified and labeled in a previous census. Over the course of this study, we followed the fate of approximately 600 canes of each species. The nonparametric Kruskal–Wallis (KW) procedure was used to test for differences between the demographic parameters, such as production and survival rates of each life-history stage, for both species at each density.

In spring 2001, floral buds were removed from six entire populations of each species to determine the effects of current reproduction on current growth. Prior to bud removal, average cane length was measured to assess the degree of similarity between these six treatment and six control populations. The control populations were randomly selected from those used in the demographic analyses (three each from low- and high-density). Due to the length and the arching, sprawling growth

form of *Rubus* canes, total cane length could be accurately measured only by harvesting canes. Therefore, we removed three senesced reproductive canes from each of the plots, which would not likely affect the growth or survival of plants remaining in the population. Average cane length per population was not significantly different between control and treatment populations (Wilcoxon Signed Ranks $Z = 0.280$, $P = 0.778$ for low-density and $Z = 0.294$, $P = 0.768$ for high-density *R. ursinus*; and Wilcoxon Signed Ranks $Z = 0.643$, $P = 0.530$ for low-density and $Z = 0.472$, $P = 0.647$ for high-density *R. discolor*) and, therefore, the populations were considered similar prior to the floral manipulation. To test for the effect of floral bud removal on growth of cane_v, three randomly selected cane_v were removed from each of the control and manipulated populations in the fall. Total cane length of each cane_v was measured in the field. Then, all leaves from each cane_v were harvested, brought to the lab, and kept in cold storage. Within ~48 h of harvesting, leaf area of all foliage was determined using a video image recorder and AgVision software (Decagon Devices, Pullman, Washington). Three leaves per cane_v were randomly selected, placed in a 65 °C oven for 48 h, and then weighed to the nearest 0.01 g. Specific leaf area (SLA; leaf area per unit leaf mass) was calculated from these data. The non-parametric wilcoxon signed ranks (WSR) test was used to examine the difference between growth parameters of fruit-removal and control populations because these data did not meet the assumptions for a parametric analysis. Demographic and cane size parameters of control populations were used in a Pearson correla-

Figure 1. A conceptual transition matrix for *R. ursinus* and *R. discolor* showing possible transitions from one year (t) to the next ($t + 1$). The dark shaded rectangles indicate the transitions (a_{ij}) associated with continuance in the same stage from one period to the next, stippled rectangles indicate a_{ij} associated with cane production and development arising from vegetative sprouting (cane_v), and hatched rectangles indicate a_{ij} associated with sexual reproduction and growth of canes originating from seeds (cane_s). Transitions without shading were not observed.

tion matrix to examine life-history trade-offs between years.

Demographic analyses

The observations made during our field censuses were used to construct stage-based transition matrices with a time interval of one year using the four life-history stages previously described for the *Rubus* species. Separate transition matrices were constructed for each of the populations over each of the transition intervals to follow the form of projection matrix models

$$\mathbf{n}(t+1) = \mathbf{A} \cdot \mathbf{n}(t)$$

where $\mathbf{n}(t)$ is a vector of the number of individuals in each of the four stages at time t , $\mathbf{n}(t+1)$ is a vector of the number of individuals in each stage at time $t+1$, and $\mathbf{A}$ is a matrix of the transition probabilities (a_{ij}). The a_{ij} for all transitions except seedling recruitment and cane_v production were calculated as the proportion of individuals in stage i at time t that contributed to stage j at time $t+1$ (Figure 1). Occasionally, an individual remained in stage i over a transition interval (Figure 1), although this was rare. Several possible transition probabilities did not occur (e.g., seedlings in one year could not become reproductive canes in the following year) and were, therefore, entered as 0's in the matrix.

Seedling recruitment and cane_v production probabilities were calculated as the number of seedlings and cane_v, respectively, produced in one year relative to the number of reproductive canes existing in the previous year. Our calculation for seedling recruitment was based on the assumption that all seedlings germinated from seeds produced during the previous year and not from the seed bank. This assumption was probably reasonable based on the rapid disappearance of *Rubus* seeds from the soil due to predation (Maxwell 1990; Kollmann et al. 1998) and the low germination probability of seeds following storage (Amor 1974) or desiccation in the field (S. Lambrecht-McDowell, personal observation).

From each matrix, we calculated the finite rate of population growth, λ , which is the dominant eigenvalue of $\mathbf{A}$. We calculated an average transition matrix for each species in both low- and

high-density populations over each transition interval. A value of $\lambda > 1$ indicates a positive population growth rate, $\lambda < 1$ indicates the population is decreasing in size, and $\lambda = 1$ indicates a stable population size. We used an analytical approximation according to Caswell (2000, 2001) for the variance (V) of λ where

$$V(\lambda) \approx \sum_{ij} \sum_{kl} \text{Cov}(a_{ij}a_{kl}) \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial \lambda}{\partial a_{kl}}$$

for each of these eight average matrices where Cov denotes the covariance between pairs of transition probabilities (a_{ij} and a_{kl}) and $\partial \lambda / \partial a_{ij}$ is a sensitivity term and denotes the effect of a change in a_{ij} on λ . We used t -tests to determine the significance of the difference between λ in low- and high-density populations over a transition interval for each species and between the species and densities for each transition interval.

Given a difference in λ between low- and high-density populations for both species, we used a life table response experiment (LTRE) to determine the contribution (c_{ij}) of each transition to the effect of population density on λ (Levin et al. 1996; Caswell 2000, 2001). The size of each c_{ij} relative to other c_{ij} indicates the relative effect of that transition on the reduction in population growth between low- and high-density populations. In this manner, the LTRE can be used to determine which transitions underlie the population-level effect of density. To calculate the c_{ij} for each species, we first calculated an average transition matrix for all populations at a given density. For *R. ursinus*, we averaged transitions from both transition intervals. However, for *R. discolor*, we only used the transitions from the 2000–2001 interval because we observed no effect of density on λ over the 1999–2000 interval for this species. We then calculated a matrix midway between the high- and low-density population matrices for each species where values in the midway matrix were averages of the corresponding values from the mean low-density and mean high-density matrices. Finally, we estimated the effect of density on λ by calculating the c_{ij} of each vital rate using the difference between the average matrix elements of high- and low-density populations and using the equation

$$c_{ij} = (a_{ij}^{high} - a_{ij}^{low}) \left(\frac{\partial \lambda}{\partial a_{ij}} \right)$$

where $(a_{ij}^{high} - a_{ij}^{low})$ is the difference (d_{ij}) between the transition values in the low- and high-density matrices and the $\partial \lambda / \partial a_{ij}$ are the sensitivity terms calculated from the matrix midway between the high- and low-density matrices.

Elasticity analysis

The elasticity of each matrix element (e_{ij}) is a measure of the proportional sensitivity of λ to proportional changes in the a_{ij} (de Kroon et al. 1986; de Kroon et al. 2000; Caswell 2001). Using the same average matrices generated for the LTRE, we calculated the e_{ij} for each a_{ij} as

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$

for each of the four average matrices. The e_{ij} values for a single matrix sum to 100% and, therefore, it is possible to sum the e_{ij} for transitions associated with the same life-history process (e.g., sexual reproduction or clonal growth) to compare the relative importance of each life-history process to λ (Silvertown et al. 1993; van Groenendael et al. 1994; de Kroon et al. 2000). Using the transition matrix in Figure 1, we identified the characteristic life-history processes for the two *Rubus* species, denoting each with a different type of shading. The e_{ij} of all transitions sharing the same type of shading, and therefore, within the same life-history process, were added.

We used numerical manipulations of seedling and cane_v production to assess the contribution of these transitions to λ and to assess the impact of potential control strategies. For each of the four average transition matrices, new λ 's were determined by modifying the seedling recruitment transition value by differing proportions (from -90 to +50%), holding all other transition values constant. Similar analyses were repeated for manipulations of the transition value for cane_v production. We also tested whether our assumption that all seedlings germinated from seeds produced during the previous year by adding an additional transition stage (seed) to the model and calculating the change in λ and elasticity values for reproduction.

Results

Trade-offs between growth and reproduction

Flower removal from all reproductive canes within a population only slightly increased cane length production by cane_v for both species. Although the average cane length produced was higher for *R. ursinus* in the flower removal plots relative to the control plots, these differences were not statistically significant at $\alpha = 0.05$ (Table 1; low-density WSR $Z = 1.244$, $P = 0.095$; high-density WSR $Z = 0.524$, $P = 0.300$). Average cane length produced by cane_v was more similar between flower removal and control plots of *R. discolor* (Table 1; low-density WSR $Z = 0.280$, $P = 0.389$; high-density WSR $Z = 0.105$, $P = 0.459$).

Table 1. Effects of floral bud removal on average cane length produced, leaf area produced per cane, and average specific leaf area in both low- and high-density populations of *R. ursinus* and *R. discolor*.

	<i>R. ursinus</i>			<i>R. discolor</i>	
	Population density	Control	Floral bud removed	Control	Floral bud removed
Cane length produced (cm)	Low	145.5 ± 23.2	228.2 ± 45.7	336.7 ± 54.1	404.5 ± 105.7
	High	106.9 ± 16.5	133.9 ± 16.9	345.1 ± 41.9	475.4 ± 135.0
Leaf area produced (cm ²)	Low	319.6 ± 72.3*	615.0 ± 176.4*	3492.8 ± 713.9	3964.6 ± 939.0
	High	156.0 ± 16.2	201.9 ± 20.2	2877.0 ± 623.2	4018.6 ± 1263.1
Specific leaf area (cm ² g ⁻¹)	Low	162.1 ± 7.7*	116.5 ± 4.7*	88.8 ± 2.6	64.6 ± 4.0
	High	130.6 ± 15.6	111.4 ± 6.4	87.1 ± 3.4	93.8 ± 2.2*

Values are the mean ± 1 SE.

* indicates a significant treatment effect at $\alpha = 0.05$ according to the nonparametric Wilcoxon Signed Ranks test.

In contrast to cane length, leaf growth responded significantly to the flower removal experiment. In low-density populations of *R. ursinus*, flower removal resulted in increased leaf area (Table 1; WSR $Z = 1.718$, $P = 0.043$) and reduced SLA (WSR $Z = 2.667$, $P = 0.004$) compared to control plots. There was a similar response in high-density populations of *R. ursinus*, but the differences were not significant at $\alpha = 0.05$ (Table 1; leaf area WSR $Z = 1.363$, $P = 0.087$; SLA WSR $Z = 1.373$, $P = 0.085$). Flower removal had no statistically significant impact on leaf area produced per cane for *R. discolor* (Table 1; low-density WSR $Z = 0.280$, $P = 0.389$; high-density WSR $Z = 0.943$, $P = 0.173$), but did significantly increase SLA for high-density populations (WSR $Z = 2.694$, $P = 0.004$; low-density WSR $Z = 1.234$, $P = 0.125$).

Correlations between growth, reproduction, and demographic parameters reveal differences between the species. For *R. ursinus*, leaf area produced per cane_v was negatively correlated with both the number of seedlings and the number of cane_v produced per reproductive cane in the previous year (Table 2; $P = 0.028$ and 0.050 , respectively), while there was no such relationship for *R. discolor* (Table 2; $P = 0.385$ and 0.695 , respectively). There was a positive correlation between seedling and cane_s survival for both species ($P = 0.049$ for *R. ursinus* and $P = 0.026$ for

R. discolor). For *R. discolor*, there was a negative correlation between cane length and both seedling and cane_s survival ($P = 0.049$ and $P = 0.007$, respectively) and between leaf area and cane_s survival ($P = 0.045$) while there was a positive correlation between cane length production and cane_s survival for *R. ursinus* ($P = 0.008$). Leaf area and cane length were positively correlated for both species ($P = 0.003$ for *R. ursinus* and $P < 0.0001$ for *R. discolor*).

Demographic patterns

Populations of the two *Rubus* species exhibited differences in rates of clonal growth, sexual reproduction, and survival and advancement of individuals to the next stage of development. The noninvasive *R. ursinus* produced more seedlings per m² in both high- and low-density populations than the invasive *R. discolor* (Table 3; KW $F = 22.89$, $P < 0.0001$), but the two species produced a similar number of seedlings per reproductive cane (KW $F = 4.55$, $P = 0.028$). *R. ursinus* also produced more cane_v per m² and per reproductive cane than *R. discolor* (Table 3; KW $F = 31.32$, $P < 0.0001$ and $F = 12.04$, $P = 0.007$, respectively). Although *R. discolor* produced fewer seedlings and cane_v, its cane_v and cane_s tended to have higher survival rates than *R. ursinus* (KW $F = 20.01$, $P < 0.001$ and KW

Table 2. Pearson correlation values between demographic parameters of control populations of the noninvasive *R. ursinus* (upper panel) and the invasive *R. discolor* (lower panel).

	Year <i>t</i>						
	Cane length	Leaf area	Cane _v production	Seedling production	Seedling survival	Cane _s survival	Cane _v survival
Leaf area	0.781**	–					
Cane _v production	–0.183	–0.576*	–				
Seedling production	–0.317	–0.630*	0.362	–			
Seedling survival	–0.006	–0.384	0.263	0.212	–		
Cane _s survival	0.723**	0.313	–0.065	0.038	0.579*	–	
Cane _v survival	–0.226	0.069	–0.796**	–0.052	–0.073	–0.145	–
Year (<i>t</i> + 1)							
Leaf area	0.837**	–					
Cane _v production	0.347	0.242	–				
Seedling production	–0.111	–0.108	0.250	–			
Seedling survival	–0.516*	–0.465	0.190	0.081	–		
Cane _s survival	–0.665**	–0.523*	0.270	0.288	0.573*	–	
Cane _v survival	0.075	–0.147	0.309	0.509	–0.020	0.246	–

* Indicates a significant difference at $\alpha = 0.05$ and ** indicates a significant difference at $\alpha = 0.01$.

Table 3. Average demographic parameters ± 1 SE for the noninvasive *R. ursinus* and the invasive *R. discolor*.

	<i>R. ursinus</i>		<i>R. discolor</i>	
	Low density	High density	Low density	High density
Seedlings (m^{-2})	2.0 ± 0.5^a	3.6 ± 0.6^b	0.3 ± 0.1^c	0.7 ± 0.2^c
Cane _v (m^{-2})	4.9 ± 0.7^a	14.7 ± 0.7^b	1.1 ± 0.2^c	1.5 ± 0.1^c
Seedlings per reproductive cane	1.1 ± 0.3^a	0.5 ± 0.1^a	0.3 ± 0.1^a	0.5 ± 0.2^a
Cane _v per reproductive cane	3.1 ± 0.6^a	2.4 ± 0.3^{ab}	1.4 ± 0.2^{bc}	0.9 ± 0.2^c
Seedling survival (%)	68 ± 16^a	69 ± 9^a	79 ± 9^a	86 ± 7^a
Cane _s survival (%)	41 ± 14^a	26 ± 13^a	58 ± 14^a	72 ± 9^a
Cane _v survival (%)	70 ± 7^a	41 ± 4^b	93 ± 4^c	98 ± 2^c

Values of the same parameter sharing letters are not significantly different at $\alpha = 0.05$ as determined with the nonparametric Kruskal–Wallis procedure.

$F = 6.22$, $P = 0.102$, respectively). Seedling survival was similar between densities for a given species (KW $F = 2.34$, $P = 0.505$).

Population growth

Rubus ursinus exhibited positive population growth rates over both transition years in both low- and high-density populations (Figure 2). However, for high-density populations, λ was very close to 1, suggesting that population size in these established populations was fairly constant. The λ in low-density populations was higher than that of high-density populations over both transition years ($t = -2.144$, $P = 0.034$). The range in λ for low-density *R. ursinus* populations was 1.22–1.92 and for high-density populations was 0.72–1.22.

The average population growth rate of *R. discolor* was positive over both transition years in both low- and high-density populations, except in high-density populations in 2000–2001 (Figure 2). Like *R. ursinus*, *R. discolor* showed an apparently higher λ in low-density populations than in high-density populations in 2000–2001 ($t = -6.353$, $P = 0.003$), but in 1999–2000, λ was approximately equal between the two population densities ($t = 0.705$, $P = 0.262$). Values of λ for *R. discolor* ranged from 0.82 to 1.76 for low-density populations and from 0.70 to 1.41 in high-density populations.

Population growth rates were similar between the species. λ was not significantly different between the species over the 1999–2000 ($t = 0.437$, $P = 0.402$ for low-density and $t = 0.898$, $P = 0.251$ for high-density) or 2000–2001 transition intervals ($t = 1.428$, $P = 0.223$ for low-density and $t = 1.439$, $P = 0.206$ for high-density).

Figure 2. The finite rate of increase (λ) for low- (open bars) and high-density (shaded bars) populations of *R. ursinus* and *R. discolor* over each one-year transition interval. Error bars = 1 SE as calculated using an analytical approximation (discussed in the text).

The LTRE revealed that the factors underlying the effects of density on λ were different for each of the species. The transition that contributes the

most to the density-dependent change in λ for each species has the largest c_{ij} . The c_{ij} for *R. ursinus* reveal that high population density caused reduced cane_v survival and, to a lesser degree, reduced cane_v production because the c_{ij} for these transitions were largest (Figure 3C). For *R. discolor*, the reduction in λ in high- relative to low-density populations was due to reduced cane_v production because this transition had the largest c_{ij} (Figure 3D). For *R. ursinus*, the transition elements that yielded the largest d_{ij} between high- and low-density populations did not produce the largest c_{ij} and, therefore, largest effect on λ (Figure 3). However, for *R. discolor*, the largest d_{ij} produced the largest c_{ij} (Figure 3).

Elasticity analysis

Comparison of the summed elasticity values for each life-history process indicated that clonal growth affected λ relatively more than sexual reproduction for both species in both low and high population densities (Table 4). For *R. ursinus*, the contribution of clonal growth and sexual reproduction to λ remained relatively constant between low- and high-density populations (Table 5). However, the relative importance of

sexual reproduction to λ increased between low- and high-density populations of *R. discolor*. The summed elasticity values for sexual reproduction were higher in *R. discolor* than *R. ursinus*, particularly in high-density populations, ($t = 0.670$, $P = 0.128$ for low-density populations and $t = 1.728$ and $P = 0.028$ for high-density populations). Similarly, clonal growth contributed slightly more to population growth in *R. ursinus* relative to *R. discolor* ($t = -1.751$, $P = 0.050$ for low-density populations and $t = -1.544$, $P = 0.075$ for high-density populations). Adding the seed transition stage to the model reduced λ for both species at both densities, but not significantly ($t = 1.95$, $P = 0.15$ and $t = 0.37$, $P = 0.73$ for *R. discolor* high- and low-density populations, respectively and $t = 1.89$, $P = 0.16$ and $t = 1.97$, $P = 0.15$ for *R. ursinus* high- and low-density populations). For both species, the summed elasticity values for sexual reproduction increased in the high-density populations, but not significantly (5% increase for *R. discolor*, $t = 0.53$, $P = 0.63$ and 1% increase for *R. ursinus*, $t = 2.12$, $P = 0.12$). In low-density populations of both species, the summed elasticity values for sexual reproduction decreased by a nonsignificant amount (4% decrease for *R. discolor*, $t = 0.96$,

Figure 3. The differences (d_{ij}) between transition values (a_{ij}) from the mean low- and mean high-density populations of *R. ursinus* (A) and *R. discolor* (B), and the contribution (c_{ij}) of each of those differences to the density-dependent change in population growth (C and D). Abbreviations for transitions from one year to the next are ss (seedling to seedling), sc_s (seedling to cane_s), c_sc_s (cane_s to cane_s), c_sr (cane_s to reproductive), c_vc_v (cane_v to cane_v), c_vr (cane_v to reproductive), rs (seedling recruitment), rc_v (vegetative cane production), and rr (reproductive to reproductive).

Table 4. Average summed elasticity values ± 1 SE for sexual reproduction and clonal growth transitions of all low- and high-density populations for each species over both transition years. Transitions included in the sum for sexual reproduction include those depicted with hatched lines in Figure 1, while transitions included in clonal growth include those with dots in Figure 1.

	Mode of reproduction	
	Sexual	Clonal
<i>R. ursinus</i>		
Low density	14 $\pm$ 10	85 $\pm$ 10
High density	13 $\pm$ 6	81 $\pm$ 6
<i>R. discolor</i>		
Low density	20 $\pm$ 8	71 $\pm$ 7
High density	32 $\pm$ 7	68 $\pm$ 8

$P = 0.41$ and 2% decrease for *R. ursinus*, $t = 1.33$, $P = 0.31$). Therefore, we conclude that our assumption that seeds produced in one year germinated in the following year did not significantly affect the results of our analyses.

For both species, changes in the average cane_v production transition value had a much larger effect on λ than proportional changes in the average seedling recruitment value, holding all other transition values constant (Figure 4). For *R. ursinus*, reducing seedling recruitment by as much as 90% had virtually no impact on λ in both low- and high-density populations while even small changes in cane_v production had a proportionately larger effect on λ . In low-density populations of *R. discolor*, the proportional effects of changes in seedling recruitment and cane_v produc-

tion on λ were similar to the effects observed in *R. ursinus* (Figure 4). However, in high-density populations of *R. discolor*, changes to the seedling recruitment and to the cane_v production transition value produced more similar effects on λ .

Figure 5 shows the percent change in λ given a 50% change in either the cane_v production or seedling recruitment transition values for each matrix of each species while holding all other transition values constant. For *R. ursinus*, a 50% reduction in seedling recruitment yielded a small change in λ (always less than 10% change), while a 50% change in cane_v production yielded a minimum 15% change in population growth (Figure 5). For *R. discolor*, although a 50% change in cane_v production generally had a larger impact on λ than a 50% change in seedling recruitment, the impact of these two transitions on λ were more similar to each other than their impacts on λ of *R. ursinus* (Figure 5). With a 50% change in seedling recruitment, λ changed by as much as 14% while a proportional change in cane_v production changed λ by as little as 7%.

Discussion

Trade-offs between growth and reproduction

The demographic trade-offs between current sexual reproduction and growth of cane_v within a clone are more evident in the noninvasive

Figure 4. The finite rate of increase (λ) for a proportional change in the average transition value of seedling recruitment (circles) and cane_v production (triangles) for *R. ursinus* in low- (A) and high-density (B) populations and for *R. discolor* in low- (C) and high- (D) density populations.

Figure 5. The percent change in the finite rate of increase (λ) for a 50% proportional change in seedling recruitment (circles) and cane_v production (triangles) versus the elasticity value (e_{ij}) for each fecundity and cane_v transition for each matrix of *R. ursinus* and *R. discolor*. For *R. ursinus*, $\lambda = 1.06 + 0.49e_{ij}$ ($P < 0.0001$) and for *R. discolor*, $\lambda = 0.06 + 0.56e_{ij}$ ($P < 0.0001$).

R. ursinus than in the invasive *R. discolor*. Trade-offs between current growth and reproduction have been observed in studies with natural and manipulated levels of reproduction for noninvasive species (Fox and Stevens 1991; Newell 1991; Ashman 1992; Nicotra 1999). However, little is known about these trade-offs in an invasive plant species. The apparent trade-offs in *R. ursinus* were driven by the physiological costs associated with reproduction, leading to relatively higher reproductive effort. A previous study of these same two species demonstrated that sexual reproduction caused decreased foliar water status and photosynthetic capacity in *R. ursinus*, leading to a reduction in annual carbon gain (McDowell and Turner 2002). These effects of reproduction

on carbon gain, however, were not apparent in *R. discolor*, thus explaining the apparent lack of growth response to floral bud removal observed in this study.

In addition to the trade-off between current growth and reproduction, plants may also exhibit a negative relationship between current reproduction and future growth and reproduction. If current and future reproduction draw on the same pool of resources, then current reproduction may deplete available resources for future growth, flower, and fruit development (Stearns 1992). Furthermore, the negative effects of reproduction on current plant size may decrease a plant's capacity to acquire resources in the future (Bloom et al. 1985) or limit the number of meristems that may develop into inflorescences (Geber 1990). The negative correlation between leaf area production per cane_v of *R. ursinus* in one year and cane_v production in the following year suggests trade-offs may exist between generations in the noninvasive *Rubus* because these two parameters, as components of clonally integrated canes, draw on the same pool of resources. Although there is a negative correlation between leaf area production in one year and seedling production in the following, this correlation may be spurious. In order for seedling production to have an effect on resource allocation to leaf area production of cane_v, the seeds from which those seedlings germinated must have been produced by reproductive canes clonally connected to the affected cane_v. In this study, it was not possible to determine the seed source of the germinated seedlings.

The demographic trade-offs between growth and reproduction within and between generations were not apparent in the invasive *R. discolor*. It is possible that such life-history trade-offs are not apparent when resources are not limiting, when different life-history functions are dependent upon separate resource pools, or when current allocation does not affect the capacity of a plant to capture resources in the future (Geber 1990; Stearns 1992). The two *Rubus* species examined in this study grow in the same open sites and, therefore, have potential access to equivalent resources. However, *R. discolor* is able to achieve higher photosynthetic rates per unit resource investment of carbon, water, and nitrogen than

R. ursinus (McDowell 2002). Therefore, resource availability may be more limiting to carbon gain in *R. ursinus* than in *R. discolor*. Furthermore, the lack of effect of reproduction on carbon gain in *R. discolor* highlights a possible mechanism underlying the apparent lack of trade-offs for this species (McDowell and Turner 2002).

Demographic patterns

Rates of production and survival of canes within populations were different for the species. The higher rate of seedling and cane_v production by *R. ursinus* on a ground area basis is due, at least in part, to the smaller size of *R. ursinus* canes; more small canes can grow in a given area than large canes. However, *R. ursinus* also produced more cane_v per reproductive cane, a value that was standardized for plant size. Although *R. discolor* produced fewer cane_v, they had a higher survival rate than the cane_v of *R. ursinus*. In fact, the noninvasive *R. ursinus* displayed a demographic trade-off between cane_v production and survival, as evidenced by the negative correlation between these two parameters. For *R. discolor*, there was a positive, although not significant, relationship between cane_v production and survival, suggesting there was no demographic trade-off between these two parameters.

Population growth and invasiveness

As plant populations become more dense, they eventually reach the site carrying capacity and are subject to density-dependent limits on recruitment of new individuals. In short-lived species such as *Rubus*, recruitment may be expected to plateau so that each year, the population merely replaces senescing canes. Clonal plants commonly show constant rates of mortality and recruitment following population establishment so that cane_v numbers remain relatively constant (Cook 1985; Hartnett and Bazzaz 1985; Meyer and Schmid 1999). For both *Rubus* species in this study, λ of the high-density populations was approximately equal to 1, suggesting that the populations had, on average, reached a plateau in population growth. Furthermore, λ was higher in low- than in high-density populations, with the exception of *R. discolor* over the 1999–2000 transition. This

pattern of population growth is similar to that of other clonal plant species (Barkham 1980; Cook 1985; Briske and Butler 1989) as well as that of the invasive, but non-clonal, *Cytisus scoparius* (Parker 2000), in response to increasing population density. The LTRE showed that for *R. ursinus*, the effect of density on λ was due to a reduction in cane_v survival with increasing population density, while in *R. discolor*, the difference was due to a reduction in cane_v production. Reduced cane_v production, rather than increased mortality, is a more commonly observed response to increased population density in other clonal plant species (Cook 1985; Briske and Butler 1989), perhaps because cane_v mortality generates a resource cost for the entire clone. The mortality of cane_v in *R. ursinus* was particularly pronounced over the 2000–2001 transition interval, along with mortality of other life-history stages, and may have arisen due to the colder than normal conditions during the winter and much drier than normal spring. *R. discolor*, which is more tolerant of seasonal and diurnal drought than *R. ursinus* (McDowell 2002; McDowell and Turner 2002), may have been less adversely affected by the climate over that transition interval.

The elasticity analysis revealed that life stage transitions relating to cane_v production and survival were relatively more important to population growth of both species than transitions relating to sexual reproduction. A reliance on predominantly clonal spread over sexual reproduction has been observed in other species of *Rubus* (Abrahamson 1975; Maxwell et al. 1993; Baret et al. 2003), as well as other plants that reproduce both sexually and clonally (Cook 1985). There are several advantages associated with the reliance on clonal growth for population expansion. Although cane_v production may require an initial investment of more resources than sexual reproduction, cane_v eventually contribute positively to the resource balance of the clone (Cook 1985), increase the capacity of the clone to recover from stresses such as defoliation (Price et al. 1992), and increase the potential for the clone to access unevenly distributed resources, such as light and water (Stuefer et al. 1996). Furthermore, production of cane_v enables a clone to rapidly capture and dominate an area, competitively excluding other species (Pitelka and

Ashmun 1985). Finally, life history processes with fewer transitions contribute relatively more to population growth than those with more transitions (de Kroon et al. 2000). Therefore, development of cane_v contributes more to population growth of *Rubus* because it takes two years for a reproductive cane to develop from clonal origins, while it takes three years for a reproductive cane to develop from seed.

Population growth rates within existing populations were similar among the species across both densities and transition intervals. Therefore, invasiveness of *R. discolor* may be due to a greater capacity for dispersal and establishment of new populations than *R. ursinus*, where invasiveness is defined as the ability to rapidly colonize sites, reproduce, and spread to new sites outside of the species' previous range. We did not explicitly measure dispersal or establishment rates of new populations for these species, but we did observe a relative increase of importance of sexual reproduction with population density for *R. discolor*. This increase was due to seedlings germinating in locations within the high-density plots that had not been previously colonized by clonal spread. The minimal physiological costs associated with sexual reproduction for *R. discolor* (McDowell and Turner 2002) mean that the importance of sexual reproduction in populations may increase without incurring negative effects on the current population. *R. ursinus* relied almost entirely on clonal spread for population growth and, therefore, had limited potential for dispersal.

Control of *R. discolor*

The elasticity analysis for *R. discolor* may be useful in determining methods for controlling this species. In order to control invasive plant species, population growth needs to be lowered to below $\lambda = 1$, so that population size will decrease. One biological control strategy suggested for several other invasive plant species is to utilize predators or pathogens to reduce flower or seed development (Shea and Kelly 1998; McEvoy and Coombs 1999; Parker 2000). Seed predation could reduce population growth of established populations of *R. discolor* by limiting dispersal, but only if seedling recruitment is reduced by at

least 70%. The most effective strategy for controlling population growth for existing populations of *R. discolor* would be to reduce cane_v production. The numerical simulations in this study showed that reducing cane_v production by as little as 30% could reduce population growth adequately to bring about eventual extinction of existing populations. Control methods that involve mowing canes or applying herbicide to foliage have proven relatively ineffective at controlling this species (reviewed in Hoshovsky 2001), probably because such methods have failed to adequately affect allocation to the belowground portions of the plant. The most effective controls for this invasive *Rubus* include the introduction of animals that graze canes to the roots from which cane_v sprout (Amor 1974; Daar 1983) or the use of herbicides applied to cut or burned stems following fruit set (Hoshovsky 2001). The effectiveness of this latter approach is likely due to the translocation of nutrients and, therefore, herbicides from reproductive canes to the roots prior to senescence. Such management tactics, in addition to reducing seedling recruitment to limit dispersal and establishment of new populations, could be effective in controlling established populations of this invasive species in the PNW.

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