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When does it make sense to target the weed seed bank?

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Weed seeds initiate most weed invasions of arable fields, yet there is relatively little information on the value of managing weed seed banks. Matrix population models were used to examine the relative importance of managing weed seed banks, in relation to other life stages, for four model weed species with varying life histories. Simulations for giant foxtail and common lambsquarters, summer annual weeds of arable fields; garlic mustard, an obligate biennial invasive weed of temperate forests; and Canada thistle, a perennial weed of pastures and arable fields, were run under conditions of varying population density and efficacy of seedling control. The models were subjected to elasticity analysis to determine what happened to weed populations when different life stages were targeted. Losses from the dormant seed bank were most important for summer annual weeds, of intermediate importance for biennial weeds, and of low importance for perennial weeds. More effort is needed to develop weed seed-bank management techniques for summer annual weed species as part of integrated weed management systems.

Nomenclature: Common lambsquarters, *Chenopodium album* L. CHEAL; giant foxtail, *Setaria faberi* Herrm. SETFA; garlic mustard, *Alliaria petiolata* (M. Bieb.) Cavara and Grande ALPET; Canada thistle, *Cirsium arvense* (L.) Scop. CIRAR.

Key words: Elasticity analysis, matrix modeling, seed bank, seed mortality, target transitions, weed life histories.

The great majority of weed control tactics, including herbicides, cultivation, mulches, and emergence forecasting tools, target the seedling stage of plant development. There are good reasons for focusing weed management efforts on this life stage: weed seedlings are easy to see, highly vulnerable to disturbances, and will quickly compete with the crop unless controlled. There are also potential costs associated with exclusively controlling weed seedlings. First, confining weed management to a narrow temporal window increases the risk of unsatisfactory weed management outcomes due to unfavorable weather (Gunsolus and Buhler 1999). Managing risks of this sort is particularly important in production systems that are less reliant upon herbicides (Barberi 2002). Second, weed seed banks are the primary source of persistent weed infestations in agricultural fields (Cousens and Mortimer 1995). Weed seed-bank density can directly affect the efficacy of weed seedling management, with greater herbicide doses required to control seedlings after large seed inputs to the soil seed bank (Taylor and Hartzler 2000). Weed seeds also drive the spread of weed patches in fields, both for annual (Steinmann and Klingebiel 2004) and perennial weed species (Blumenthal and Jordan 2001), and are the only means of population increase for annual weed species. Is managing the weed seed bank sufficiently important that it is worth the effort to develop new tools for this purpose?

This study used a modeling approach to identify conditions under which reducing the weed seed bank is an important management goal. Four weed species were used as model representatives for three different life histories: giant foxtail and common lambsquarters, summer annuals; garlic mustard, an obligate biennial; and Canada thistle, a perennial. Giant foxtail and common lambsquarters, both important weeds of field crop production systems in the Midwest U.S. Corn Belt, were chosen to represent two contrasting patterns in annual weed life history: giant foxtail produces modest numbers of seeds with relatively low dormancy and low seed-bank persistence (Buhler and Hartzler 2001), whereas common lambsquarters produces enormous numbers of highly dormant seeds (Forcella et al. 1992). Garlic mustard is a widespread invasive weed of forested ecosystems (Nuzzo 1999), with few options for control. Canada thistle has long been a troublesome weed in pastures and a wide variety of agronomic crops (Donald 1990).

Densities of these species were varied in four separate simulations to determine how density-dependent feedbacks to population growth and trade-offs between seed and safe-site limitation (Maron and Gardner 2000) affected the relative importance of managing different weed life stages. Safe-site theory predicts that when seed-bank densities are low, changes in seed inputs to, and persistence within, the soil seed bank should have a direct effect on population dynamics. In contrast, safe-site limitation occurs when the seed bank is so high, or when regeneration-niche requirements are so stringent, that the number of propagules exceeds the availability of suitable microsites for regeneration. Empirical and modeling studies show that, in reality, most plant populations have some degree of both seed and safe-site limitation at a wide range of seed-bank densities (Boyd and Van Acker 2004; Maron and Gardner 2000). Efficacy of seedling control was also varied in simulations to determine the de-

gree to which management of various weed life stages could make up for lapses in seedling management.

Materials and Methods

Modeling Approach

Matrix population models (Caswell 2001) were used to examine the relative effect of targeting different life stages (Figure 1) on the population dynamics of common lambsquarters, giant foxtail, garlic mustard, and Canada thistle. Models followed the general form

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t \quad [1]$$

where **n** is a vector with i rows representing the number of individuals in each life stage i at time t and $t+1$, and **A** represents the annual projection matrix with i rows and j ($= i$) columns containing all life stage transition probabilities (a_{ij}) for the weed species being modeled (Table 1). All models were deterministic (i.e., a_{ij} were held constant during the course of a simulation) and nonlinear, because of density dependence in seedling recruitment, seedling survival, rosette and plant survival (in biennial and perennial species), and fecundity. Density dependence was imposed on these transitions by assuming negative exponential decay of parameter values as population size increased and by multiplying each density-dependent a_{ij} by $e^{-\mathrm{k}\mathbf{n}_{ti}}$ (Jordan et al. 1995), where k is a coefficient expressing the degree of density dependence and $\mathbf{n}_{ti}$ is the number of individuals within a given life stage i at time t. Values of k were chosen that resulted in populations converging within three model generations on seed-bank densities consistent with ranges reported in the literature (Donald 1994; Drayton and Primack 1999; Forcella et al. 1992).

The central question of this study was, "What happens to the relative importance of weed seed mortality in limiting weed population growth rate, compared with mortality at other life stages, as efficacy of seedling control and life history are varied?" Perturbation analyses, including sensitivity and elasticity analysis, are powerful tools for asking "what if" questions of this sort (Caswell 2000). Sensitivity analysis, which has been used frequently in the weed science literature (Bussan et al. 2000; Gonzalez-Andujar and Fernandez-Quintanilla 1991; Jordan et al. 1995), examines the effect of additive perturbations to demographic parameters on population growth rate. In contrast, elasticity analysis looks at how small proportional changes to each demographic rate a_{ij} affect the proportional change in overall population growth rate, λ when all other a_{ij} are held constant. It is expressed as

$$E_{ij} = \frac{a_{ij}}{\lambda}\frac{\partial\lambda}{\partial a_{ij}} \quad [2]$$

where E_{ij} is the elasticity of λ to proportional perturbations in a_{ij}; and $\delta\lambda/\delta a_{ij}$, the partial derivative of λ with respect to a_{ij}, is the sensitivity of λ to additive changes in a_{ij} (Caswell 2001). In other words, an elasticity value of 1 would imply that a 10% change in the value of a_{ij} results in a 10% change in λ. An elasticity value of 0.5 would indicate that a 10% change in a_{ij} would result in only a 5% change in λ. Because elasticities examine proportional perturbations, they allow for an unbiased comparison of parameters that have greatly different magnitudes or differ in their units, and facilitate comparative analyses of populations under favorable and limiting conditions (Davis et al. 2004). An extension of Equation 2, making use of the chain rule for differentiation, allows the calculation of elasticities of λ to lower-level demographic parameters (i.e., the individual life-stage transitions, such as germination and seedling survival, making up each a_{ij}; see Figure 1), such that

$$E_x = \frac{x}{\lambda}\frac{\partial\lambda}{\partial x} = \frac{x}{\lambda}\sum_{i,j}\frac{\partial\lambda}{\partial a_{ij}}\frac{\partial a_{ij}}{\partial x} \quad [3]$$

where E_x represents the elasticity of λ to proportional perturbations in x, which in turn represents a lower-level demographic parameter (Caswell 2001).

To obtain elasticities for density-dependent matrix models, Equation 3 was evaluated at a specific population density (Grant 1998). Model behavior was explored at low and high population densities, with values chosen to fall within published ranges for the study species. Giant foxtail and common lambsquarters elasticities were evaluated at low and high densities of 200 and 15,000 dormant seeds m^{-2}, and 200 and 150,000 dormant seeds m^{-2}, respectively (Davis and Liebman 2003; Forcella et al. 1992). Garlic mustard and Canada thistle elasticities were evaluated at low densities of 500 seeds m^{-2}, 100 rosettes m^{-2}, and 8 plants m^{-2} and high densities of 2,200 seeds m^{-2}, 384 rosettes m^{-2}, and 40 plants m^{-2}, stable age distributions for these species (Caswell 2001; Donald 1994; Drayton and Primack 1999). Entering the population density for a given life stage into the negative exponential function for density dependence yielded a proportional coefficient for each density level and parameter. These coefficients were multiplied by the relevant a_{ij}, resulting in a new **A** matrix at the chosen population density.

The influence of variation in seedling control on the relative importance of mortality in other life stages was investigated by computing E_{ij} for all a_{ij} as seedling mortality was varied from 0 to 100%. All calculations were performed within MATLAB.[1]

Model Parameters

Matrix models for each species were parameterized using values from the weed science literature (Table 1). Demographic parameters for giant foxtail (Davis and Liebman 2003) and garlic mustard (Drayton and Primack 1999) were obtained from whole life-cycle data sets collected within a single time and location. Data collected in this fashion are the most desirable for population dynamics modeling purposes, as the covariances between parameters remain intact (van Tienderen 1995). Demographic parameters for common lambsquarters and Canada thistle were estimated from mean values obtained from literature reviews (Donald 1994; Freckleton and Watkinson 1998). Parameter covariances were not necessarily intact within these data sets, but the large number of values comprising the means for each parameter gives some degree of assurance that the parameter estimates are within reasonable ranges for these species.

Results and Discussion

Elasticity Analyses

Annual Species

The elasticity of giant foxtail population growth rate (λ) to changes in overwinter seed-bank persistence (Es_w) main-

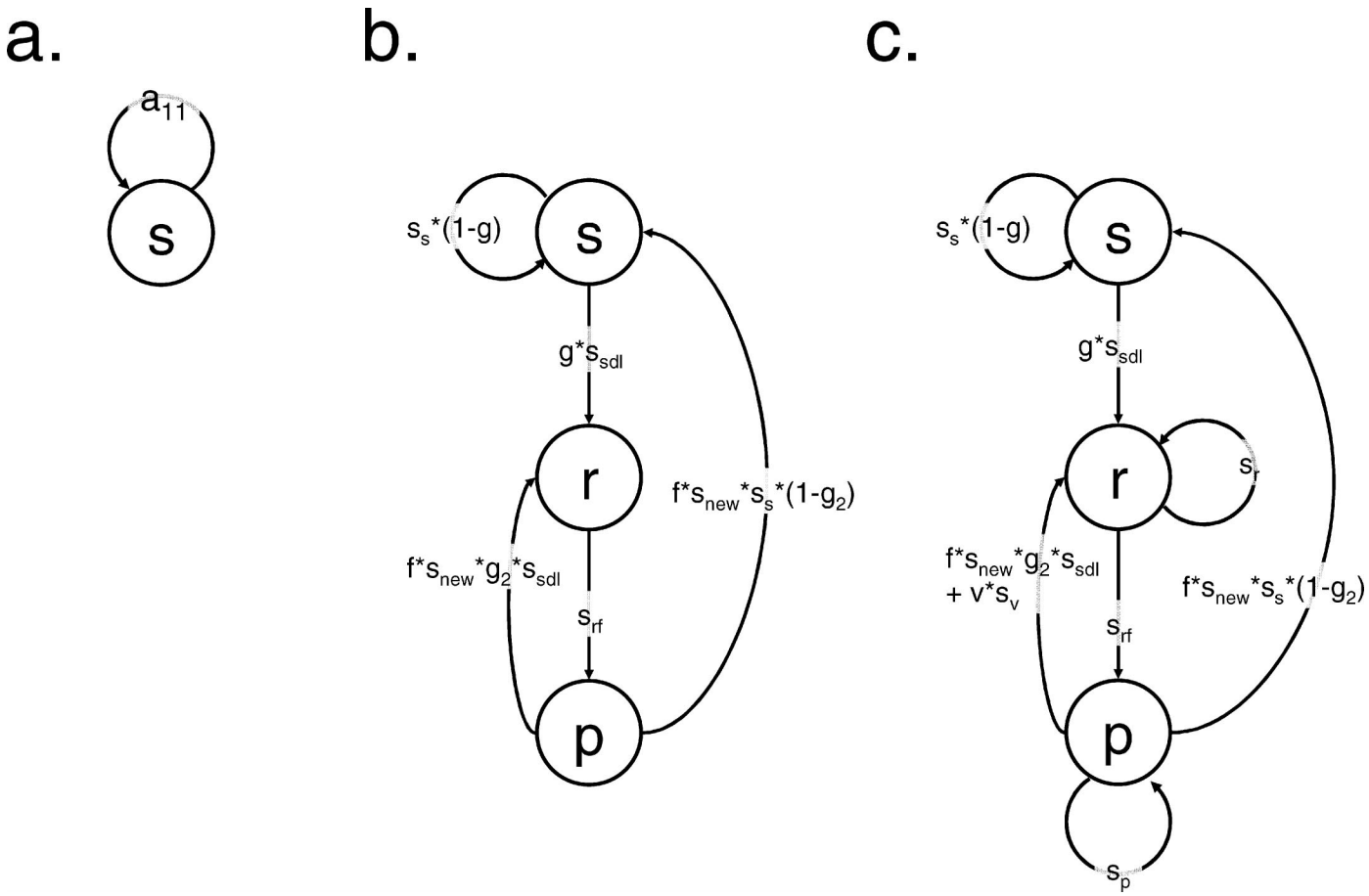

FIGURE 1. Life cycle diagrams for (a) annual, (b) biennial, and (c) perennial weed species. Circles represent life stages; s, seed; r, rosette; and p, plant. Arrows represent life-stage transitions and are labeled with the lower-level demographic rates making up each transition (see Table 1 for explanation of parameter abbreviations). For the annual weed species giant foxtail and common lambsquarters, the annual transition rule $a_{11} = s_{new} \times s_w \times g \times s_{sdl} \times f + s_w \times s_s \times (1 - g)$, where s_w is overwinter seed survival; g, germination; s_{sdl}, seedling survival; f, fecundity; s_{new}, survival of newly shed seed; and s_s, spring/summer seed survival.

tained a value of 1 over all conditions studied (Figures 2a and 2b). The constancy of Es_w can be understood by examining the annual weed life cycle represented in Figure 1a. As there is only one stage (dormant seeds within the soil seed bank) that maps across years, the matrix is simply a function that evaluates to a single number when all the parameter values are specified. In terms of the parameters describing the important events in the life cycle, this function is

$$a_{11} = s_w \times g \times s_{sdl} \times f \times s_{new} + s_w \times s_s \times (1 - g) \quad [4]$$

where s_w represents overwinter seed-bank persistence, g represents seedling recruitment, s_{sdl} represents survival of seedlings to reproductive maturity, f represents fecundity, s_{new} represents the survival of newly shed seed, and s_s represents spring/summer seed-bank persistence. The first string of parameters in a_{11}, $s_w \times g \times s_{sdl} \times f$, describes the aboveground pathway for the annual life cycle, in which seeds germinate, seedlings survive to reproductive maturity, new seeds are shed, and seeds enter the seed bank. The second string of parameters in a_{11}, $s_w \times s_s \times (1 - g)$, describes the belowground pathway for the annual life cycle, in which seeds remain dormant and survive at some rate until the following growing season. Because s_w appears in both the above- and belowground pathways, changes in this parameter are directly proportional to changes in λ, making it a bottleneck in the life cycle of annual weeds. No other lower-level demographic parameter appears in both the above- and belowground pathways, hence Es_w was greater than the elasticity of λ to changes in all other demographic parameters.

The above result is universal to models of the population dynamics of annual weeds (Davis et al. 2004; Gonzalez-Andujar and Fernandez-Quintanilla 1991; Jordan et al. 1995) because the annual weed life cycle forces all individuals to pass through the dormant seed stage. In the following sections, results from this study extend upon previous modeling work by elucidating some of the ramifications of seed-bank density, control efficacy, and life history upon target transitions.

Varying the proportion of giant foxtail seedlings surviving weed control affected the relative importance of controlling s_w in comparison to other parameters (Figures 2a and 2b). If very few, or no, seedlings survived control, then the only parameters allowing the weed population to persist in the field were the seed-bank parameters s_w and s_s. This was reflected in high values for E_{sw} and E_{ss} in comparison to reduced values for E_g, E_{ssdl}, E_f, and E_{snew}. As the proportion of seedlings surviving control increased, the relative importance of maintaining a dormant seed bank to persistence of the weed population in the field decreased, whereas the aboveground pathway increased in importance due to the

TABLE 1. Demographic rates used to parameterize matrix population models for giant foxtail (SETFA), common lambsquarters (CHEAL), garlic mustard (ALPET), and Canada thistle (CIRAR).

Parameter abbreviation[a]	SETFA	CHEAL	ALPET	CIRAR
s_w	0.90[b]	0.98	0.10	0.20
g	0.44	0.10	0.50	0.60
f	200	20,000	600	1500
s_s	0.50	0.98	—[c]	—
s_{sdl}	0.95	0.95	—[d]	0.10
s_{new}	0.90	0.90	0.90	0.90
g_2	—	—	0.001	0.35
s_r	—	—	0.13	0.10
s_{rf}	—	—	0.50	0.25
v	—	—	—	26
s_v	—	—	—	0.19
s_p	—	—	—	0.30
δ_g	0.0001	0.00001	0.001	0.001
δ_s	0.001	0.001	0.001	0.001
δ_f	0.004	0.01	0.001	0.001

[a] Parameter abbreviations: s_w, overwinter seedbank persistence; g, seedling recruitment from the seedbank; f, fecundity; s_s, spring/summer seedbank persistence; s_{sdl}, seedling survival to reproductive maturity; s_{new}, postdispersal survival of newly shed seeds; g_2, seedling recruitment from newly shed seeds; s_r, rosette survival in the rosette stage; s_{rf}, rosette survival to flowering; v, vegetative reproduction; s_v, survival of vegetative propagules; and s_p, plant survival in the plant stage. In the last three rows of the table, δ_g, δ_s, and δ_f represent density-dependence parameters for germination and seedling and rosette survival to maturity and fecundity.

[b] With the exception of f and v, fecundity and vegetative propagation in seeds plant^{-1} and ramets plant^{-1}, the demographic parameters in this table are all unitless rates.

[c] For ALPET and CIRAR, seed-bank persistence was represented on an annual basis by s_w, rather than splitting it into seed survival during the winter and during the growing season.

[d] For ALPET, s_r was not included in the model because s_{rf} encompassed both the seed-to-seedling and seedling-to-rosette transitions, which together made up an annual transition.

impact of recruitment, growth, and seed production on weed population size. This was reflected in decreasing values of s_s and increasing values of E_g, E_{ssdl}, E_f, and E_{snew}, asymptotically approaching E_{sw} as more and more seedlings survived control. Even when all seedlings survived control, E_{sw} remained high because s_w determined the number of seeds that would survive the winter and be available for recruitment into the aboveground pathway.

Variation in the density of the dormant giant foxtail seed bank shifted the relation between control efficacy and tradeoffs in the relative importance of the below- and aboveground pathways. At a density of 200 giant foxtail seeds m^{-2}, the relative importance of controlling the belowground pathway was greater than that of the aboveground pathway only when very low proportions of seedlings survived control, and the elasticities of λ to changes in the aboveground pathway quickly became similar to that for E_{sw} (Figure 2a). At a seed-bank density of 15,000 giant foxtail seeds m^{-2}, however, there were two substantial changes in elasticity patterns. First, E_g, the elasticity of λ to germination, fell below 0.25. The reduced effect of changes in germination on population growth rate in relation to other parameters, is consistent with an increase in safe-site limitation at higher seed-bank density. Second, E_{ssdl}, E_f, and E_{snew}, decreased in relative importance to E_{sw}. In other words, at a higher seed-bank density, controlling the weed seed bank had a proportionally greater effect on weed population growth rate over a much wider range of seedling control efficacies (Figure 2b).

This result may seem counterintuitive at first, especially because the trade-off between seed and safe-site limitation would seem to predict that as seed-bank density increases, changes in seed number should become less important to overall population dynamics. One way to understand this result is to think of the seed bank as having momentum, like a flywheel. As the seed-bank density increases, so does its contribution to population momentum. No empirical data have shown persistence of dormant seeds in the seed bank to be density dependent, thus the model does not assign density-dependent functions to s_w and s_s. In contrast, aboveground parameters are bound by density dependence. Therefore, as seed-bank density grows, the proportional contribution of the aboveground pathway to population size is constrained by fierce competition (Ross and Harper 1972) and shrinks in comparison to the unrestrained growth of the seed bank.

To see how elasticities correspond to changes in numbers of individuals within a population, consider how a 50% change in s_w and s_{sdl} influences changes in seed-bank density over a single year (Table 2). At an initial density of 200 seeds m^{-2}, a 50% decrease in s_w from 0.90 to 0.45 will change ΔN (the additive change in seed bank density) from 8,528 to 4,164, whereas a 50% decrease in s_{sdl} from 0.90 to 0.45 will change ΔN from 8,528 to 4,854. The reduction in seedling survival at this population density causes a similar change in the number of new individuals added to the population as an equivalent reduction in overwinter seed survival. At an initial density of 15,000 seeds m^{-2}, a 50% reduction in s_w changed ΔN from 5,686 (a growing population) to $-4{,}657$ (a shrinking population), with a corresponding 50% reduction in λ from 1.38 to 0.69. The number of new seedlings and mature plants and their reproductive capacity in this scenario remained unchanged from the base parameter values, but the newly produced and dormant seeds were disappearing much faster. In contrast, a 50% reduction in s_{sdl} at Nt = 15,000 seeds m^{-2} changed ΔN from 5,686 to 4,492, only a 6% reduction in λ from 1.38 to 1.30. Under this scenario, there were fewer reproductively mature plants than in the reduced s_w scenario, but the population continued to grow strongly because gains from newly produced seeds, as well as residual population density from old seeds, were not eliminated because of low seed-bank persistence. It is worth noting here that a 50% reduction in seed-bank persistence is obviously much more difficult and costly to achieve than a 50% reduction in seedling survival. Cost-effectiveness of potential control measures is an important consideration, as discussed in the concluding section.

Elasticity analyses for common lambsquarters (Figures 3a and 3b) followed the same general patterns as those for giant foxtail, but the curves were all shifted to the left on the x-axis. High levels of dormancy and high seed longevity in the common lambsquarters soil seed bank, coupled with extremely high fecundity for this species, meant that tactics aimed at the dormant seed bank during the growing season would have a greater impact upon population growth rate than tactics aimed at other life stages only at very high levels

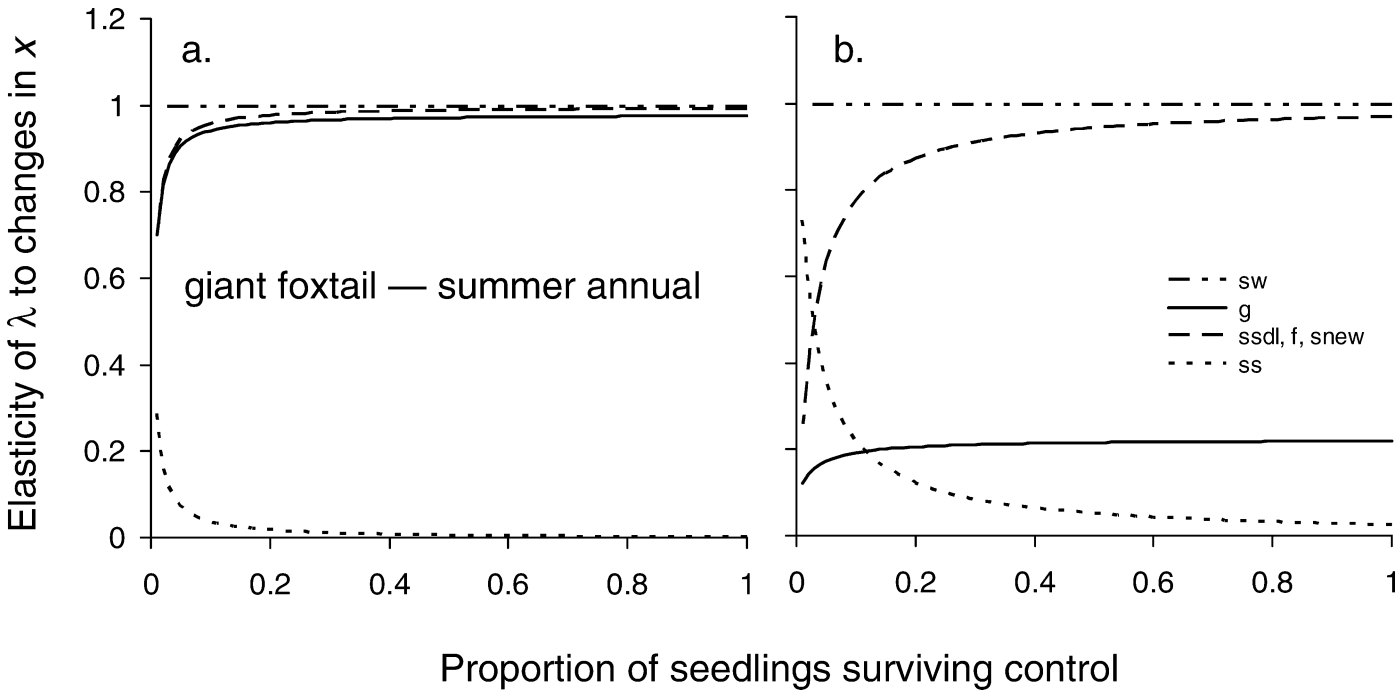

FIGURE 2. The elasticity of giant foxtail population growth rate (λ) to changes in overwinter seed survival (s_w), germination (g), seedling survival (s_{sdl}), fecundity (f), survival of newly shed seed (s_{new}), and spring/summer seed survival (s_s) evaluated at seed-bank densities of (a) 200 seeds m^{-2} and (b) 15,000 seeds m^{-2}.

of seedling-control efficacy. At an initial seed-bank density of 150,000 seeds m^{-2}, density-dependent feedback to germination reduced the importance of changes in this parameter to the population growth rate, consistent with safe-site limitation at high seed-bank density. As with giant foxtail, E_{sw} of common lambsquarters remained equal to 1 over all conditions, but the high fecundity of this species kept the relative value of changes in the aboveground pathway high over a wide range of population density and control efficacy. These findings are in agreement with other models of management effects on common lambsquarters population dynamics (Freckleton and Watkinson 1998).

Garlic Mustard

Changes in garlic mustard seed-bank persistence had an important effect on λ, relative to changes in survival of newly produced seeds, seedlings, and rosettes, only when very few garlic mustard plants survived control. This result held at both low and high population densities (Figures 4a and 4b). As greater proportions of garlic mustard plants survived control, reflecting current management constraints for garlic mustard, the elasticity of λ to changes in the survival of newly produced seeds, seedlings, and rosettes rapidly became greater than the elasticity of λ to changes in persistence of old seeds that were already part of the soil seed bank.

Canada Thistle

As life histories progressed from annual to biennial to perennial in this study, seed-bank persistence became less important, and aboveground life stages became more important. In contrast to the annual weed species, in which seed-bank persistence uniformly had the greatest impact on λ, Canada thistle λ was most responsive to changes in rosette survival over all conditions studied (Figures 5a and 5b). Survival of new seeds and seedlings was second in importance to rosette survival. All other life stages were a distant third,

TABLE 2. Comparison of the impacts of a 50% reduction in overwinter seed-bank survival (s_w) or seedling survival (s_{sdl}) on changes in population size at low and high initial seed-bank density (N_t).

N_t	Parameter s_w	Parameter s_{sdl}	New seedlings	Mature plants	Input to seed bank	Dormant seed bank	N_{t+1}	ΔN[a]	λ
seeds m^{-2}			plants m^{-2}		seeds m^{-2}				
200	0.90	0.90	86	71	8,677	51	8,728	8,528	43.6
	0.45	0.90	86	71	4,339	26	4,364	4,164	21.8
	0.90	0.45	86	36	5,003	51	5,053	4,854	25.3
15,000	0.90	0.90	1,473	304	14,598	6,087	20,686	5,686	1.38
	0.45	0.90	1,473	304	7,299	3,044	10,343	−4,657	0.67
	0.90	0.45	1,473	152	13,405	6,087	19,492	4,492	1.30

[a] The additive change in seed-bank density is represented by ΔN, where $\Delta N = N_{t+1} - N_t$, where the proportional change is represented by λ, where $\lambda = N_{t+1}/N_t$.

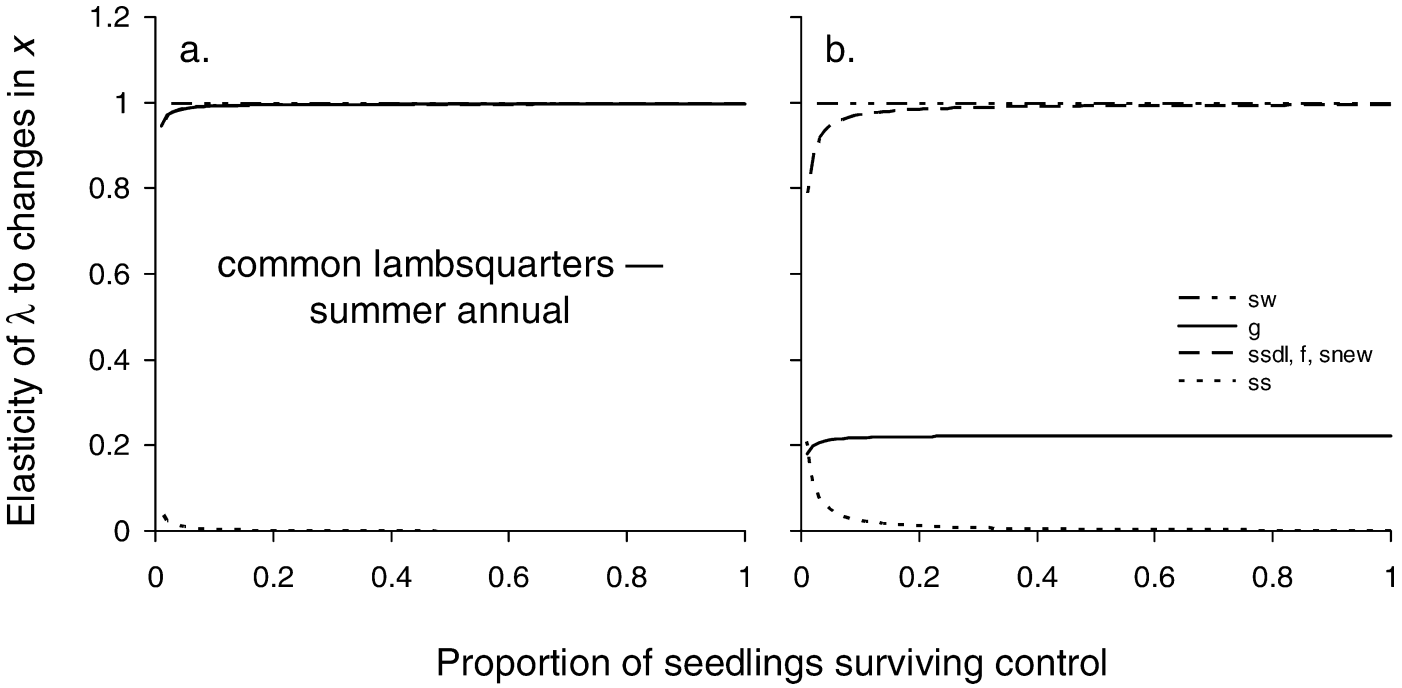

FIGURE 3. The elasticity of common lambsquarters population growth rate (λ) to changes in overwinter seed survival (s_w), germination (g), seedling survival (s_{sdl}), fecundity (f), survival of newly shed seed (s_{new}), and spring/summer seed survival (s_s) evaluated at seed-bank densities of (a) 200 seeds m^{-2} and (b) 150,000 seeds m^{-2}.

with seed-bank persistence having almost no effect on population growth rate at all. Why should survival of the rosette stage have been more important than survival of mature plants? Rosette survival was a bottleneck in the life history of Canada thistle because entry of new individuals into this stage represented a loss to the seed bank, no reproduction was possible at this stage, and all individuals had to pass through this stage to become reproductively mature. Tactics targeting rosettes would have reduced the number of rosettes and eliminated the multiplicative effect of these rosettes becoming reproductively mature. Tactics targeting only mature plants would have reduced reproduction in a given year, but would not have reduced the large future reproductive potential of the rosette population.

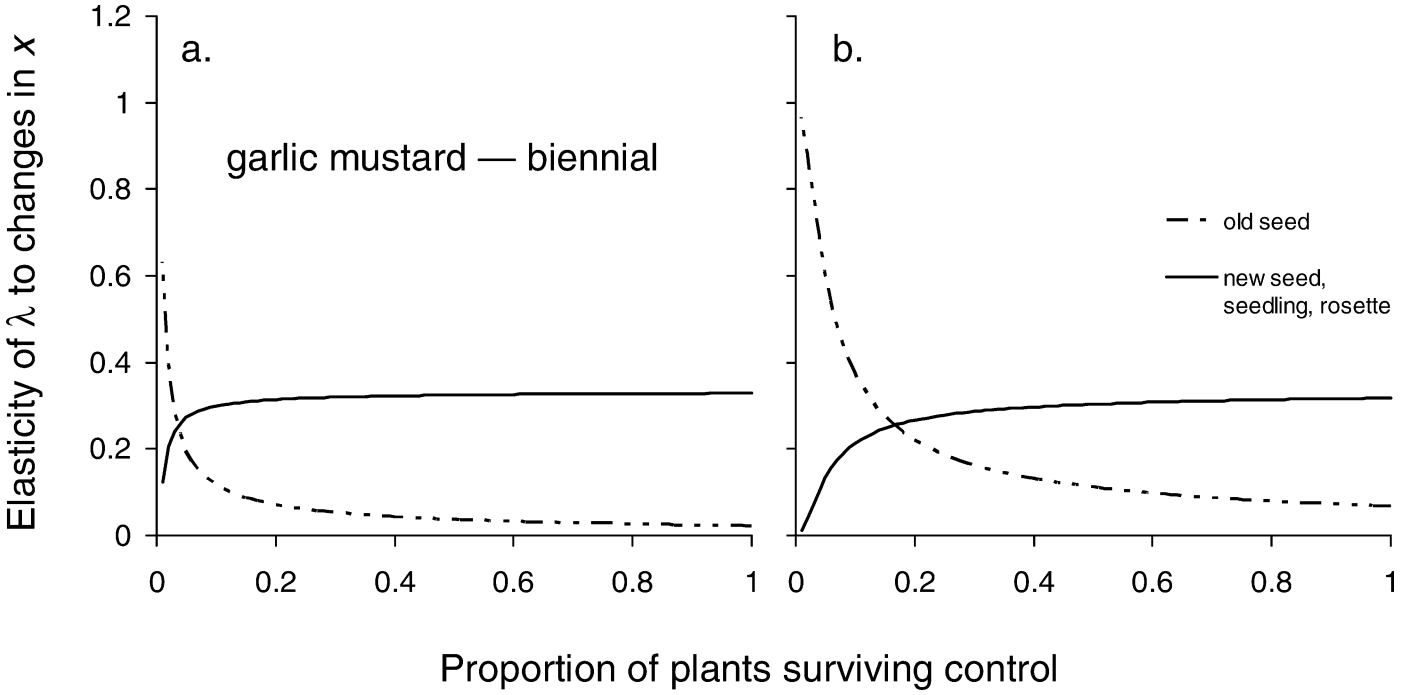

FIGURE 4. The elasticity of garlic mustard population growth rate (λ) to changes in survival of old seed, newly shed seed, seedlings, and rosettes, evaluated at (a) low population density (seeds = 500 m^{-2}, rosettes = 100 m^{-2}, and plants = 8 m^{-2}) and (b) high population density (seeds = 2,200 m^{-2}, rosettes = 384 m^{-2}, and plants = 40 m^{-2}).

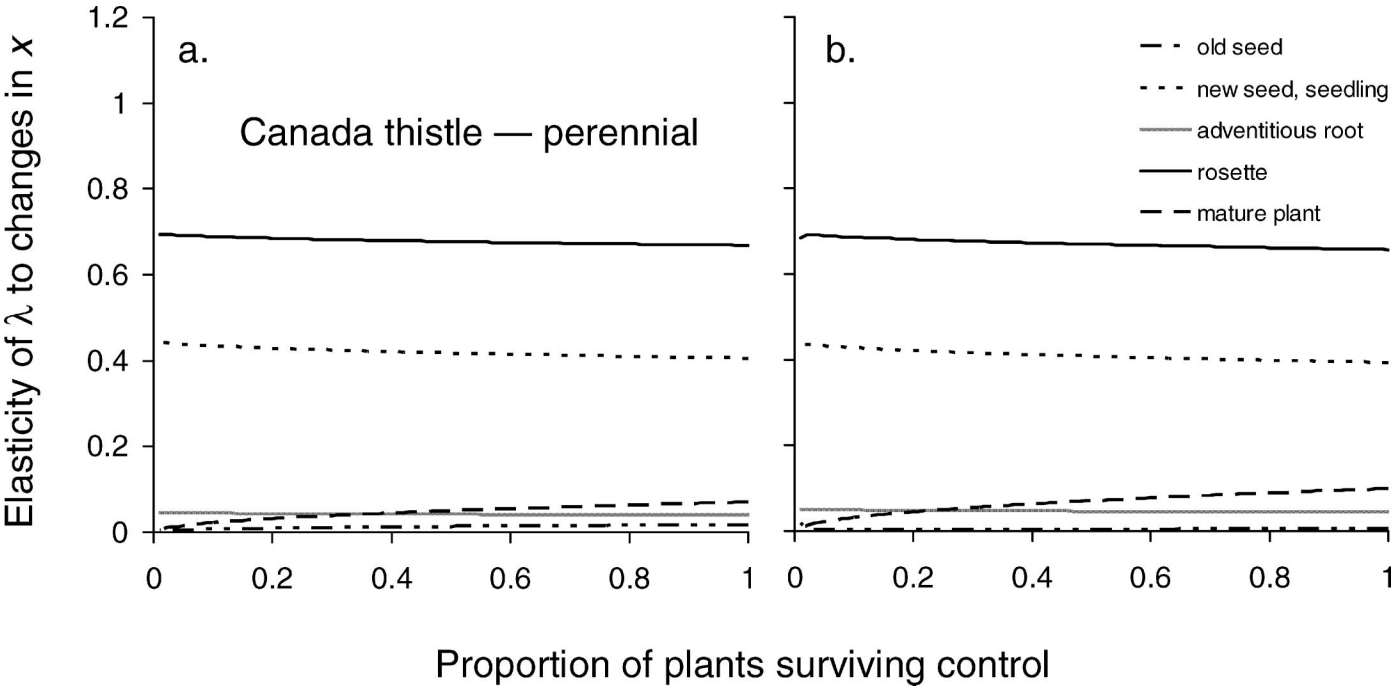

FIGURE 5. The elasticity of Canada thistle population growth rate (λ) to changes in survival of old seed, newly shed seed, seedlings, adventitious roots, rosettes, and mature plants evaluated at (a) low population density (seeds = 500 m^{-2}, rosettes = 100 m^{-2}, and plants = 8 m^{-2}) and (b) high population density (seeds = 2,200 m^{-2}, rosettes = 384 m^{-2}, and plants = 40 m^{-2}).

Implications for Management and Future Research

Using giant foxtail and common lambsquarters as model weed species yielded useful insights for targeting weed seed-bank control in annual weed species. For weed species with modest fecundity and low persistence in the weed seed bank, such as giant foxtail, tactics aimed at controlling overwinter seed bank persistence are proportionally more effective in reducing population growth rate than tactics aimed at aboveground life stages. For weed species with high fecundity and high seed-bank persistence, there is a rough equivalence in the importance of tactics aimed at reducing overwinter seed-bank persistence and tactics aimed at aboveground life stages. When should we target the weed seed bank? For annual species such as giant foxtail and common lambsquarters, it always makes sense. In weed management systems with highly effective seedling control, adding seed-bank management measures may be the best option for further optimization of weed management outcomes.

The elasticity analyses presented here only provide one criterion for targeting weed life stages for control: the relative impact of changes in vital rates on population growth rate. Another obvious criterion for assembling integrated weed management strategies is economic return to management effort (Buhler 2002; Bussan and Boerboom 2001; Cox et al. 1999; Lindquist et al. 1995). Chemical control of weed seedlings dominates contemporary weed management because herbicides are relatively inexpensive and effective when used judiciously. Are there cost-effective measures for reducing weed seed survivorship? Direct interventions for increasing mortality of dormant seeds in the soil seed bank are rare and, currently, too costly for extensive production of field crops (Melander and Jørgensen 2005; Wayland et al. 1973). Cropping system design for increasing postdispersal weed seed predation (Westerman et al. 2006, this issue) and microbial attack of weed seeds (Hallett 2005) may offer a cost-competitive alternative. Another approach to reducing weed seed-bank persistence is to exploit germination biology. One such method is the stale seedbed approach, used to deplete the seed bank before planting crops. A stale seedbed is created by stimulating germination through tillage (Caldwell and Mohler 2001) or use of chemical germination stimulants (Dyer 1995) and eliminating newly emerged seedlings, rather than by attempting to increase mortality of dormant seeds in the seed bank. The development of direct and indirect methods for reducing weed seed-bank persistence is a rich area for further study.

Because tactics for effectively controlling garlic mustard plants on an extensive scale are not yet available, targeting seed-bank persistence would not appear to be an important practice for this species (Figures 4a and 4b). Elasticity analysis indicates instead that techniques for control of aboveground stages are most important. Biocontrol agents that attack the rosette and seed pods of garlic mustard have been identified (Blossey et al. 2001) and are currently in quarantine. Studies are currently underway to create recommendation domains, with respect to regional variations in garlic mustard demography, for the release of these species (Landis et al. 2005).

Aboveground life stages were most important for Canada thistle control, but an interesting feature of the elasticity analysis was the relatively high importance of controlling survival of newly produced seeds. This finding is consistent with previous studies showing successful biocontrol of invasive thistles in North America using predispersal seed predators as control agents (Crawley 1989).

None of this is to say that, armed only with today's available weed management tactics, one should abandon management of aboveground life stages in favor of seed-bank

management. Rather, these results argue the importance of developing more effective means of reducing weed seed inputs to the seed bank and reducing weed seed-bank persistence as complements to seedling control within an integrated weed management system.

Sources of Materials

[1] MATLAB 2004, v. 7.0.1. The MathWorks, 3 Apple Hill Drive, Natick, MA 01760.

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