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Authors: Maxwell, Bruce D., Lehnhoff, Erik, and Rew, Lisa J.

Source: Invasive Plant Science and Management, 2(1) : 1-9

Published By: Weed Science Society of America

URL: https://doi.org/10.1614/IPSM-07-054.1

Invasive Plant Science and Management 2009 2:1–9

Research

The Rationale for Monitoring Invasive Plant Populations as a Crucial Step for Management

Bruce D. Maxwell, Erik Lehnhoff, and Lisa J. Rew*

Many land managers are faced with trying to optimize management of invasive plant species based on budget constraints and lack of knowledge of the true potential of the species. Generally, ''early detection rapid response'' (EDRR) is the assumed best management strategy and tends to drive management regardless of the invasion stage or possible variation in the invasion potential of the population. We created a simulation model to evaluate the optimal management strategy to reduce the rate of invasion of nonindigenous plant species. The strategies were specifically chosen to assess the value of information from monitoring populations. We compared four management strategies and a no-management control over a 20-yr period in the context of a management area: (1) managing a fixed number of populations at random each year (EDRR random), (2) managing an equivalent number of populations along a road each year (EDRR road), (3) managing half of the fixed populations that were determined by monitoring to be sources of new populations (monitoring every year), and (4) managing an equivalent set of source populations only on even years, leaving the odd years for monitoring (monitoring every other year). EDRR random location without regard to population invasion potential, and monitoring every year targeting management on populations determined to be invasive (sources for new populations), were the most successful strategies for reducing the increase in total number of populations. The model simulations suggest that managers could dedicate 50% of their management time to monitoring without risk of accelerating invasions or reducing the impact of their weed management program.

Key words: Invasive species management, metapopulation dynamics, population colonization, information value, early detection rapid response.

Early detection of invasive plant species followed by a rapid management response with the intent to eradicate has become the mantra of most land managers (DiTomaso 2000; Rejmánek 2000; Simberloff 2003). The EDRR strategy is logical and represents an economic optimum approach if detection and eradication probabilities are high (McNeely et al. 2003; Naylor 2000; Rejmánek et al. 2005). Detection and eradication probabilities are likely maximized at ports of entry (e.g., Rejmánek and Pitcairn [2002] documented eradications in California), but as an invasion progresses onto a continent, probability of multiple and frequent introductions at the regional or lower scale areas increases, and subsequent probability of detection and eradication are likely to decline (Myers et al. 2000). Once an invasion has taken hold on a continent, management strategies may be made more efficient by determination of the potential for a species to be invasive based on its traits and the environments available for it to invade (Peterson and Papes 2003; Rejmánek et al. 2005). Determining if a species is invasive can be difficult and requires a few considerations. First, determination of invasion potential must be shifted from a focus on species to a focus on populations of suspect species. Second, populations must be selected for monitoring across the widest array of environments where they have become established. Third, each population must be measured to determine their relative potential to be invasive according to the environments where they were found. The relative invasion potential becomes a prioritization for management of populations in the environments where the species are most

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DOI: 10.1614/IPSM-07-054.1

* Professor, Post Doctoral Research Associate, and Assistant Professor, Department of Natural Resources and Environmental Science, Montana State University, Bozeman, MT 59717. Corresponding author's Email: bmax@montana.edu

Interpretive Summary

Land managers are often challenged with invasive plant management budgets that will not allow treatment of all the populations in a management area. Our limited informal survey of managers indicated that most invasive plant species management is driven by the desire to manage as many populations as possible in a growing season following the EDRR philosophy. Thus, using the efficiency of travel, invasive species populations are treated primarily along roads without regard to their potential for further spread or stage of invasion. Furthermore, conventional thinking is centered on the idea that managing fewer populations by taking time to monitor to detect source populations will only increase the rate of invasion by not maximizing the number of populations managed. If populations of invasive species represent a range of invasion potentials, then one can assume that there may be value in determining which populations are more likely to be sources of further invasion. The simulations conducted with our model conservatively suggest that monitoring populations to identify source populations will not hamper invasive species management under budgets that only allow portions of the total populations to be managed. These simulations also suggest that efficient evaluative techniques for identifying source populations could improve management of species that have recently arrived in a management area. There may be a narrow window of opportunity where the metapopulation is small enough and detectable, and the invasion has not progressed too far, where EDRR will be a successful approach to management. The simulations suggest that EDRR will only be successful if at least 67% of the patches of an invasive species can be found and eliminated. The value of monitoring increases as the ability to detect populations decreases. Therefore, land managers may be wise to adopt a new mantra: ‘‘early detection, rapid monitoring, and thorough management.’’

invasive. Measurements of invasive potential of a population would include determining if the population is a source for new populations (colonies) and assessing changes in density and changes in spatial extent of the population (Lehnhoff et al. 2008).

The ‘‘tens rule’’ suggests that only 10% of the species reaching a new area will be able to grow, but maybe not reproduce in the new environment. Only 10% of those species that can survive in the new environment will become naturalized, and only 10% of those will become invasive (Williamson and Fitter 1996). Thus, the tens rule suggests that there is variation in the invasion potential of introduced species. The lag phase suggests that invasion potential may change over time, where a species may undergo evolutionary changes or reaches an ecological threshold where it becomes invasive (Dietz and Edwards 2006; Hobbs and Humphries 1995). Regardless, the variation in invasion potential coupled with the common constraint of limited budgets for invasive plant management drives a need for prioritizing populations for management. Populations of any species, invasive, rare, native, or nonnative, show variation in their growth rates across different environments (Crawley 1997; Mack et al. 2000; Williamson and Fitter 1996). The knowledge of variation in population dynamics within a species prompts the question of how one may focus management on the populations that present the greatest potential for creating new populations to maintain the invasion (Gilpin 1990).

Management focused on eradication of weed populations has had some limited success at the early stages of invasion (Myers et al. 2000; Rejmánek and Pitcairn 2002). However, management of invasive plants has rarely caused local, let alone total, eradication once invasions have reached regional scales (e.g., present in more than 1,000 ha [2,471 ac]) (Rejmánek and Pitcairn 2002). The eradication strategy is almost exclusively implemented with use of herbicides. Unfortunately, the predominately used herbicides tend to be only moderately selective (Cota 2004). Therefore, the management runs the risk of removing the native species that might be most likely to provide overlap in resource use and phenology and therefore represent the greatest competition for the invasive species (Hobbs and Humphries 1995; Zavaleta et al. 2001). Evaluation of different control practices and their impact on the invasive species and the surrounding ecosystem is another crucial part of invasive plant prioritization (Rew et al. 2008). Cost-benefit analysis needs to be conducted with quantitative assessment that considers not just the impact of the invasive species, but also the impact of the management on the nontarget environment.

Prioritization of invasive plant species populations for management through monitoring could be an important step in conducting cost-benefit analysis. Field comparison of management strategies with appropriate controls and replication across environments would be prohibitive. Therefore, we initiated a simulation study to determine under what conditions population prioritization with its associated cost could improve invasive plant species management once an invasion is regionally established but in the early stages of local invasion. Our specific objectives were to compare four management strategies and a no-management control over a 20-yr period on a simulated region with different numbers of initial invasive plant species populations (patches). The management area was meant to simulate a ranch, county, U.S. Forest Service, Bureau of Land Management, or U.S. National Park Service District where most of the nonfarm invasive plant management decisions are made. We made specific assumptions about the potential of populations to be sources of new populations and to go extinct naturally and with management. We compared the following four strategies for managing 15 (early invasion) and 30 (late invasion) initial populations in a virtual management area:

(1) Managing 10 randomly located populations per year in the management area. This strategy is equivalent to the EDRR, but does not constrain the location of populations selected for management.

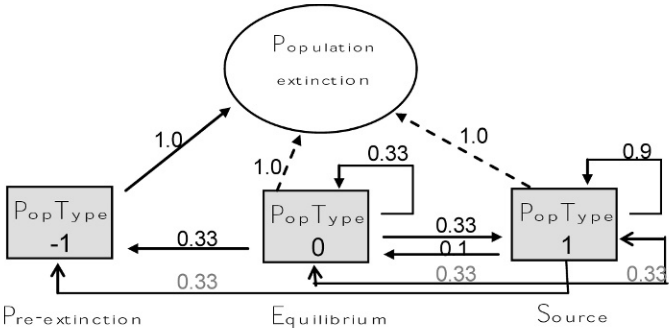

Figure 1. Diagrammatic model of the metapopulation model, with three states or population types (-1 = pre-extinction, 0 = equilibrium, +1 = source of new populations), transitions (solid arrows with filled points) with probability of annual transition values above, annual creation of new populations from source populations (solid arrows with open points), and annual response to management (dashed arrows) with transition probabilities above.

(2) Managing 10 populations per year at random along a road. This strategy follows the logic of EDRR but constrains the location of populations selected for management to roads. This may be the most commonly applied strategy for invasive plant management.

(3) Managing 5 randomly located populations per year that were determined by monitoring to be sources of new populations. This approach places emphasis on monitoring populations and assumes that source populations can be distinguished from other population types. In addition, management is restricted to the source populations once they are identified. Unfortunately, identification of the source populations through monitoring requires time so only half of the populations can be managed when monitoring occurs under a fixed budget.

(4) Managing 10 randomly located source populations only on even years, leaving the odd years for monitoring, was the final strategy considered.

Therefore, we assumed a constant budget for managing the species and manipulated the amount of time dedicated to management to stay within the set budget. This removed the need for assigning costs to the control and monitoring activities.

Thus, we could compare the overall efficacy of the different proposed management strategies by comparing the number of populations of the invasive species in the management area over time as a result of each management strategy. We were then able to knowledgeably formulate hypotheses about optimal management by varying the assumptions about the populations and their potential to be invasive, to determine how each influenced the management outcomes.

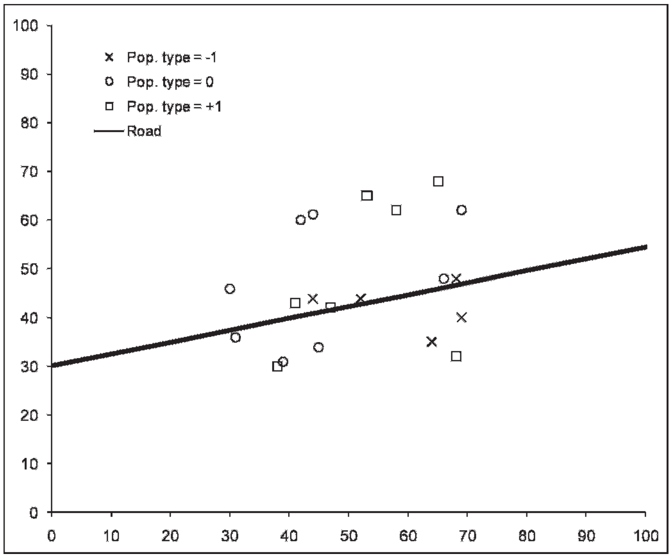

Figure 2. Random location of 15 initial populations (patches) and road (line) running through a virtual management area.

Materials and Methods

A simulation model was designed to include a minimum set of key processes to make objective comparisons among management strategies (Figure 1). A simulated management area was created where initial populations (15 or 30) were distributed at random in the central portion or along a road of a 100 by 100-cell map of a management area (Figure 2). Simulations resulted in a growing number of populations spatially expanding from the initial source populations.

The general form of our models followed that of Valverde and Silvertown (1997). Populations were classified as one of three types: PopType = -1, those that had become established but were going to go extinct naturally in the next year; PopType = 1, source populations that could produce up to two new populations each year (invasive); and PopType = 0, populations that were in equilibrium (neither going extinct nor sources of new populations) (Figure 1). Twenty viable propagules were produced per source population per year. Successful colonization of new populations from the propagules at a location was determined according to a modified Weibul dispersal kernel (probability distribution) (Kot et al. 1996) (Equation 1).

$$N = e^{\left(a - b\sqrt{d}\right)} \qquad [1]$$

Where N is the density of individuals at distance (d) from the source and converted to a probability by $p_{new}(d) = N/(1 + N)$. The parameter a was set to 5 and b to 3 for short-distance dispersal simulations, and b to 2 for long-distance dispersal simulations. Distance from source (d) was calculated for each nonoccupied map cell within a 25-

pixel-radius neighborhood, then used to calculate the probability of a new population ($p_{new}[d]$). Long-distance dispersal simulations reduced the number of viable propagules dispersed from source populations to 5. The number of viable propagules (20 or 5) and the dispersal neighborhood size were selected to create metapopulation growth rates (λ_M) that ranged from 1.0 to 1.2 which spanned empirical estimates for an herbaceous plant species that was not regarded as invasive (Valverde and Silvertown 1997). New populations had equal probability of becoming classified as one of each of the types described above and were distributed to unoccupied locations. This assumption could be equivalent to no habitat preference or effect on potential for a population to be a source of more colonies.

Populations of type −1 in 1 yr would always go extinct in the next year. Populations of type 0 in 1 yr had an equal chance of becoming one of the other types (−1 or 1) or remaining type 0. Populations that were of type 1 in the current year had a 10% probability of becoming type 0, otherwise they remained of type 1 (Figure 1). All transitions between population states were held constant over time, and metapopulation growth rates (n_{t+1}/n_t, where n was the number of populations in the management area at time t) over the 10-yr simulation period were calculated as the geometric mean (Equation 2) of the growth rates between each year (Valverde and Silvertown 1997).

$$\lambda_M = \sqrt[9]{\prod_{t=2}^{t=10} \frac{n_{t+1}}{n_t}} \qquad [2]$$

where λ_M is the metapopulation growth rate ranging from 0 to ∞ and was used to compare the different management strategies (Freckleton and Watkinson 1998).

A road was placed on the map as a straight line that would approximately bisect the initial infested area to ensure that some populations would occur along the road (within 1 map unit north or south of the road). All replications of the simulation runs were started with the same initial population distribution (Figure 2). The model continues to add populations to the map until the map is fully occupied (after approximately 130 yr). There is no density-dependence; only eventual space limitation decreases the metapopulation growth to equilibrium ($\lambda_M = 1.0$). Thus, we restricted our simulations of metapopulation behavior to the early stages (first 20 yr) of an invasion to retain realistic assessments of the selected management strategies.

Model parameters were set to create early and late invasion scenarios with a range of metapopulation growth rates to determine the conditions where each invasive plant management strategy would have greatest success. Simulations were conducted with 15 and 30 initial populations representing early and late detection of invasion, respectively. The initial population numbers represent 0.15 and 0.3 percent cover of the management area. Such frequencies are within the observed range (0.002 to 4.98%) for 20 nonnative herbaceous dicot species sampled over 134.6 ha in the northern range of Yellowstone National Park (Rew et al. 2004). Percent infested, however, is not a useful characterization of the initial conditions of the metapopulation for the simulations that we conducted. Absolute number of populations and the proportion of those managed are the more useful characterizations for the early phases of invasion that were the focus of this study. The initial proportion of populations managed at the initiation of the simulation period was 67% with the early invasion scenario (15 populations) and 33% with the later invasion scenario (30 populations). Initial populations were divided into 25% classified as going to extinction (PopType = −1), 35% as sources of new populations (PopType = +1), and 40% as at equilibrium (PopType = 0). Initial populations were placed either randomly but towards the center of the management area, or within one map cell on either side of the road. Variation in metapopulation growth rate was accomplished by varying the number of viable propagules released from source populations from 5 (mean $\lambda_M = 0.96$) to 50 (mean $\lambda_M = 1.3$). These propagule numbers may seem low, but because of the model assumption of equal habitat quality across the map, the number of successful colonizations per propagule was high, making up for the low number of propagules.

The model operated under the assumption that management of the populations would result in them going extinct (i.e., management had 100% efficacy) regardless of the population type. The set of management strategies selected for comparison, as well as the initial conditions, represent a range of scenarios and approaches currently practiced or that could be implemented. Management success was evaluated based on the number of populations maintained in the management area and the metapopulation growth rate over a 20-yr simulation period. Metapopulation growth rate was considered the superior measure of management strategy performance because it more realistically characterized metapopulation dynamics under the model assumption of static transitions, which lead to exponential growth (Freckleton and Watkinson 1998). We compared four strategies for managing populations in the management area. The first strategy selected 10 populations per year at random locations to manage. This strategy represents selecting 10 populations regardless of their type (−1, 0, or +1) and making them go extinct (eradication). This strategy was referred to as the EDRR approach with the caveat of no constraint with regard to the spatial location of populations selected for management. The second strategy managed 10 populations per year regardless of type at random locations except they had to be within one map unit of the road. This represents a common EDRR strategy implemented by land managers of just treating populations along roads. The third strategy managed 5 population per year that were determined by monitoring to be sources of new populations (population type = +1). The critics of monitoring populations believe that the time and money taken for monitoring would be better spent directly on managing populations. Thus, this strategy tests the alternative to the more conventionally accepted EDRR approaches to management. The fourth strategy managed 10 source populations only on even years leaving the odd years entirely dedicated to monitoring. Thus, this strategy is an alternative in support of monitoring but applied differently over time.

All simulations were replicated 50 times for each management strategy including "no management" as a control. The mean and standard deviation in number of populations of the invasive species in the virtual management area were tracked for each of the 10 replications and for 20 simulation years. Variation in population numbers is a result of the probabilistic form of the model using uniformly distributed random values between 0 and 1.0, to determine if a transition event occurred or a particular population type was selected. Inconsistent distributions of numbers of populations resulting from different management strategies restricted the use of standard statistical comparison among treatments after 6 and 12 yr of simulated time. Therefore, the actual distributions from 50 replications of each strategy were used to determine the probabilities of difference between key strategies using bootstrap sampling of the distributions, and tallying the proportion of results when a value from a strategy was less than the no-management control or managing 10 populations of random type along a road (EDRR road) which was regarded as the "standard" strategy.

Monitoring was assumed to be omniscient in identification of source populations, but required the same amount of time and money required to manage an equal number of populations. For example, if the land manager has a budget to manage 10 populations per year and crews were allowed to monitor populations half the time, they could discover 5 source populations with the monitoring, but only have time and budget remaining to manage 5 populations. There was concern that monitoring could not possibly identify source populations immediately; therefore, the model was modified to assume that monitoring would not successfully identify 5 source populations until after year 3. In year 1, it was assumed that the 5 populations to manage would be selected at random regardless of their type, and in year 2, only 2 source populations could be identified and the rest would be selected at random. Year 3 through 20 would select 5 source populations. Similar logic could be applied to the EDRR random strategy because it would likely take longer to find populations away from the road than along the road. However, this situation could be highly variable, and dependent on the vegetation type and how it could restrict viewing. Thus, no penalty was issued on number of populations to manage when they were located away from the road.

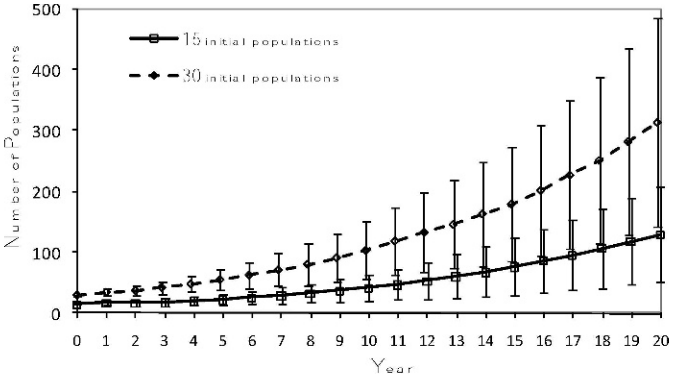

Figure 3. The total population numbers in the simulated management area, including one standard deviation–error bars, as a result of 10 replicate simulations of 20-yr periods with 15 and 30 initial populations and no management.

The model was coded in Microsoft Visual Basic as a macro in Excel and is available from the corresponding author.

Results and Discussion

Simulated metapopulations with no management increased exponentially from 15 or 30 initial populations in the management area (Figure 3). Initial population number in the management area had little influence on the unmanaged metapopulation growth rate (λ_M was 1.127 starting with 15 populations, and 1.124 starting with 30 populations). The no-management control always resulted in the greatest number of populations in the management area, and in the highest λ_M.

Management of populations was only able to slow the invasions (not cause decline) over the 20-yr simulation when starting from an early detection scenario (15 populations) or a later detection scenario (30 populations). When detection was allowed to occur earlier in the invasion ($\leq$ 10 populations), some management strategies could consistently drive the metapopulation to extinction or set it on a trend to extinction. The EDRR that restricted management to roadsides was the least effective management strategy for reducing the number of populations, regardless of the initial conditions or parameter value changes. This result was disconcerting considering the prevalence of management restricted to roadsides. Managing 10 populations per year of unknown type along the road had only a 0.54 probability of reducing the number of populations, more than no management after 6 yr, and 0.55 probability after 12 yr (Table 1). Managing 10 populations per year of unknown type (EDRR random), but not restricted to the roadside, was consistently the most effective strategy for reducing the number of populations in the management area over the first 10 yr (Figure 4).

Table 1. Metapopulation growth rates for each management strategy, and the probability that management strategies would allow fewer populations than no management and the standard management approach (random populations managed along roads). Simulations assumed short distance dispersal and 15 centrally located initial populations in the management area.

		Year 6		Year 12	
Treatment	λ_M	Probability strategy < no management	Probability strategy < standard	Probability strategy < no management	Probability strategy < standard
No management	1.127	—	0.46	—	0.45
Eradicate 10 random populations/year	1.048	0.99	1.00	0.98	0.98
Eradicate 10 random populations along road/year (standard)	1.124	0.54	—	0.55	—
Eradicate 5 source populations/year	1.006	0.97	0.97	0.98	0.99
Eradicate 10 source populations on even years	1.051	0.89	0.89	0.89	0.90

However, managing 5 source populations per year using monitoring to identify the source populations became the most effective strategy for reducing the number of populations in the management area after 10 yr (Figure 4). The monitoring to detect and manage source populations every year was the only strategy that reduced the metapopulation growth rate to near equilibrium (λ_M = 1.006) over the 20-yr simulation for the early invasion scenario (Table 1). It was assumed that half of the time dedicated to invasive plant management, crews were making measurements that would allow determination of which populations were sources of new populations, and using that knowledge to restrict management to the source populations. The simulations suggested a 0.98 probability that managing 5 source populations per year would reduce population numbers more than no management after 12 yr, and a 0.99 probability that it would reduce populations below the standard approach of managing 10 populations per year of unknown type along the road (Table 1). The simulations suggest that the strategy of using half of the management time for monitoring was not as effective for reducing the number of populations if management was only conducted on even years, and odd years were totally dedicated to monitoring. When initial number of populations was increased (Figure 5), or initial populations were restricted to occur along the road (Table 2), the monitoring and managing of 5 source populations continued to be the most effective strategy for slowing the invasion if the simulation was run for more than 10 yr.

The results were consistent when dispersal distance was varied and metapopulation growth rates were held between

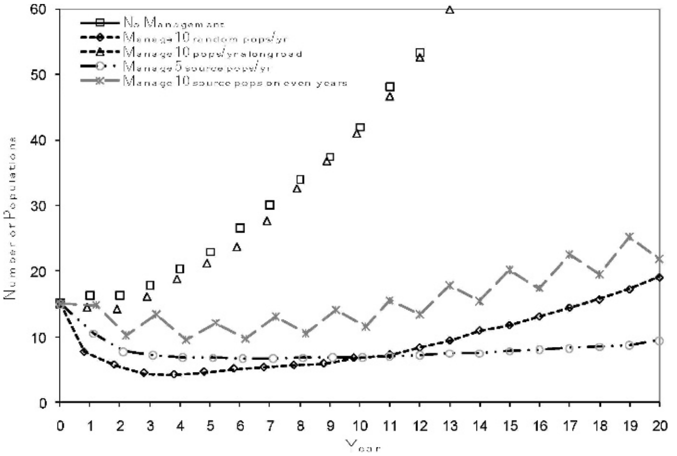

Figure 4. Mean population number in the management area in response to different management strategies simulated with 15 initial populations randomly distributed in the center of the map.

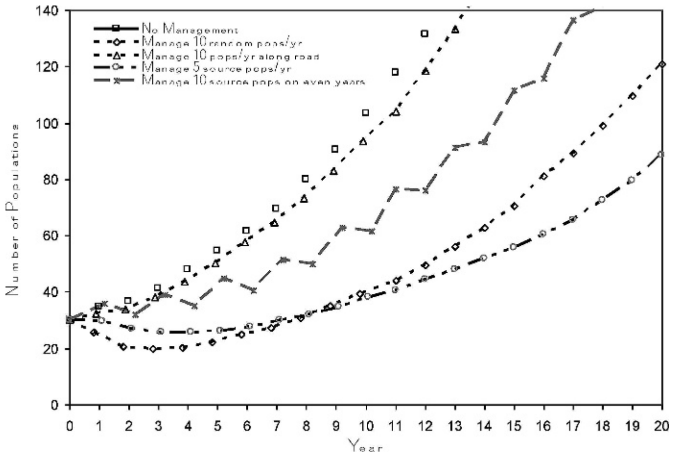

Figure 5. Mean population number in the management area in response to different management strategies simulated with 30 initial populations randomly distributed in the center of the map.

Table 2. Metapopulation growth rates for each management strategy, and the probability that management strategies would allow fewer populations than no management and the standard management approach (random populations managed along roads). Simulations assumed short distance dispersal and 15 centrally located initial populations along the road in the management area.

Treatment	λ_M	Year 6		Year 12	
		Probability strategy < no management	Probability strategy < standard	Probability strategy < no management	Probability strategy < standard
No management	1.122	—	0.21	—	0.22
Eradicate 10 random populations/ year	1.054	1.00	0.94	0.99	0.94
Eradicate 10 random populations along road/year (standard)	1.108	0.79	—	0.78	—
Eradicate 5 source populations/year	0.965	1.00	0.94	1.00	0.96
Eradicate 10 source populations on even years	1.040	0.94	0.75	0.96	0.84

1.0 and 1.3 (data not shown). Simulation results starting with 15 populations distributed along the road indicated some improvement in the standard road management strategy (Table 2). The probability of management restricted to the road reducing the population below that of no management increased from 0.55 to 0.78 after 12 yr of simulated invasion. The initial roadside distribution of populations may simulate the earliest stages of invasion, where the road serves as a vector of introduction, but new populations disperse away from the roadside. The management strategies that included monitoring and managing source populations every year, or randomly choosing populations to manage without regard to their location (EDRR random), continued to be most effective for reducing the number of populations and decreasing the metapopulation growth rates over the 20-yr simulation (Table 2). If the habitat for the invasive species was restricted to the roadside, the road limited management strategy may perform much better relative to the other strategies (simulations not conducted).

Results presented thus far indicate little difference between the EDRR random location management approach and the monitoring and managing source populations approach in the first 10 yr following initiation of management. Further simulations were conducted to determine under what unmanaged metapopulation growth rates and initial conditions one of these management approaches may be more likely than the other to reduce the metapopulation growth rate. Metapopulation growth rate was varied by increasing the number of viable propagules dispersed by source populations, and the metapopulation growth rates in response to EDRR random, and monitoring and managing source populations every year, were compared (Figure 6). The results suggested that the monitoring and managing source population strategy may be more effective than the EDRR random strategy for metapopulation growth rates between 1.05 and 1.15 over a 20-yr management period (Figure 6). It is not clear how significant the differences were between metapopulation growth rates in the range $\lambda_M = 1.0$ to 1.2, but improved methods to monitor metapopulation growth rates may help identify which of these two strategies may be most effective for management of an invasion. The simulations suggested that if newly introduced populations can be identified early enough, and a high proportion of them (> 67%) can be controlled (made to go extinct) then knowledge of which populations are sources (monitoring) will not be as valuable for managing the metapopulation. The simulations clearly demonstrated the reliance of the EDRR random management strategy on early and high population detection rates and high management efficacy (population removal), if budgets restrict the number of

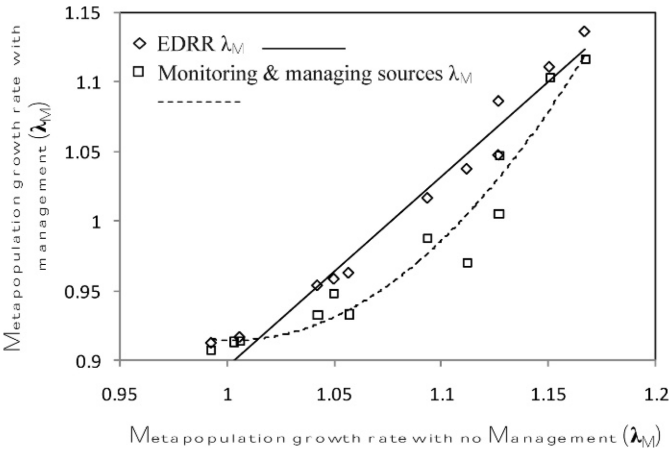

Figure 6. Metapopulation growth rates in response to the early detection rapid response (EDRR) random, and the monitoring and source population management every year strategies, plotted against metapopulation growth rate without management for 20 yr with 15 initial populations, short distance dispersal, and 25 viable propagules produced annually by the source populations.

populations that can be eradicated. These aspects may not be easy to achieve, and thus further support the value of targeting management based on knowledge of the potential of population to be sources of further invasion (monitoring).

Results of the simulations consistently indicated that monitoring to identify source populations, even with delay in the success of monitoring and only being able to manage half the populations, was an effective strategy when detection limitations allowed more than 10 populations to be present before initiation of management. When simulations were started with less than 10 populations, the EDRR random and the monitoring and management of source population approaches would frequently cause total extinction, supporting both strategies. However, detection would become limiting as more populations were able to become established, particularly away from the roads. Thus, the value in identifying source populations increased as the number of years of simulation was increased. Early detection is, by definition, plagued by the fact that the species occurs with low frequency and thus becomes increasingly costly to detect in the early phase of an invasion. Thus, invasions may rarely be detected early enough for EDRR to be the most effective strategy for reducing the invasion rate into a management area. Even with the penalty of not being able to manage as many populations because time is committed to monitoring, the value of knowing which populations are sources and would thus be the target of management becomes more valuable as an invasion progresses.

The success of the monitoring based strategy is dependent upon the ability to efficiently and rapidly differentiate between source and nonsource populations. If source population occurrence could be correlated with environmental variables that are easy to map, and thus allow the ability to interpolate monitoring results across management areas and regions, then the number of populations managed could be increased over time on the fixed budget, and the strategy may be even more effective. These dependencies define a research agenda that includes development of field methods that will efficiently quantify the invasion or source potential of populations, and determine the ability to interpolate results.

The model used for the above assessment of invasive plant monitoring and management strategies has several limitations that should be considered along with the conclusions that have been drawn. The model does not consider spatial heterogeneity or habitat preference in the management area and it does not directly combine the influence of existing populations on the probability of new populations. In addition, the model is limited by artificial classification of the population types, when in reality, populations represent a continuum of invasion potential (Mack et al. 2000). The model predicts exponential unregulated invasion, but includes the equally unrealistic, but offsetting assumption, of eradication of all managed populations. The transition rates between population types could be altered, but without empirical base we chose to assume equal transition rates between population types. The management approaches that include monitoring assume a cost associated with monitoring, but no cost was assumed for finding populations away from the road (EDRR random strategy). The model limitations tend to be offsetting, and thus are unlikely to change the generalized result, but they restrict use of the model to predict species-specific dynamics because the parameters do not lend themselves to empirical derivation.

Acknowledgment

The authors would like to thank the USDA-ERS PREISM Program for funding of this project, Cooperative Agreement Number: 433AEM-4-80111.

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Received November 28, 2007, and approved September 18, 2008.