Risk analysis and management decisions for biological control agents:

Perspectives from theoretical ecology

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INTRODUCTION

Although estimates vary, there is broad agreement that invasive species impose major costs on the U.S. economy. The USDA FY 2001 budget for invasive species activities alone exceeded $580 million. In addition to direct economic damages, invasive species can disrupt the provision of non-market environmental goods and services (e.g., by adversely impacting water quality) or present risks to public health (e.g., West Nile Virus). Although the total area affected is uncertain, the Bureau of Land Management estimates that over 4,000 new acres are lost to the spread of invasive weeds each day on all western public lands. Due to the widespread distribution of invasive plants on extensively managed lands, conventional weed control technologies (chemical pesticides or physical removal) are often impracticable, uneconomic, and/or ineffective. Biologically-based controls offer many advantages in the effort to develop ecologically sound and sustainable approaches to the long-term management of destructive invasive plant species; however, biological control is also not without risk. Furthermore, given the complexity of ecological interactions, the efficacy of biological control agents for controlling plant pests or noxious weeds is more difficult to evaluate and demonstrate than the more predictable effect of pesticides, for example. Therefore, the use of any non-indigenous organisms must be developed, evaluated and used in a wise and effective manner.

Since the 1950s, the regulatory approach to permitting decisions regarding the release of biological control agents has been safety assessment. This assessment has consisted primarily of host range analysis to determine whether the proposed agent could feed or oviposit on non-target species. In most cases, however, absolute safety is unattainable. The host range of the proposed agent may be uncertain or known to include non-target species. In order to be efficacious, a biological control agent must attain a viable population size, either through replenishment or natural reproduction. Uncontrolled growth of the biological control agent population, however, may pose the potential for adverse effects on non-target species or ecosystem functions, either directly

or indirectly. Similarly, spread of the biological control agent beyond the target site may have unintended negative consequences. The Plant Protection Act of 2000 recognized both the potential negative consequences and beneficial aspects of biological organisms to control plant pests and noxious weeds. Consequently, the regulatory criteria are expanding to consider both the risks and benefits of proposed environmental introductions of biological control agents for the management of invasive plant pests and noxious weeds.

In spite of concerns over its effectiveness, over the irreversibility of biocontrol releases, and over potential unintended effects on desirable non-target plants (Simberloff and Stiling 1996; 2003), biological control remains a highly cost-effective means for controlling invasive weeds on regional scales not amenable to chemical control methods (Hill and Greathead 2000). With the increasing threat of biological invasions due to continuing globalization of the economy (Williamson 1996), the recognition of the threats posed by invasive species to our nation's biotic heritage (Pimentel, Glenister et al. 1984), and with the elevation of the priority of invasive species in both the domestic and international policy arenas, the demand for continued effective biological control measures is not likely to diminish. However, given the concerns mentioned above, there is a clear need for more effective risk analysis methodologies for biological control agents (Simberloff and Stiling 1996; Lonsdale, Briese et al. 2001; Louda, Pemberton et al. 2003).

These methodologies, to be both effective and efficient, will need to rely heavily on quantitative methods including ecological modeling and results from theoretical ecology. These types of methods have proven useful in other applications (Morris and Doak 2002; Pastorok, Bartell et al. 2002) Mathematical and simulation models provide the best way to integrate information from multiple studies on potential biological control agents, and to provide a firm basis in ecological first principles for formulation of release programs. In addition, mathematical and simulation models are the only way to extrapolate known information to the regional scale, which is essential for successful

biological control.

In this paper I briefly review established guidelines for environmental risk assessments in general as well as the state of the science in risk assessment for biological agents proposed for release to control invasive plants. The specific scope of this document covers insects to be introduced for the biological control of invasive plants (i.e., weeds); this excludes biocontrol agents for insect and other pests, as well as pathogenic biocontrol agents (e.g., mycoherbicides). I also review some results from theoretical ecology that might prove useful in risk assessment for biological control agents. I then synthesize these three themes by presenting a brief hypothetical example which shows the relationships among the established ecological risk assessment framework, screening processes for biological control agents for invasive plants, and general principles of ecological theory. I conclude with some recommendations for the conduct of risk assessments for biological control agents. My goal is to provide independent scientific input for the formulation of methods and processes for risk analysis of biological control agents to ensure that the analytic processes used are firmly rooted in sound scientific principles.

THE STATE OF THE SCIENCE

Ecological risk assessment

The process of ecological risk assessment was established by the U.S.E.P.A. (1992) as a way to evaluate the chances of adverse environmental effects of exposure by environmental receptors to various stressors. Typically, the stressors considered are various toxic chemicals, and the adverse effects are toxic effects on the receptors, which are individuals or populations. In the case of biological control agents, the control agents themselves are the stressors, the receptors are non-target host plants, and the effects to be evaluated are adverse effects on native species.

Chemical risk assessments are always directed at a particular assessment endpoint, such as response of growth or fecundity to toxicity. These endpoints are

typically focused on effects of chemical contaminants on individuals. However, since the quantities of interest are usually population-level effects (i.e., changes in abundance), ecological models are often used to perform the necessary extrapolation from the measurement endpoint (e.g., a toxic or teratogenic effect) to the assessment endpoint (the environmental characteristic or feature that is to be protected from risk, such as the abundance of some sensitive species).

There are four phases recognized in the process of ecological risk assessment, as follows:

1) Problem formulation: In this phase, one identifies the features of the system, the stressors and receptors present in the system, the endpoints that will be considered. In addition, one must carefully formulate a conceptual model of the system (cite Landis), and specify questions and objectives.

2) Exposure analysis: In this phase, the mechanisms of contact between stressor(s) and receptor(s) are characterized, and the magnitude and frequency of contact are assessed. For most risk assessments, exposure analysis will include a GIS component or some other spatially-explicit analysis.

3) Effects analysis: In this phase, the effects of stressors on receptors are estimated, often based on toxicity thresholds or exposure-response relationships. The effects analysis phase also includes that process of hazard identification, and may conclude with hazard identification for some types of discrete endpoints.

4) Risk characterization: Finally, the effects and exposure analyses are integrated to obtain an estimate of the probability of a negative effect on the receptor. In addition, it is important to assess uncertainty, confidence in the results, and the ecological significance of any risks identified.

In this document, we advocate the position that the process of risk assessment for weed biological control agents would be substantially improved by following the basic outline of the process of ecological risk assessment. Such a process would, as mentioned above, consider the biocontrol agent to be the stressor and non-target host plants to be the

receptors. The measurement endpoint might be some measure of damage to or oviposition on the non-target host.

Specific risks of weed biological control agents

What sorts of exposures and effects can be expected to be identified in risk analyses of biological control agents? The typical effects are most likely to be oviposition and damage on non-target plants by the control agent, leading to mortality of individual non-target host plants and possibly to reduced viability of local populations of the non-target host species. Here we briefly outline some of the identified patterns in these hazards, following closely the review of Louda et al. (2003).

A broad range of severity of non-target effects has been identified in those cases in which non-target effects have been documented (Simberloff and Stiling 1996; Louda, Pemberton et al. 2003). Although near relatives of the target pest host plant are the most likely non-target hosts, indirect effects on many plant species are possible if biological control agents alter plant competitive hierarchies or patterns of resource availability and use (Lonsdale, Briese et al. 2001; Louda, Pemberton et al. 2003). Classical biological control agents, to be effective, must have good dispersal ability; this implies that successful agents will almost inevitably disperse away from the agroecosystems in which they are usually released, and into natural areas in which they may encounter populations of threatened or endangered plant species.

For these reasons, the usual host-specificity studies, although useful, are not sufficient to adequately characterize the risks of introductions of weed biological control agents (McEvoy 1996). Even given the rather obvious suggestion that generalist control agents should be avoided (Lonsdale, Briese et al. 2001; Louda, Pemberton et al. 2003), there is still a need for better testing of proposed control agents, using more kinds of ecological, behavioral, life-cycle, and genetic information (McEvoy 1996; McEvoy and Coombs 1999; Schaffner 2001). These data must be integrated into population-level assessments of the risk of non-target effects, and risk criteria should be used in the

selection of agents (Simberloff and Stiling 1996). The results presented here are intended to provide some specific guidance for specific types of data that need to be collected, and how they could be integrated into a comprehensive risk assessment.

Insights from theoretical and empirical ecology

Plant-herbivore interactions

The complex interactions between herbivory of various types and other biotic and abiotic factors greatly influence plant community structure and persistence. Huisman and Olff (1998) found that multi-species interactions play an important role in terrestrial plant-herbivore systems. Using an ecosystem featuring a small plant species and a tall plant species (favored by increased soil productivity), and a generalist herbivore and specialist herbivore (dependent on the small plant species), the authors reviewed field data and constructed a multi-species plant-herbivore model. In the absence of the generalist herbivore, the tall plant species out-competes the smaller species and becomes dominant, resulting in disappearance of the small plant and its specialist herbivore. With the inclusion of the generalist herbivore, the two plant species no longer compete for light, and all species in the model coexist. Thus two herbivore species acting together influence plant community dynamics (Huisman and Olff 1998).

Along the same lines, Van de Koppel et. al. (1996) show that nutrient enrichment can destabilize or destroy plant-herbivore systems. They use field data from a salt marsh along with plant-herbivore models to examine grazing and plant standing crop in areas of differential productivity. In highly productive areas of dense vegetation, grazing pressure remains low due to low herbivore foraging efficiency (no large herbivores occur in this system, and small herbivores like rabbits have difficulties in thick plant cover). Here, plants in productive areas do not experience herbivore control and a strong feedback loop between reduced herbivory and increased plant growth exists. With the introduction of cows into highly productive areas, small herbivores returned to these areas after the cattle removed dense vegetation. Again, the presence of a generalist herbivore can affect the structure and diversity of a community.

Herbivory can influence plant communities through a “feedback loop” in which herbivores affect the success and location of plants. This in turn affects the foraging behavior of herbivores and causes repetition of the cycle (Seabloom and Riechman 2001). In a model of the effects of gopher feeding patterns on annual plant distribution and gopher foraging efficiency, the authors document increasing plant abundance with increasing gopher density and a concomitant increase in gopher foraging efficiency. In contrast, Weisberg et. al. (2002) modeled an elk-plant system and showed that increased elk numbers reduced the biomass of palatable plant species and intensifies intraspecific competition.

Many studies have helped illumine the effects of resource availability on herbivory and plant community structure. Sarkar and Ray (1993) use a mathematical model of a resource-based plant-herbivore system with nutrient recycling to illustrate how the supply rate of external resources combined with both herbivore mortality rates and loss of plant biomass shape the dynamics of the system. For small perturbations of an assumed plant-herbivore “steady-state”, the system will return to equilibrium provided the supply rate of external resources falls between two definite threshold values. If the herbivore mortality rate reaches a critical value for which the supply rate of external resources reaches its upper threshold value, plant and herbivore populations will oscillate with small amplitude around the “steady-state” value. If, on the other hand, the supply rate of external resources *exceeds* its upper threshold value, large-amplitude non-constant periodic oscillations of plant and herbivore populations result. Increased input to the system can increase the oscillatory behavior.

Hawkes and Sullivan (2001) remind us that, in order to predict the resource conditions under which plants will be most affected by herbivory, we must understand how plant *recovery* from herbivory interacts with the resource environment. High resource levels and a lack of herbivory strongly increase plant growth and reproduction. Monocot herbs with basal meristems grew more after herbivory in conditions of high resource availability, while dicot herbs and woody plants grew more after herbivory in

conditions of low resource availability. There exists a functional split between basal-meristem monocots and dicot herbs/woody plants in how resources influence plant recovery from herbivory. No single model, therefore, can account for all possible plant responses to herbivory.

Additionally, plants can respond to herbivory by reducing the quantity and quality of tissues appealing to herbivores. Morris (1997) notes that plants respond to herbivory with both broad-scale (entire plant) and localized induced defenses (chemical deterrants, etc.), but that measuring the impact of localized changes proves difficult because plant tissues suffering direct damage may represent a food source lower in quantity *and* quality than comparable ungrazed tissue. He uses nonlinear models to separate the confounding effects of prior herbivory on quantity and quality, and presents three alternative possibilities: *1)* Only food quantity affects herbivore performance; *2)* Herbivores must eat more food to achieve a given performance level when food quality is low, but can still achieve maximum performance when fed ad. lib.; and *3)* Damage-induced changes in plant quality could affect herbivores by reducing the maximum performance level – reduced plant quality inhibits performance even if food is superabundant. Morris then fits the models to field data involving Colorado potato beetle larvae and plants damaged to differing extents by adult beetles. Prior damage reduced average beetle mass at pupation due to lower quantity and quality of food, but beetle survival proved subject only to food quantity.

In another study, Underwood and Rausher (2000) demonstrated that a plant's genotype can affect the quality of that plant as a resource. They used Mexican bean beetles on soybean plants and found that beetle populations on different plant genotypes exhibited significantly different recruitment curves. These curves predict differences in equilibrium population sizes, and differences in the magnitude and period of population fluctuations. Therefore, differences in quality among plant genotypes can affect long-term herbivore population dynamics.

Finally we come to the concept of "grazing optimization" – the idea that primary productivity/plant fitness increases with grazing and reaches a maximum at a moderate level of herbivory (de Mazancourt, Loreau et al. 1998). Grazing optimization can occur when: *1)* the proportion of nutrients lost along the herbivore pathway (e.g. excretion) is sufficiently smaller than the proportion lost throughout the rest of the ecosystem; and *2)* the amount of nutrients entering the system exceeds a threshold value (dependent on the sensitivity of plant nutrient uptake rates to increases in soil nutrient availability). However, grazing optimization will occur with more likelihood in ecosystems where large losses of limiting nutrient occur, or where herbivores bring in nutrients from outside the ecosystem (de Mazancourt, Loreau et al. 1998). Conversely, herbivores can prevent grazing optimization. Herbivory can cause changes in the composition of the plant community by eating mostly plants with nutrient-rich tissues and consequently promoting the persistence and abundance of plants with either nutrient-poor or chemically defended tissues (slow to decompose). In this scenario, herbivores do not cause grazing optimization. On a long-term basis, however, primary production depends on the balance between nutrient inputs and outputs of an ecosystem. Grazing optimization can occur if herbivores recycle nutrients efficiently and leave the less efficient plants (de Mazancourt, Loreau et al. 1998). Also, increasing efficiency of herbivore nutrient recycling can lead to mutualistic relationships between plants and herbivores if plant reproduction proves proportional to primary production (de Mazancourt, Loreau et al. 2001). Jaremo et. al. (1999) evaluate plant-herbivore interactions with respect to three different fitness criteria – absolute fitness, relative fitness, and mean absolute fitness – and conclude that mean absolute fitness may aid in distinguishing mutualistic and antagonistic plant-animal relationships.

Both Parsons et. al. (2001) and Tiffin and Inouye (2000) suggest ways to improve plant-herbivore study methods. Parsons et. al. describe the pressure on modelers to reduce the level of model detail in areas where biological processes are "understood". Modeling grazing as a non-spatial process can produce inaccurate results, especially with the use of a logistic growth function (plants) and large bite depth (herbivores). The authors compare the performance of a non-spatial model using a logistic growth function

and acceptable bite depth to a fully spatial bite-scale model that uses a modified growth function more responsive to residual vegetation states (severe grazing versus light grazing, for example). The modified growth function appeared less sensitive than the conventional logistic function to choice of scale, and gave good approximations even when the grazing system was modeled as a homogenous, continuous, non-spatial entity.

Tiffin and Inouye (2000) compare the accuracy and precision of the estimates of plant tolerance to herbivory obtained with natural versus imposed herbivory. Using natural herbivory allows plants to experience the timing, distribution, and damage that they would in the wild but can bias results by failing to recognize microenvironmental variables that affect plant fitness *and* herbivore density and food preferences. Using imposed herbivory avoids this problem. However, plants may respond differently to simulated damage than they do to natural damage. It is difficult to simulate natural distributions and intensities of herbivory, and imposing damage on a large number of plants requires monumental effort. Also, unmeasured effects from greenhouses or herbivore exclusion methods may exist. The authors conclude that using natural herbivory results in better precision. This proves important because a researcher's ability to detect genetic variation in plant tolerance to herbivory depends on the precision with which tolerance is measured.

Pest and disease studies

Many researchers have attempted to model pest-host interactions with the eventual goal of reducing pest-induced damages. Dobesberger (1998) used a stochastic simulation model to derive a damage function for the spruce budworm on balsam fir. His model could predict the mean percentage of stemwood volume increment lost as a function of mean budworm larval density among trees in a forest stand for both clumped and random budworm attack patterns. Aggregation of larvae resulted in less growth loss than did a uniform attack pattern. Low to moderate levels of larvae could induce defensive or compensatory growth mechanisms in trees. The author concludes that pest suppression to maintain budworm populations may constitute the best response to these pests.

Knudsen and Schotzko (1999) produce an individual-based simulation model of the spatial and temporal population dynamics of the Russian wheat aphid on oat plants (non-preferred host) and wheat plants (preferred host). Oat crops represent poor quality aphid food, and aphids therefore move rapidly between plants. These aphids do not stay in one place long enough to become infected by the fungus *Beauveria bassiana* and die; the aphid population instead persists on oat plants at slightly reduced levels. On wheat plants, however, patterns developed with pockets of both infected and healthy aphids. In this system, plant quality is good and aphids stay on one plant until they reduce its quality to the point where leaving in search of a new plant becomes more beneficial than staying. Aphid populations that escape infection with the fungus persist and spread, while infected population perish. Pest proliferation depends on the effect of the plant host on aphid behavior. The fungus reduced the rate of aphid population increase, but failed to cause a negative population growth rate. Aphid populations able to escape infection will continue to grow.

Van den Bosch and De Roos (1996) developed a structured population model of the dynamics of a **S**(usceptible)-**I**(nfective)-**R**(emoved) type epidemic in an orchard with rouging and replanting. They found that rouging when the number of infections on a tree reaches a threshold resulted in a dynamically varying age at rouging, and that this dynamically varying time-delay produced periodic model solutions. Steady-state analysis showed that increasing the rouging threshold beyond a certain "key-value" increased tree lifespan, as did increasing the death rates of infected sites. Decreasing the tree density in the orchard also increased tree lifespan. They concluded that, when the life-history parameters of a disease are such that the chosen rouging threshold is slightly above the final value of the S-I-R epidemic, periodic disease outbreaks occur.

Gibson et. al. (1999) developed a stochastic model for the dynamics of a plant-pathogen interaction, and fit the model to observations of the fungal pathogen *Rhizoctonia solani* in radish plants in both the presence and absence of the antagonistic fungus *Trichoderma viride*. They determined the extent to which observed variability

among replicates of a given treatment could arise from inherent stochasticity in the infection process, and discovered which aspects of disease transmission were most affected by the biological control agent *T. viride*. They could estimate the probability of successful biological control and analyze effects of fine-tuning critical parameters.

Ghersa and Roush (1993) investigated weeds as crop pests. They compared the impact on crop yields of reducing weed dispersal ability with the effect of increasing crop ability to compete for resources. Weed research currently emphasizes manipulation crop genotypes in an attempt to shift competitive relationships between crops and weeds in favor of crops. However, the mutability and variability of weed populations, combined with stochastic processes in the crop environment, make breeding for crop response to weed pests difficult. The authors argue that strategies designed to manage weed dispersal and distribution prove better than plans that aim to augment crop competitive ability, and that we need a better understanding of weed dispersal.

Finally, Thomas (1999) advocates increasing our knowledge of the action and interaction of various additional pest control strategies and moving away from the existing single-technology, pesticide-dominated pest control paradigm in order to improve the efficacy of pest control. We must integrate biological control and knowledge of host-plant resistance to control insect pests. He suggests that partial plant resistance and partially effective biological control be combined to result in additive reuctions of pest densities. Current resistance screening and evaluation procedures fail to examine the effects of resistance on pest predators and leave positive interactions between plant resistance and biocontrol agents unidentified. Partially resistant plants that, when combined with biocontrol agents could provide successful pest control, are often rejected. He also believes that better understanding of host-parasite interactions and microbial pest control could help. For example, hosts infected by a biopesticide can infect new hosts by horizontal transmission whether already dead or still alive: this can prolong the effects and increase the impact of a single spraying. Infected hosts prove more vulnerable to predation, therefore increasing the speed of pest kill. Also, biopesticides are species-specific and conserve natural predators, as opposed to chemical pesticides that kill most

insects. Application of biopesticides causes reduced pest feeding rates. Thomas also cautions that pest response to biocontrol can vary with environmental and internal temperatures – screening conducted in a lab does not necessarily reflect field conditions and can lead to erroneous conclusions and the resultant selection of inappropriate biopesticides.

Biological control of weeds

In addition to insect pests, weeds can also reduce survival and reproduction of other plants. Smith et. al. (1993) constructed a deterministic model of the population dynamics of the parasitic weed *Striga hermonthica* in a millet cropping system with biological control of the weed provided by *Smicronyx umbrinus*. The biocontrol agent affects weed seeds by preventing weed plants from producing seeds and consequently reducing the soil seed bank. *S. hermonthica* seeds are long-lived, and the weed can build up substantial seed banks very quickly. *Sm. umbrinus* has almost no effect on the density of emerged weed plants until it destroys almost 80% of the soil seed bank annually and therefore is not a good biocontrol agent of *S. hermonthica* once the weed establishes. *Sm. umbrinus* could prove effective in situations where the weed seed bank is already limited – in controlling new infestations, or where other control methods have already reduced the seed bank (Smith, Holt et al. 1993; Smith and Webb 1996).

Conversely, Smith et. al. (1997) made a deterministic difference equation model of the population dynamics of the weed *Rottoboellia cochinchinensis* with biological control provided by the head smut *Sporisorium ophiuri*. This weed has a very short-lived seed bank (unlike the weed in the previous paragraph), and control methods that prevent input into the soil seed bank should have a long-term controlling effect on the weed. The model estimates that long-term control of the weed requires a constant annual infection rate by the head smut. The smut alone probably will not provide satisfactory control, but could be effective if combined with one or two manual weedings per year.

Lonsdale et. al. (1995) looked at biocontrol of a tropical weed (*Sida acuta*) by a chrysomyelid beetle that reduced annual weed seed production. They adapted an annual

plant model and used it to predict density of weed flowering in the next year resulting from beetle impact on the seed bank. Over time, the density of the weed would fall to a level dependent on beetle search efficiency. However, the model contains uncertain estimates of some plant parameters, and needs more information about the grazing patterns and population dynamics of the beetle. The model shows that the presence of seed carry-over usually lowers plant density but, where herbivory is patchy, it reduces the rate of population extinction.

Exotic species

Managers can use ecological modeling techniques to predict invasive plant species dynamics and control the spread of such plants. Higgins et. al. (2000) developed a spatially explicit, individually-based model that predicts rates and patterns of alien plant spread, and then scaled this model up to a spatially explicit landscape-scale simulation. They then used the model to explore strategies and funding schedules for clearing exotic plants from the Cape Peninsula of South Africa. Comparisons between the fine-grained local-scale and coarse –grained landscape scale models revealed no significant artifacts introduced into model behavior as a result of the scaling up process. They found that clearing low density stands of juvenile exotics first, high density juvenile stands next, and adult stands last proved the most rapid, cost-effective control strategy. Strategies that cleared high density stands first were expensive and took longer to eliminate exotics. The faster the clearing rate, the less expensive the clearing operation. However, the authors noted the existence of a "critical clearing rate" above which costs did not decline significantly. Strategies that gave priority to sites of high native plant biodiversity proved even more effective in preserving native species. Delaying clearing operations both increased eventual total costs and exacerbated the negative impacts of exotics on native plant communities.

Marco and Paez (2000) warn that researchers cannot consider only the life history traits of an exotic species and expect to accurately predict invasion outcomes; they must also examine demographic studies of the exotic across the range of environmental conditions in which it occurs. They examined the interactions between exotic *Gleditsia*

triacanthos and native *Lithraea ternifolia* in two different environmental scenarios in Argentina ("good" and "bad" habitat for each species). In this case, the invader gorws faster, reproduces at an earlier age, produces more seeds, has larger seeds, disperses farther, and has higher germination percentages than the native. The authors used matrix models to predict and project consequences of differences in growth rates between the two species, and reaction-diffusion models to predict rates of spread. The matrix models help pinpoint those plant life stages contributing the most to population growth, and therefore help researchers understand how to control exotics. Typically, biologists consider disturbance an aid to exotic spread and a hindrance to native plant persistence. In the system the authors examined, *L. ternifolia* needs disturbance to establish itself. They concluded that forest managers here need to maintain moderate disturbance levels to prevent native extinction, but should not create disturbance in areas with deep soils because these sites are more amenable to invader establishment.

Finally, Keane and Crawley (2002) examine the validity of the Enemy Release Hypothesis. This hypothesis predicts that, when a species is introduced to a new region: *1)* its specialist enemies will not occur in the new region; *2)* host switching by specialist enemies of native plants will prove rare; and *3)* generalist enemies will have greater impacts on native plants than on exotics. The authors first note that if a plant species is introduced to a region that supports closely related native species, the specialist enemies of those natives may also attack the exotic. Exotic plants may not escape their natural enemies because these may have been introduced with the exotic. They see no reason why generalist enemies of native plants should display less inclination to attack exotics; these enemies may indeed be better at attacking natives, but natives should concurrently have better adaptations enabling resistance to native generalist enemies. Even if enemies have a reduced impact on exotics, the exotics may not necessarily become invasive; the climate of the region of introduction may prove unsuitable, or the exotic may fail to capitalize on "enemy release" because it is naturally less competitive than native plants.

The authors do document some evidence for the Enemy Release Hypothesis. Managers implementing biological control strategies have discovered that importation of enemies of exotics can control the exotic plants. However, introduced exotic enemies can also become invasive due to the fact that they are free of natural enemies and competitors for their host in the new region. Other researchers have observed host switching by enemies native to the region of exotic introduction, but found the effects of host switching minimal. The absence of specialist enemies and lower relative impact of generalist enemies on exotics proved more important in such cases. The authors suggest that validation of the Enemy Release Hypothesis could occur through the performance of enemy exclusion experiments (where *all* enemies are excluded). In these experiments, the exotics may benefit a bit, but if the hypothesis is correct and natives are *more* affected by enemies, native species should benefit much more than exotics from enemy release, and should display increased competitive ability.

Parasitoid-host models

Modeling has increased our understanding of parasitoid behavior and its relationship to host dynamics, and has also allowed for more meaningful evaluation of the suitability of particular parasitoids for biological control. Simple models of host-parasitoid interactions show that parasitoids tend to drive all but the most fecund of their host species extinct – host species coexistence requires a way for the less fecund species to increase when rare. In this vein, Hastings and Godfray (1999) explored the extent to which host fidelity among parasitoids influences population dynamics and contributes to host species coexistence. They modified a basic model of a generalist parasitoid and several host species to include the idea that the species of host a parasitoid emerges from influences its own host choice. Models show that this parasitoid learning can contribute to the coexistence of two host species regulated by the same parasitoid. This occurs if host fidelity is strong enough to provide the less fecund host a means of increasing when rare.

Hsu et. al. (2001) transform a Michaelis-Menten type ratio dependent predator-prey model to a Gause-type predator-prey system. They note that ratio-dependent models

can produce richer and more reasonable biological dynamics than classical prey-dependent predator-prey models. These models avoid the "paradox of biological control" (this states that you cannot have a low and stable prey equilibrium density, though there are many instances of successful control where prey remain at densities less than 2 percent of their carrying capacity). They also fail to produce the "paradox of enrichment" (the idea that enriching a predator-prey system and thereby increasing carrying capacity will cause an increase in the equilibrium density of the predator but not of the prey, thus destabilizing the positive equilibrium). These models allow mutual extinction as a possible outcome of predator interactions with prey. In their model modification, the authors found that the asymptotic behavior of model solutions is independent of carrying capacity, but relates to prey capture rate. The time-lag in predator numerical response neither caused nor prevented mutual extinction.

Flinn and Hagstrum (1995) developed a discrete, distributed-delay model of parasitoid population growth as a function of grain temperature, and coupled this model to an existing model of the rusty grain beetle. Their model accurately predicted the time and magnitude of peak parasitoid density, and predicted population dynamics well for 175 days. However, the model overestimated parasitoid efficacy, probably by overestimating the attack rate. Changing the *timing* of parasitoid release had a greater effect on host density than did releasing more parasitoids. Releasing parasitoids at a density equal to the density of their host should result in adequate host population reductions.

Meier et. al. (1994) note that equilibria of host-parasitoid systems within the framework of general Nicholson-Bailey models tend toward instability. Stability occurs only when host fertility does not exceed a threshold level and if superparasitism proves unsuccessful. They then discuss the global behavior of the Hassell-Waage-May model using KAM theory and illustrate its sensitivity to small perturbations capable of creating radically different patterns of host-parasitoid dynamics.

Kean and Barlow (2000) monitored the density of the pest weevil *Sitona discoideus* and its parasitoid *Microtonus aethiopoides* in New Zealand, where the parasitoid serves as a biocontrol agent. They constructed a model that showed the parasitoid reducing weevil density by 75%, and indicated that the parasitoid could maintain this level of control. Biological surveys corroborated model predictions. The weevil sex ratio was female-biased, but parasitoids attacked male weevils more often. The model included explicit dispersal in a coupled map-lattice metapopulation (Kean and Barlow 2000). Metapopulation structure had little effect on the local dynamics, except for things like initial rates of parasitoid spread or response to local perturbations. The model results were consistent with observed data from New Zealand and mimicked successful biological control.

DeGrandi-Hoffman et. al. (1994) describe a model capable of simulating host and parasitoid interactions, parasitism rates, and plant damage. The model can simulate many different species of herbivorous insects, parasitoids, and plants because specific parameters of insect and plant biology are entered through menus at the beginning of simulation. The model can simulate augmentative releases of parasitoids. The authors suggest their model can aid in screening and selection of parasitoids that may be effective biocontrol agents. It can simulate the biology and behavior of many different pests and parasitoids.

Muller-Graf et. al. (2001) investigated and modeled host-parasite interactions between the pest cockroach *Blatella germanica* and its nematode parasite *Blatticola blattae*. Hosts were usually infected with only one male and one female parasite. Parasites significantly impacted the survival rate of cockroach larvae and larval maturation time, but had no effect on adult roach survival. Infected female roaches produced fewer first oothecae than uninfected females. The model indicated that the parasite suppresses host populations by 11%; this parasite is not good enough to serve as a roach control agent.

Lane et. al. (1999) constructed a Thompson-Nicholson-Bailey model of host-parasitoid dynamics that incorporated effects of parasitoid fecundity and host density dependence to examine the idea that, all else equal, a more fecund parasitoid species will provide better biocontrol because of its ability to kill more hosts over the course of an individual's lifetime. The model predicted that high parasitoid fecundity and search efficiency coupled with a moderately aggregated attack pattern minimized host equilibrium abundance. The authors used the BIOCAT database of biocontrol introductions to look for positive correlations between parasitoid fecundity and successful biological control, and found nothing. The taxonomic order of the host served as a source of confounding variability. When they ignored effects of host taxa, the authors found that less fecund parasitoids provided more successful control than more fecund species. Parasitoids can provide long-term pest control without the existence of a stable host-parasitoid equilibrium. Overall, host taxonomy has the greatest effect on the success of biological control. Low parasitoid fecundity is not necessarily bad.

Getz and Mills (1996) considered a model of host-parasitoid dynamics where the attack rate of female parasitoids has both egg-limited and search-limited components. A higher degree of spatial heterogeneity is insufficient on its own to stabilize interactions between parasitoids and otherwise unregulated hosts in a discrete time model. The interaction cannot be stable unless the proportion of hosts escaping parasitism has a sufficiently clumped distribution. The more the encounter rate of female parasitoids is egg-limited instead of search-limited at low to moderate host densities, the more efficient a control agent the parasitoid will be.

O'Neil et. al. (1996) used a state-variable predator-prey model (PREDPREY) that uses a distributed-delay function to represent the temperature dependent development of predator and prey to describe the population dynamics of the generalist predator *Podisus maculiventris* and the exotic Mexican bean beetle in soybean crops. They found the model a reasonable approximation of actual system dynamics. *P. maculiventris* has a significant impact on within-season beetle dynamics and on overwintering populations. Its effectiveness depends more on developmental and reproductive rates than on search or

survival rates. *P. maculiventris* had the greatest impact on beetle populations early in the season at relatively low beetle densities, rather than late in the season when densities are higher. Natural enemies like *P. maculiventris* can serve as "buffers" to prey population growth. They can prevent or delay pest outbreaks instead of suppressing outbreaks that have already begun.

Van Roermund et. al. (1997) studied biological control strategies of the greenhouse whitefly by the parasitoid *Encarsia formosa* with a simulation model of the parasitoid-host interaction on tomato plants. They based the model on the biology of both insect species and on the search and parasitization behavior of individual parasitoids (related to host plant characteristics and temperature). The model included stochasticity and spatial structure based on the location coordinates of plants and leaves. The model agreed well with observed dynamics of the parasitoid and host. The authors found that the degree of whitefly control provided depends greatly on the "giving-up time" of the parasitoid (how long it stays on the same leaf). Variation in giving-up time creates host refuges from parasitoid attack. When this variation was excluded from the model, the hosts nearly became extinct. Lower rates of leaf production by tomato plants increased whitefly control by causing whitefly adults to stay longer and oviposit more on a particular leaf. The same number of hosts then are distributed among fewer leaves: this aggregated host distribution increased parasitoid efficacy. The authors conclude by noting that their model can be used to evaluate many parasitoid release strategies on different crops under different greenhouse conditions.

Several studies address systems containing two parasitoid species. Murdoch et. al. (1996) constructed a stage-structured model of the competitive displacement of parasitoid *Aphytis lignanensis* by *A. melinus* on California red scale in the inland valleys of Southern California. *A. melinus* can obtain female offspring from smaller scale than can *A. lingnanensis*, and can obtain two female offspring from larger scale (this is noteworthy because only female parasitoids kill hosts, and because red scale is a citrus pest). The model recognizes three juvenile scale stages. *A. lignanensis* must have a much higher successful search rate than *A. melinus* to overcome its natural disadvantage. *A. melinus*

usually wins in competition by suppressing the third juvenile scale stage. The other parasitoid needs this stage (which is larger) to produce female offspring, and *A. melinus* suppresses this stage below the level needed for *A. lignanensis* maintenance. The better competitor suppresses total scale density to its lowest level, but the parasitoid that wins in competition is the best control agent *only* if the juvenile scale stage it suppresses to win is also the main source of crop damage.

Gutierrez et. al. (1993) use a unified ratio-dependent supply-demand driven tritrophic model of an African cassava plant system. They compare the model to field data and examine successful biological control of the cassava mealybug with the exotic parasitoid *Epidinocarsis lopezi* and the unsuccessful control of the mealybug by *E. diversicornis*. Without immigration, the numerical responses of the parasitoids could not explain mealybug dynamics. Rainfall and a fungal pathogen suppress mealybug populations enough during the wet season that *E. lopezi* can control them in the dry season. *E. lopezi* can produce female offspring on smaller hosts than *E. diversicornis* can, and is five times better at finding hosts than *E. diversicornis*. In cases of multiple parasitism on the same host, *E. lopezi* displaces *E. diversicornis*.

Tuda and Bonsall (1999) address the problems inherent in coupling the evolutionary and population dynamics of host-parasitoid interactions, noting that evolution can alter the ecological dynamics of interactions. They examine the effects of life history on population persistence and stability with a Nicholson-Bailey model with intraspecific competition between two parasitoids for a host. The model uses two forms of host, one that is competitively inferior but better defended and vice versa, and two forms of parasitoid, one that is more virulent but a worse competitor and vice versa. The trade-off in the parasitoid proves less important to system dynamics than the trade-off in the host, and genetic variability in the host promotes stability in either case. If hosts evolve resistance to parasitoid attack, but parasitoid populations don't have enough variability to coevolve, biological control may fail and an economic problem result. Host resistance to attack by one parasitoid species does not guarantee resistance to different

species. Multiple release strategies of different parasitoids proved advantageous to long-term pest control.

AN EXAMPLE

To illustrate one possible way in which an ecological model could be used for exposure analysis for weed biological control agents, I present analyses of a simple individual-based model of herbivorous insect behavior in the presence of two host plants. Individual-based models, although computationally intensive, are relatively easy to formulate, analyze and interpret (Fahse, Wissel et al. 1998). In addition, although individual-based models are typically parameter-rich, the parameters are typically quite easy to estimate from behavioral observations (Blanche, Casas et al. 1996; Turchin 1998).

The model simulates movement by individual herbivorous insects through a fractal environment containing three habitat types (pest host plant, non-target native host plant, and non-host matrix habitat), as well as oviposition on those three habitat types. Results are presented for simulations of insect movement as both a simple random walk, and a more realistic correlated random walk (Othmer, Dunbar et al. 1988; Routledge 1990; Zollner and Lima 1999). The fractal environments are simulated as neutral landscapes, specifically two-dimensional fractional Brownian motion processes. Neutral landscape models are used in landscape ecology as a means of generating artificial or simulated landscape patterns with known properties, constraints, and structuring processes (With 1997; With and King 1997). There are a number of classes of neutral landscape models that have been proposed and used by different researchers. The most useful of these classes of model are amenable to spectral synthesis. Spectral synthesis is the use of spectral basis functions such as wavelet transforms or Fourier transforms to represent neutral landscape models (Keitt 2000). The spectral approach also encompasses a number of different types of scaling relations, although all variants of spectral synthesis rely fundamentally on a scaling relation between amplitudes and frequencies of environmental (spatial or temporal) fluctuations. One of the most useful neutral landscape

models is the fractional Brownian motion or fBm (Keitt 2000). Fractional Brownian motion is controlled by a parameter H called the Hurst exponent; this parameter appears in the scaling relation between the expected variance of increments to the process and their separation distance.

The basic algorithm for the model is as follows:

1) Generate a fBm landscape with a given H value, and scale it so that the values lie between zero and one.
2) Divide the fractal landscape into three habitat types using two different cutoff values. Values of the fBm which are less than the first cutoff value are designated as the native non-target host plant, values of the fBm which are between the two cutoff values are labeled as non-host matrix habitat, and values of the fBm which exceed both cutoff values are designated as the target pest host plant.
3) Release insects in the three-phase fractal habitat. Insects are released at the point with the highest value of the original two-dimensional fBm, to simulate release of biological control agents at a location with high pest density. Because the individual insects are assumed to not interact (e.g., through interference (Stillman, Goss-Custard et al. 1997)), the movements of many individual insects through a habitat can be simulated in a simple loop.
4) Allow the simulated insects to move through the habitat with different average move lengths (assumed lognormally distributed) in the three habitat types. Allow insects to oviposit on the pest host plant or on the non-target host plant when in the corresponding habitat type; these two types of oviposition events may differ in their probability. For each move, record the habitat type the insect lands in, and whether or not it oviposits there. For simulation runs in which insect movement was modeled as a correlated random walk, one additional parameter specified the spread of the distribution of turning angles; this was a beta

distribution scaled to the interval $-\pi$ to π, with a mean turning angle of zero.

Each simulation run includes 200 simulated habitats, each with 2000 insects; each insect is allowed to make 100 moves. Default parameter values are shown in Table 1.

To investigate the effects of the details of habitat structure and movement behavior on the potential damage to a native plant caused by a biocontrol agent introduced to control a related pest plant, we studied variation in three parameters for both simple and correlated random walk models of insect movement. Effects of changes in the Hurst exponent (which control the "grain" of the habitat) on number of ovipositions on the native host plant are shown in Figure 1. Effects of changes in the mean move length of the insect on number of ovipositions on the native host plant are shown in Figure 2. Effects of changes in the probability that the insect will oviposit on the native plant, given that it is on a native plant, on number of ovipositions on the native host plant are shown in Figure 3.

The Hurst exponent of the fBm process generating the habitat appears to have very little effects on potential non-target impacts by the biological control agent for both simple and correlated random walk models of insect movement (Figure 1). The variability of potential non-target impact across replicate habitats is quite large. This indicates that the specific arrangement of habitat patches of the two plant species in the landscape may be more important in determining non-target impacts than the "grain" of the environment.

Ovipositions on the native plant decrease asymptotically with increasing mean move length on the native, non-target plant species for both simple and correlated random walk models of insect movement (Figure 2). The low variability shows that this result is robust across a range of specific patch arrangements. This result makes intuitive sense; short move lengths on the native plant will tend to keep the insect on or near its current habitat patch, increasing the risk of non-target impacts.

Ovipositions on the native plant increase with increases in the probability of oviposition on the native plant species given that the insect is already in a patch of the native plant for both simple and correlated random walk models of insect movement (Figure 3). This result also has low variability across replicate realizations of the landscape. This result is also intuitively reasonable.

Taken together, these results suggest that risks of non-target impacts may be strongly influenced by the details of the movement patterns of biological control agents in target and non-target host plant habitats. The specific details of insect movement that appear to be relevant are readily measured in field trials.

DIRECTIONS FOR FUTURE RESEARCH

We have shown that simple individual-based models of the movement of herbivorous insects in heterogeneous environments can tell us a great deal about the risk of non-target impacts of biological control agents introduced to manage invasive plants. Although the models presented here rely on simulation of neutral landscape models, the algorithms could easily be modified to simulate movement on known spatial habitat configurations perhaps derived from remote sensing data. The models could easily be made more realistic in application to specific insect-host plant systems, and all the models' behavioral parameters can be estimated based on simple field measurements of oviposition and movement behaviors.

Although the models allow for fairly sophisticated simulation of individual movements, they do not at present allow for interactions between individual insects as they move through their habitat. We are currently working on development of models that allow for this type of behavior. However, the models as they now stand could begin to provide useful guidance for risk assessments for proposed weed biological control agents.

There are several areas of research that need additional development before a protocol for comprehensive risk assessment for weed biological control agents can be firmly recommended. The specific areas that we will discuss here are applications of modeling to relevant questions concerning weed biological control agents, empirical studies of herbivorous insect movement, and example applications of the ecological risk assessment framework to weed biological control agents.

Modeling studies should focus on the importance of the movement of biological control agents through the environment in determining their potential non-target impacts. Individual-based approaches are likely to be advantageous in terms of parameter estimation, interpretability, and predictive power; such models allow assessment of impacts via simulation, and, although relatively parameter-rich, have modest data requirements. Applications of such models have the potential to allow more extensive and explicit exposure analyses than have typically been conducted in the past.

Additional insights and guidance for both risk assessment and control agent selection could come from applications of matrix population models, a primary tool in conservation biology (Heppell, Walters et al. 1994; Botsford 1996; Levin, Caswell et al. 1996; Hoffmann 1999; Fieberg 2000; Caswell 2001; Fieberg and Ellner 2001; Harding, Doak et al. 2001; Lennartsson and Oostermeijer 2001; Rae and Ebert 2002; Sherman and Runge 2002). In particular, elasticity analysis is a form of perturbation analysis of matrix population models that allows one to determine the rate of change of population growth rate in response to changes in individual vital rates (Caswell 2001). This allows vital rates to be ranked in order of their influence on population growth. Elasticity analyses of host plant life histories could be used to reveal which target host plant life cycle stages would be most sensitive to the impacts of a control agent. This information could then be used in control agent screening or selection. Also, elasticity analyses on non-target host plants could be compared with those for target host plants to see if the most sensitive life-cycle stages coincide. If so, the risk of non-target impacts would be higher than if not, and would need to be carefully assessed.

Additional studies of herbivorous insect movement are also needed, preferably focused on proposed weed biological control agents. In particular, risk assessment of proposed weed biological control agents requires measurements of critical parameters that determine host search success in complex environments, in natural systems as well as in agroecosystems. Specifically, such studies should estimate the move length and turning angle distributions that could be used to parameterize a correlated random walk model.

Finally, we need peer-reviewed examples in the literature of full-on regional comprehensive risk assessments (Landis and Wiegers 1997; Walker, Landis et al. 2001; Moraes, Landis et al. 2002; Obery and Landis 2002), as case studies from which to learn; the *Tamarix-Diorhabda-Frankenia* system might be a good place to start. Given that biocontrol agents can disperse far from the initial release area, questions of scale would need to be thoroughly addressed in such studies.

RECOMMENDATIONS

Specific recommendations arising from the research reported here include the following:

1) Risk assessment for biological control agents should follow the standard protocol for ecological risk assessment with appropriate modifications as outlined above.

2) Potential uses of demographic elasticity analysis in risk assessment for proposed weed biological control agents should be thoroughly explored, as outlined above.

3) Following the problem formulation phase of the risk analysis, hazard identification and effects analysis should be performed. If the proposed

agent poses a significant hazard to non-target species, the assessment should proceed with an exposure analysis.

4) Individual-based models should be given serious consideration for any exposure analysis that proves necessary. The data required to estimate the movement parameters of such a model are relatively easy to collect.

5) Risk assessments should be explicitly linked with cost-benefit analyses in a unified decision-theory framework (Simberloff and Stiling 1996; Shea, Amarasekare et al. 1998).

Finally, and perhaps most importantly, practitioners of such risk assessments need to cultivate an attitude of humility about the predictive ability of their models, about specific risks, and about their risk assessments.

TABLES

Table 1. Default parameter values used in individual-based simulations.

Parameter	Meaning	Value
H	Hurst exponent of fractional Brownian motion	0.5
n	Number of grid cells in x and y direction in fractal habitat	128
p_native	Cutoff value to convert continuous fBm habitat to three-phase habitat	0.15
p_matrix	Cutoff value to convert continuous fBm habitat to three-phase habitat	0.7
mu_pest	Mean insect move length in pest host plant habitat	5
mu_native	Mean insect move length in native host plant habitat	10
mu_matrix	Mean insect move length in non-host habitat	30
CV_pest	Coefficient of variation of insect move length in pest host plant habitat	0.10
CV_native	Coefficient of variation of insect move length in native host plant habitat	0.10
CV_matrix	Coefficient of variation of insect move length in non-host habitat	0.10
p_ov_native	Probability of oviposition on native host plant	0.05
p_ov_pest	Probability of oviposition on pest host plant	0.2
num_hab	Number of fBm habitats to generate for each parameter combination	200
num_bug	Number of insects per fBm habitat	2000
num_move	Number of moves per insect	100

FIGURES

Figure 1. Results of individual-based simulation showing effects of Hurst exponent on number of ovipositions on the native plant; results for the simple random walk model of insect movement are shown in the top graph, while results for the correlated random walk model of insect movement are shown in the bottom graph. In a risk analysis, this could be considered a measure of exposure. Error bars represent one standard deviation, taken across the 200 replicate habitats.

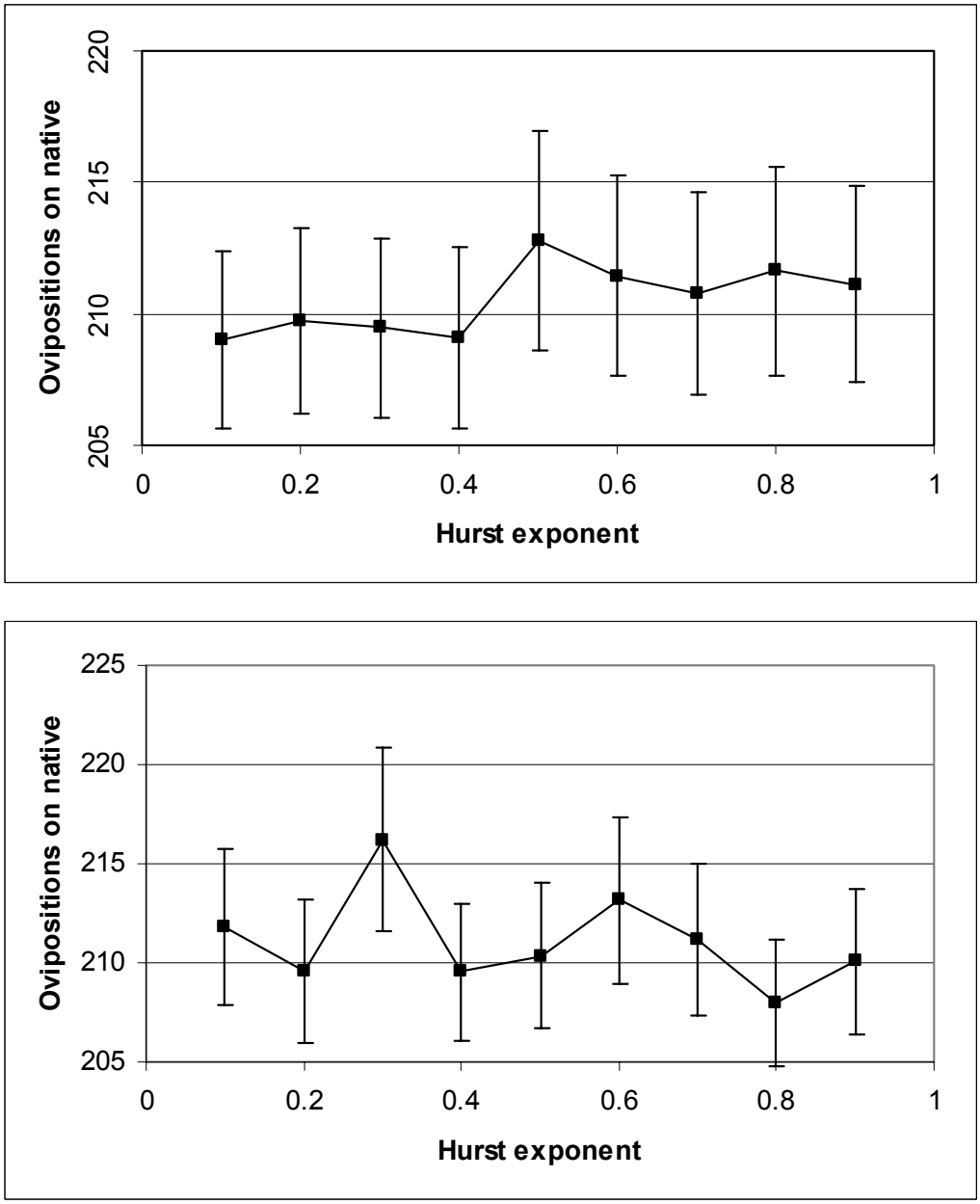
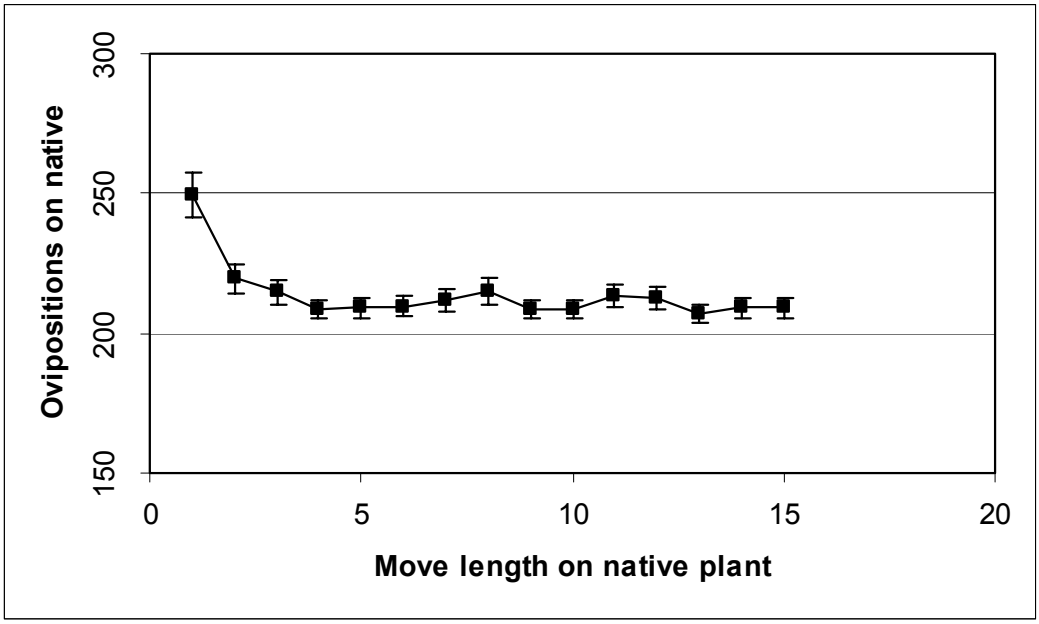


Figure 2. Results of individual-based simulation showing effects of mean insect move length in the native host plant habitat on number of ovipositions on the native plant; results for the simple random walk model of insect movement are shown in the top graph, while results for the correlated random walk model of insect movement are shown in the bottom graph. In a risk analysis, this could be considered a measure of exposure. Error bars represent one standard deviation, taken across the 200 replicate habitats.



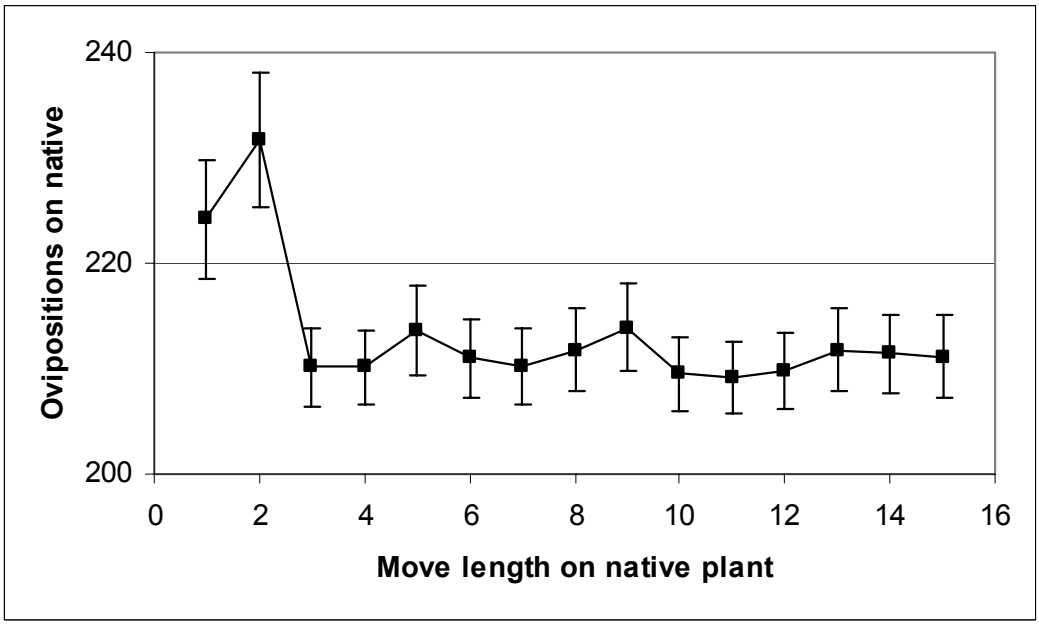
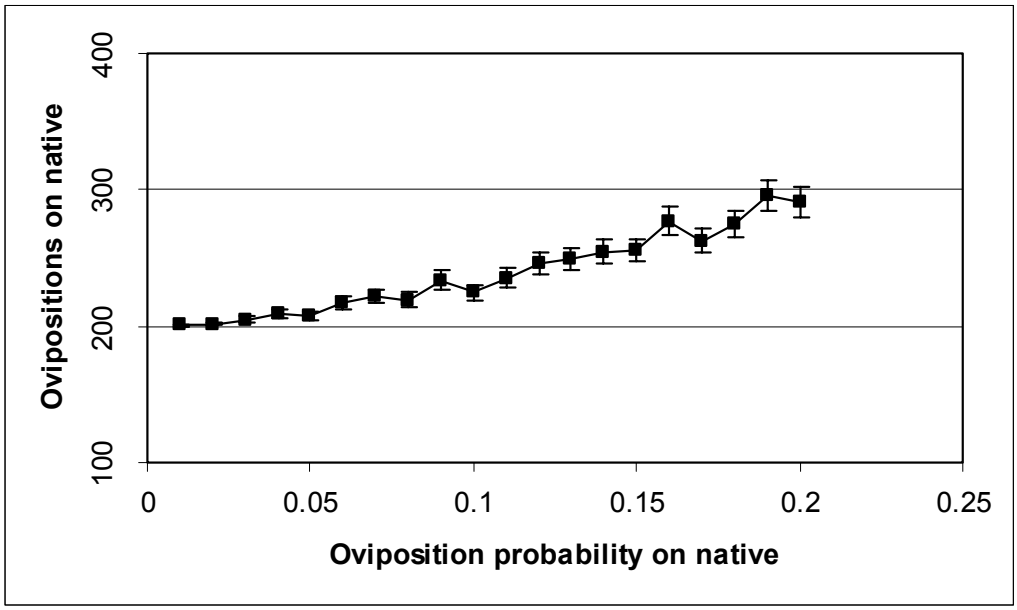
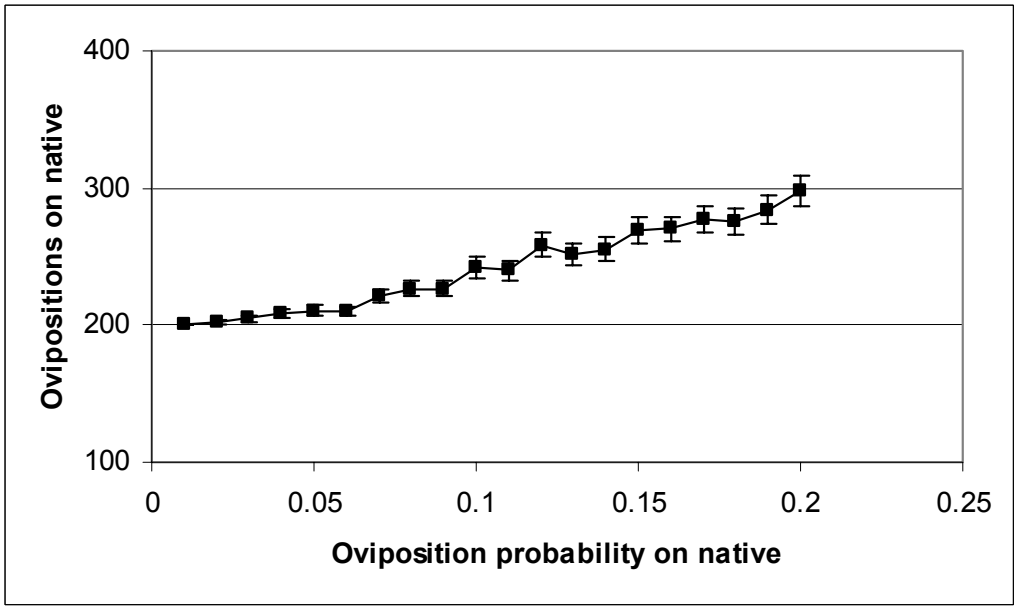


Figure 3. Results of individual-based simulation showing effects of oviposition probability on the native host plant on number of ovipositions on the native plant; results for the simple random walk model of insect movement are shown in the top graph, while results for the correlated random walk model of insect movement are shown in the bottom graph. In a risk analysis, this could be considered a measure of exposure. Error bars represent one standard deviation, taken across the 200 replicate habitats.





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