

Chapter 3. Plant Invasions and Their Management

Steve Radosevich, Oregon State University

THE INVASION PROCESS

The susceptibility of plant communities to plant invasion can be influenced by many factors. These factors include the species composition, community structure, site resource availability, and disturbances to the original plant community. *Invasibility* is a term used to describe the environmental, site-level factors that affect the susceptibility of an area to invasion by an exotic plant species. Biological traits of the invading species also have an effect on site susceptibility and spread of the invasive plant. Most non-indigenous plants invade latitudes similar to those of their native occurrences (**Figure 3-1**); however, the function of the “invader” may be fundamentally different in its new environment than in the local vegetation from which it originally arose (Rejmánek 1996). For example, invading exotic species may have genetic or life history traits that allow them to preempt site resources or avoid predators better than indigenous species, allowing them to be successful invaders.

It is convenient to explore plant invasions as a three-phase process (**Figure 3-2**): *Introduction*, *Colonization*, and *Naturalization* (Groves 1986; Cousens and Mortimer 1995), and we will discuss invasions in term of these three phases. However, Richardson et al. (2000) consider the process of invasion differently, as one which includes introduction, naturalization, and invasion. Invasion, according to Richardson et al. (2000) includes a special class of vegetation that can enter and occupy already fully inhabited plant communities without further assistance from humans or the environment.

While the phases of invasion are of human construct, they help us understand how the process works at different ecological and geographical scales, because they can be organized according to known stages of plant population growth (Sauer 1988; Forman 1995; **Table 3-1**).

How Plant Populations Grow

The two graphs in **Figure 3-3** show how populations grow over time. The top graph is based on a number of experiments with organisms that range from microbes to higher plants and animals. The bottom graph indicates the population growth rate of cheatgrass in the Great Basin through the first half of the last century. Both graphs demonstrate the process of invasion as depicted in **Figure 3-2**.

The top graph in **Figure 3-3** demonstrates two variations of plant population growth over time. The solid line indicates geometric growth, which is growth in an unlimited environment. Except in very special circumstances, such as a newly disturbed site or one high in fertility and free of vegetation, this pattern of growth is hypothetical.

The dashed line in the top graph of **Figure 3-3** represents logistic population growth. Logistic growth is the way plant populations grow normally in environments limited by resource availability (i.e., water, nutrients, sunlight) or the presence of other vegetation.

Plant density as well as resource limitation can create the logistic pattern of growth because the presence of many plants (versus only a few) limits environmental resources. K in this graph represents the carrying capacity of an environment for a plant population that is limited by its own density or the density of another plant.

The bottom graph in **Figure 3-3** represents actual data that shows the increase in the area occupied by cheatgrass throughout the Great Basin of North America. It spread initially at a geometric rate, occupying most available sites, and its population growth then slowed as the carrying capacity of the entire Great Basin was reached and new sites to invade

became limited (from Radosevich et al. 1997).



Figure 3-1. Cheatgrass (*Bromus tectorum*), a native to Eurasia, can successfully invade areas with similar environmental conditions such as Dinosaur National Monument, a natural area in the Great Basin, Utah/Wyoming.

Figure 3-2. Diagram of the invasion process according to Cousens and Mortimer (1995)

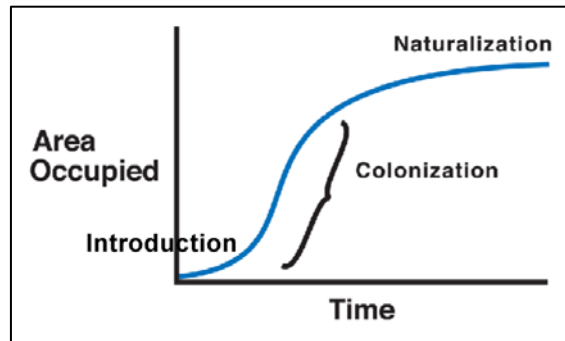


Table 3-1. Ecological processes, patterns, and scales at different phases of plant invasion. Adapted from Radosevich et al. (2003).

Phase	Ecological Process	Ecological Scale	Geographical Scale
Introduction	Immigration Survival	Species recruitment	Individual (plant)
Colonization	Germination/sprouting Growth Dispersal (short-distance) Death (mortality)	Patch expansion	Population
Naturalization	Germination Dispersal (long- distance) Death (mortality)	Range expansion	Meta-population (satellite populations)

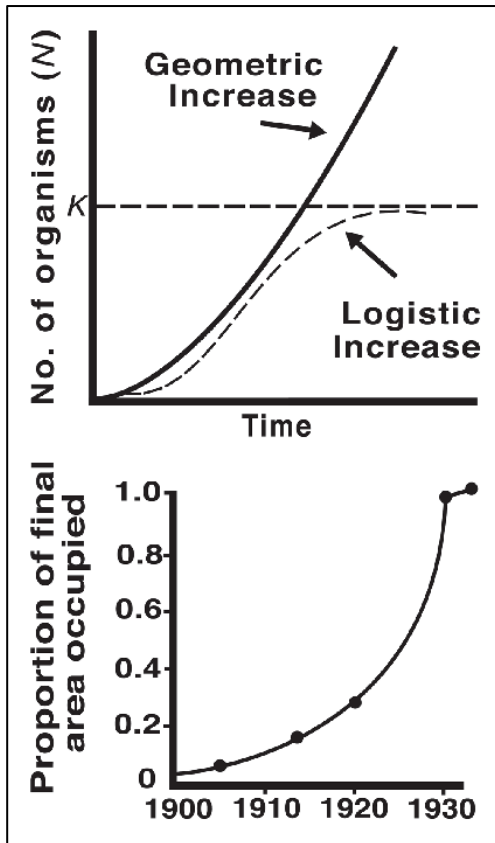
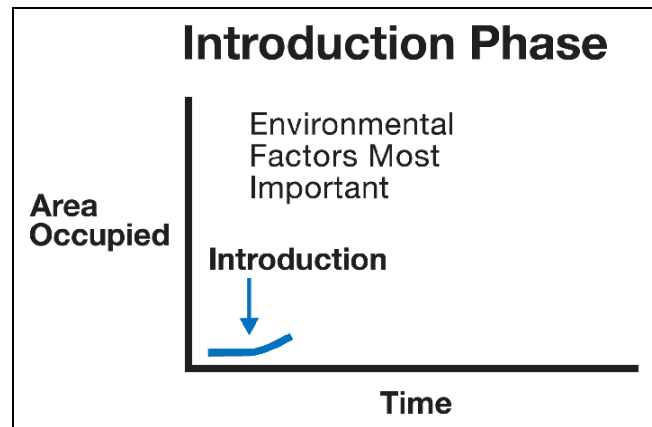


Figure 3-3 (left). Population growth rates of an idealized plant (top graph) and cheatgrass (bottom graph; modified from Radosevich et al. 1997)

Figure 3-4. The introduction phase of the invasion process according to Cousens and Mortimer (1995).



INTRODUCTION PHASE

Population growth curves can be generated for any species. For invasive plants, it is only the ability to establish (introduction), and the rate of growth (colonization) in a new environment that are believed to differ from that of other plants.

Small populations of invasive plants often go undetected during the introduction phase (**Figure 3-4**, expanded from Figure 3-2). In fact, plant invasions are most likely to fail at this point due to unpredictable events like drought and disease (Mack 1995), or because of a lack of a minimum critical population size necessary for the population to genetically maintain itself (Latore et al. 1998).

Environmental factors that favor establishment are probably most important during this phase of invasion because introduced seeds have to compete with the established flora that is already well adapted to the site. Many

ecologists have recognized the importance of

diverse plant communities in maintaining vigorous ecosystems, and research suggests that the chances of exotic plant invasion diminish with increased species diversity (Burke and Grime 1996; Tilman 1997). On the other hand, some research also suggests that species-poor communities resist invasions better than species-diverse ones (Levine and D'Antonio 1999; Stohlgren 1999). Regardless of the number of indigenous species present on a site, it appears that sites already inhabited with local native species resist introductions of invasive species better than sites where native plant populations are low or weakened. Can you think of situations in your own land management area where this is the case? Do you think that your area is less invulnerable because the native plant community is more diverse or less diverse?

Characteristics of Introduction

One-percent (1%) rule. The inflow of exotic plant species into new regions is a continuous process and many believe it is happening at an ever-faster rate. However, research suggests that only a few of the many alien species that arrive in a new region actually become established there, and then only a small percentage of the established species go on to become invasive. For example, Williamson (1996) estimated that only 10% of all species introduced into the British flora actually became established, and then only 10% of those were invasive enough to be considered as pests. He presented this finding as the “1% rule” for plant invasions, which has since been supported by other scientists. For example:

- Kowarik (1995) reports that of 3,150 woody species introduced into Brandenburg and Berlin, Germany, 10% spread beyond the initial site of introduction, 2% became established, and only half of those naturalized. Kowarik noted that this ratio was 10:2:1 for all the Central European flora of vascular plants (12,000 species).
- Weeda (1987), examined a number of alien species in the Netherlands. He estimated that approximately 75 species, or 1% of the total, penetrated the natural vegetation, thus supporting the later estimates of Williamson (1996) and Kowarik (1995).
- Kornas (1990) found that of the 799 plant species introduced around Montpellier, France, 692 species failed to become established.

Lag Time. Although some invasive species may experience rapid population growth after introduction (usually insects, like the African bee), most invasive plant species have a substantial lag time between initial introduction and subsequent population growth. For example, Kowarik (1995), in his historical reconstruction of the invasion dynamics of 184 alien woody species, found that only 6% of the species had spread within 50 years after their first introduction to the area.

Twenty-five percent lagged up to 100 years, 51% lagged for 200 years, 14% for up to 300 years, and 4% for more than 300 years. Life form also had a significant affect on lag phase. On average, trees had a longer lag phase (170 years) than shrubs (131 years). Lag times for herbaceous species are much shorter (decades or less) than for either trees or shrubs. Horticultural or ornamental plants are believed to be a source of new introductions of many potentially invasive plant species.

According to Crooks and Soule (1999), three categories of population lag can be recognized:

1. Inherent lag times caused by normal population growth (**Figure 3-3**), which will vary among species.
2. Prolonged lag times caused by environmental factors related to improving ecological conditions for the organism. These conditions can be either natural or caused by humans, and include soil disturbance and nutrient enrichment, climate change, dispersal vectors, and intra-specific interactions.
3. Genetic factors that usually improve fitness. Some species have a so-called “general purpose” genotype that enables them to grow over a wide range of environments. If an introduced species lacks such characteristics, it will be confined to a restricted area until a genetic change occurs through recombination, introgression, or, to a lesser degree, mutation, and then adapt to the new environment. The likelihood of overcoming genetic lag or fitness deficit is proportional to the population size and the rate of genetic adaptation (Crooks and Soule 1999).

Disturbance and Habitat Porosity (Site Invasibility). Disturbance is believed to be a major factor favoring plant introduction and the overall invasive process. Grime (1979) defines disturbance as the removal or damage of plant biomass. Pickett and White (1985) view disturbance more completely as “any

relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources or substrate availability or the physical environment.” Disturbance may be caused by large-scale events such as fire, floods, and storms, or smaller-scale events like soil turnover or vegetation removal by animals or humans (Hobbs 1991).

Plant introduction may be the direct result of destruction of vegetation, or it may indirectly result from changes in resource levels or other conditions that subsequently favor population growth through the ecological processes listed in Table 3-1. Likewise, disturbance does not always lead to plant invasion, but it may provide a temporary location or “safe site” for a potential invasive species to establish a founding population.

Some form of disturbance usually accompanies the successful introduction and subse-

quent colonization of invasive plant species. For example, Humphries et al. (1991) lists a number of major “environmental” weeds in Australia, along with their association with at least one type of disturbance (**Table 3-2**). In Table 3-2 we also see that multiple disturbances usually increase the chance of successful plant introduction and invasion. Hobbs and Atkins (1988) also observed that disturbance in general, and multiple disturbances in particular, increased the density and biomass of introduced species. On the other hand, Apert et al. (2000) believe that stress; i.e., environmental factors that limit the growth of vegetation, can also contribute significantly to invasability. Apert also provides evidence that environmental disturbances that are either greater or less than the evolutionary level for a site contribute to the susceptibility of sites to invasive plants.

Table 3-2. Species identified as the most serious environmental weeds in Australia, and types of disturbance favoring spread and/or establishment (derived from Humphries et al. 1991)

Species	Disturbance Type
Acacia gum	Cattle dung, floating
Buffelgrass	Floods, cattle
Bitou bush	Rabbits, cattle, roading, sandmining, natural disturbances
Rubber vine	Drought followed by floods, fire, grazing
Water hyacinth	Human interference, nutrient enrichment
Catclaw mimosa	Clearing, water level fluctuations
Bridal creeper	?
Retama	Flooding
Mission grass	Vehicular spread along roads, small-scale disturbance by pigs, bandicoots
Velvet mesquite	Flooding
Giant salvinia	Human transport, nutrient enrichment
Tamarisk	Flooding, high rainfall years
Bengal clock vine	Edge or gap formation

Porosity. Scientists often use mathematical models to describe how plant populations grow. A common way to study the growth and movement of invasive species is through reaction-diffusion models. These models contribute a parameter of population growth that describes the openness or porosity of the community to further invasion by another species.

We will illustrate this concept two ways: by viewing a [porosity animation](#) (turn on your speakers), and reading through the following information describing the diagram below.

Consider two adjacent plots of land. Area A is a sagebrush community with yellow starthistle; Area B is a sagebrush community without yellow starthistle.

The degree of movement of starthistle in this example depends upon habitat porosity; that is, the number of vacant sites present in area B, availability of the sites to occupancy, and the number of vacant sites occupied by other species in the plant community. The rate of introduction differs over time based on the amount of area (vacant sites) open to possible establishment of the invading plant, in this case yellow starthistle. It also demonstrates the importance of disturbance in creating such niches, or safe sites, for successful establishment of the new species.

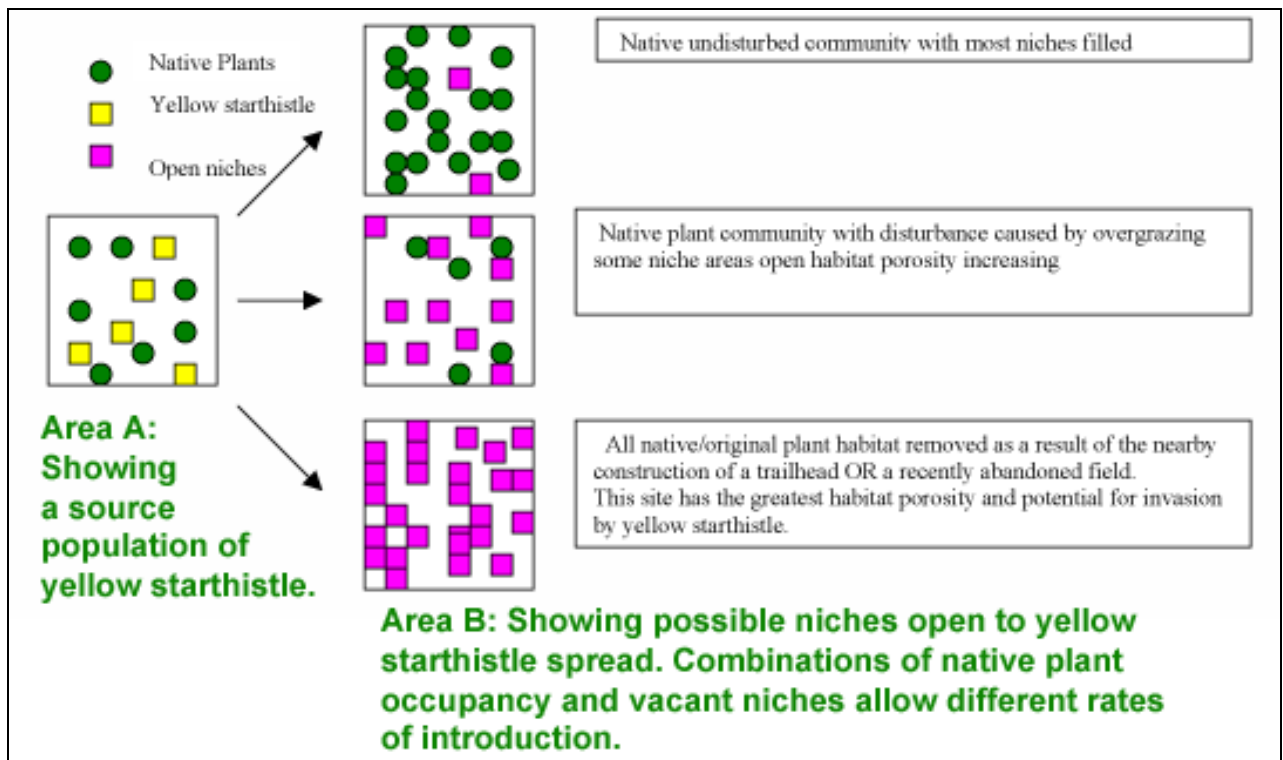


Figure 3-5. Example of environmental porosity

COLONIZATION PHASE

Colonization is characterized by geometric, exponential, population growth (Figure 3-2). During this “explosive” growth phase, the new plant species often becomes apparent and control efforts to halt its spread begin. This rate of spread is similar to the population growth rate of an organism in an ideal, resource-limitless environment and is therefore believed to be more a function of intrinsic biological characteristics of the species than of its growing environment.

For this reason, the colonization phase (Figure 3-6, expanded from Figure 3-2) of an invasive species is sometime referred to as its intrinsic rate of increase. It is thought to depend more on biological factors than environmental ones, though both can be important at times.

Biological Factors

There is no clear-cut description or list of attributes that make a plant species more invasive than another. However, some useful generalizations have been made. For example Rejmánek (2000) lists the following biological characteristics as being responsible for invasiveness:

- The ability of an individual or population to maintain relatively constant fitness over a wide range of environments. This is equivalent to Baker's (1974, 1995) “general purpose genotype.”
- Small genome size that is usually associated with short minimum generation time, short juvenile period, small seed size, high leaf area ratio, high seed size, high leaf area ratio, high relative growth rate.

- Dispersed easily by humans and animals.
- Ability to vegetatively propagate. This is an especially important characteristic in aquatic environments (Auld et al. 1982; Henderson 1991) and at high latitude (Pysek 1997).
- Alien plants belonging to exotic genera are more invasive than are alien species with native congeners. This may be partly because of an absence or limited number of resident natural enemies for that species (Darwin 1859; Rejmánek 1999).
- Plant species without dependence on specific mutualisms (root symbiosis, pollinators, seed dispersers, etc.) (Baker 1974; Richardson et al. 2000).
- Tall plants tend to invade mesic plant communities.
- Persistent seed banks; that is, seeds with different inherent dormancies that provide a random appearance through time and guarantee their survival and persistence.

Two Ways to Colonize: Sources and Satellites

Colonization occurs when plants in an introduced, founding (original) population reproduce and then increase sufficiently to become self-perpetuating. Cousens and Mortimer (1995) describe the radial expansion of such self-perpetuating patches or sources as an advancing front on all sides with a rate of increase that conforms to the following equation:

$$((\text{change in } A) / (\text{change in } t)) / A = 2\pi r 2t$$

where A equals the area occupied by the new species, r is the radius of the expanding population, and t is time in years or generations.

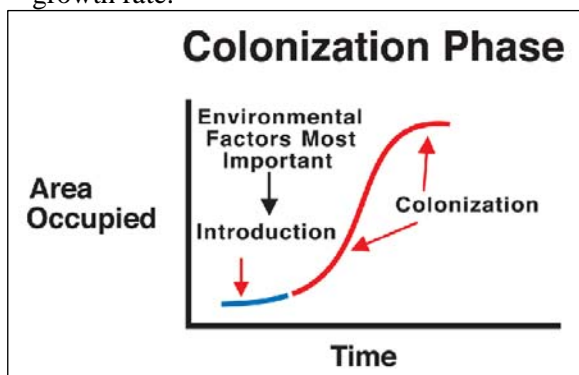


Figure 3-6. The colonization phase of the invasion process according to Cousens and Mortimer (1995).

From the equation we see that a patch should grow by half the distance of each previous generation (Cousens and Mortimer 1995), assuming successful recruitment continues within the founding population and the rate of expansion is constant (**Figure 3-7**). Although this model of expansion seems intuitively reasonable, it has received only limited examination in field studies with invasive plant species (Auld and Coote 1980; Moody and Mack 1988, Cousens and Mortimer 1995).

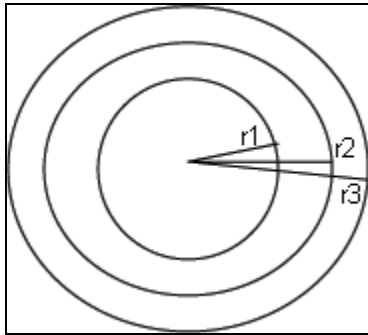


Figure 3-7. Diagram depicting patch expansion. The source patch will expand at a rate of half the distance of the previous generation (year).

It is also possible for some individuals from the founding source population to disperse widely (**Figure 3-8**) and to produce new satellite populations of the species. In this case, dispersing individuals that form satellite populations should have the same environmental requirements as the original introduction. Satellite populations will usually continue to grow, form their own patch, and eventually behave as a new source.

Thus, colonization by an invasive species can continue geometrically both from advancing fronts from existing patches, and from the wide-ranging satellites that arise from them. Caswell et al. (2003) present compelling evidence that aerial spread of invasive plants is most dependent on the annual dissemination of these widespread satellite populations. As you read about colonization, think about the populations in your management area; are they expanding as fronts or as satellite populations?

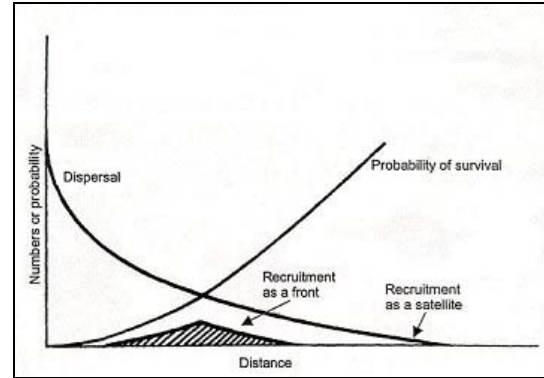


Figure 3-8. Recruitment of new genotypes as a function of the number of dispersed seeds and the probability of juvenile survival (From Cook, 1980, in O.T. Solbrig, ed., "Demography and Evolution in Plant Population"s; modified from Radosevich et al. 1997).

Source populations. In the absence of continual "safe site" availability, the advancement of source populations (patches) of invasive plant species is influenced most by the biological characteristics that influence their population growth. Thus, attempts to diminish patch size, and therefore colonization rates, should concentrate on the intrinsic biology of the species. For example, Maxwell et al. (1988, **Figure 3-9**) used a population demographic approach to examine population growth and management options of leafy spurge (*Euphorbia esula*).

Maxwell et al. (1988), following Watson (1985), divided the life history of leafy spurge into five stages: seeds, buds, seedling, vegetative shoots, and flowering shoots (Figure 3-9, top diagram). By identifying these stages, the process of population growth was determined. It was found that three important transitions must occur for patch growth to proceed; basal buds to vegetative shoots (G2), the number of basal buds that flowering shoots produced (V5), and the number of basal buds that vegetative shoots produced (V4). These three transitions were sensitive to their own density.

When these three density-dependent functions were simultaneously included in

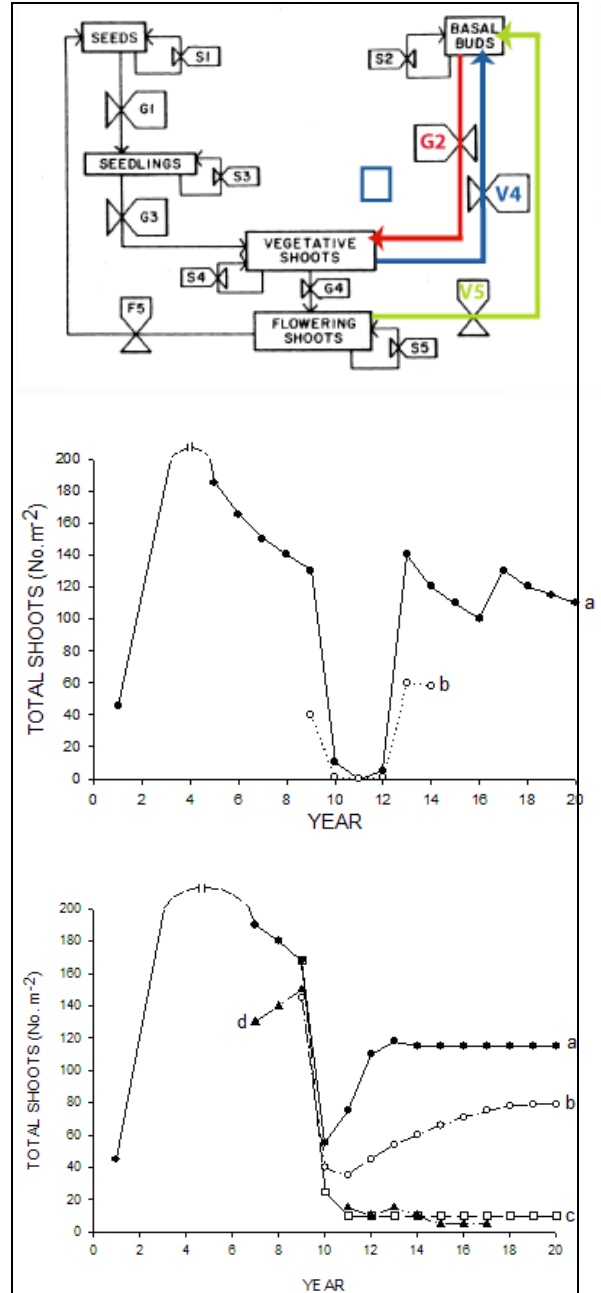
the model, initial exponential growth resulted, followed by decline and eventual stabilization of the simulated population (Figure 3-9, middle graph). They then subjected the simulated population of leafy spurge to several management tactics: a single application of picloram (Figure 3-9, middle graph: see a) and several levels of a foliage-feeding herbivore (Figure 3-9, bottom graph: see a, b, and c).

Also shown in Figure 3-9 (bottom graph: see d) is the actual effect of sheep grazing on real populations of leafy spurge. This example demonstrated how well the dynamics of population growth can be predicted from basic biological information. It also demonstrates the degree of patch reduction (i.e., slowed local colonization rate) that can be achieved by targeting particular life stages of the plant during management, in this case transitions G-2, V-4, and V-5. On the other hand, attempts to reduce the overall (regional) population spread of an invasive species are usually more effective if control tactics are focused on satellite populations originating from large patches.

Figure 3-9. Top diagram shows the five stages of leafy spurge life history and the three important transitions that must occur for patch growth to proceed: basal buds to vegetative shoots (G2), the number of basal buds that flowering shoots produced (V5), the number of basal buds that vegetative shoots produced (V4).

Middle graph shows leafy spurge population simulation and an application of picloram simulated at year 10 (a), and the observed effects (b).

Bottom graph shows population simulation with the introduction of a foliage-feeding herbivore at year 10 that removes (a) 40, (b) 50, and (c) 60 percent of stems. Observed effects from sheep feeding on leafy spurge also are shown (d) (modified from Maxwell et al. 1988 in Radosevich et al. 1997).



Satellite populations. Populations of invasive plant species also expand by satellite populations that are often isolated from their source. The equation of Cousens and Mortimer (1995) presented earlier also suggests that such satellite populations, because they are younger, should expand most rapidly. However establishment of a new satellite requires the existence of a vacant site for a dispersing propagule to occupy. Prevention of vacant sites by minimizing environmental porosity is thus a key to reducing the colonization rate of invasive species. Still, satellite populations will exist on the landscape. A relevant research and management question therefore emerges; i.e., whether to contain the “source” or “satellite” populations of an invading species after successful introduction has occurred.

Cousens and Mortimer (1995) and Moody and Mack (1988) suggest that the preferred containment strategy would be to remove satellite populations as they occur over space and through time, since these populations expand more rapidly and potentially cover greater area than the front of a source population. For example, Ghersa et al. (2002) determined that satellite populations of johnsongrass that were uniformly distributed over a previously vacant area occupied that area more quickly than the advancing front of its adjacent source population. Nonetheless, this strategy of expansion has received relatively little experimental attention by many field scientists. Land managers also continue to control source rather than satellite populations of invading species (Moody and Mack 1988; Cronk and Fuller 1995; Zamora and Thill 1999), perhaps because such populations are much more obvious than the smaller satellite populations or because control tactics seem more effective.

In linear habitats that are often disturbed as well, such as roads or riparian areas, it may be impossible to find long-distance-dispersed satellite populations. In these cases it would probably be best to contain source populations of invasive species; e.g., Japanese knotweed, since they can be located.

NATURALIZATION PHASE

A species is becoming naturalized in its new environment when it successfully establishes new self-perpetuating populations, is dispersed widely throughout a region, and is incorporated into the resident flora.

As previously discussed, a lag time of years to decades is usual between the time of first arrival and the eventual rapid occupation by a naturalizing invading species (Figures 3-4, 3-6). During subsequent colonization some individual plants disperse, survive, and produce new populations away from the founding or source populations (e.g., Forcella and Harvey 1983; Forman 1995; Ghersa and Leon 1999; Figure 3-8). Such “outliers” push the range of an invading species more rapidly than is possible by normal dispersal and patch development (Silvertown and Lovett-Doust 1993; Caswell et al. 2003).

At some carrying capacity, K , the population approaches a quasi-threshold density where its population growth may remain near one (1); that is, it may stabilize and not expand very quickly (Figures 3-2 and 3-3). The K density occurs when niche occupancy and available resources limit the rate of spread. This phase is controlled by environmental factors, so predictions of risk for populations approaching K should also focus on environmental parameters. Most agencies remove weeds from their target list (e.g., noxious weed lists) in this phase as they are too difficult and expensive to eradicate or control (see **Figure 3-10**).

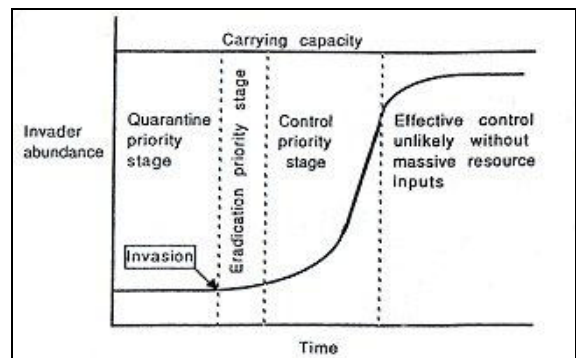


Figure 3-10. Management strategies used in relation to the invasion process (after Chippendale 1991).

ENVIRONMENTAL FACTORS THAT INFLUENCE POPULATION GROWTH

Habitat Suitability for the Invasion Process

Disturbed ecosystems (by either human or natural causes) often have a higher susceptibility to invasions than those with long periods in late successional phases. An explanation for semi-arid and grassland vulnerability to invasion by exotic plant species is that these areas have spatially open niches; that is, sites that are devoid of vascular plants for some or most of the year (Baker 1986). However, it is important to note that biological factors may influence invasion as well. For example, plants that have life forms dissimilar to the native vegetation have also invaded some ecosystems. The conversion to annual grasslands from tussock grasslands in California and the invasion of *Opuntia stricta* into Australia (a cactus where no members of Cactaceae existed previously) are examples where biological characteristics play an important role in the invasion process.

The environmental factors most responsible for population growth and persistence of invasive species are soil, climate, and land use.

Soil

Many studies show that both plant growth (e.g., Ecological Site Descriptions for Forestland and Rangeland, NRCS 1997, 1998) and plant invasions occur within certain ranges of soil types (Hueneke et al. 1990). Although soil-mapping units often have indistinct boundaries, species are usually most productive within certain soil types. The isolation of soil mapping units delineating soil types that each target species finds suitable could provide a criterion for studying the spread of invasions.

Climate

Climate also drives both abiotic and biotic thresholds for growth in ecosystems. For example, the retreat of forests to mountainous areas over the last 10,000 years is a direct result of changing climate

(Betancourt et al. 1990). Climate can change habitat suitability over short time scales through drought, and seasonal frost and flooding (Nilson and Muller 1980). Invasive plant species tend to adapt well to a variety of habitats, but usually invade areas with climates similar to those of their native range first, and then adapt to other climates later (Panetta and Mitchell 1991); however, notable exceptions also occur (Mack 1995). Topography and elevation also influence climate and the species that can grow at a given location.

Land Use

The condition of the land is a third general driving component in habitat suitability and invasion. Changes in land use are thought to be the single most important factor in species extinction (Cousens and Mortimer 1995) and to have strong influences on invulnerable sites (Elton 1958 as cited by Hodkinson and Thompson 1997). Humans to some degree have modified most of the world's ecosystems and this has direct effects on invasion suitability. Some ecosystems are altered by the presence of the invasive plant itself (D'Antonio and Vitousek 1992) through an increase in fire frequency, nitrogen depletion, or allelopathic chemicals. Other species are adapted for change in land use where native species are not; e.g., resilience to grazing pressure in the Great Basin (Mack and Thompson 1982).

MANAGEMENT BASED ON THE INVASION PROCESS

Land managers routinely use several general strategies based on the invasion process to manage invasive plant species. Various tools may then be employed depending on the prevalence and abundance of the plants detected. The most common strategies used against invasive plants and their relationship to the invasion process are shown in **Figure 3-10**. To view this figure as an animation click on [management animation](#) (text but no sound).

PREVENTION

Like many other pest management problems or disease epidemics, prevention is a key tool used against exotic invasive plants. The most common forms of prevention are national, state, or local quarantines. Because of the 1% rule for successful introductions, quarantine, if successfully implemented, can be a very effective management approach.

Early Detection and Eradication

Since exotic invasive plants usually have a long lag period following introduction but before exponential growth during colonization, they can usually be eradicated at that time if recognized. Thus, early detection and rapid response (EDRR) usually requires an informed and vigilant public and the ability to remove the new population once detected. Land managers who can act quickly to eradicate an exotic invasive plant usually avoid the long-term costs of containing the plant and the damage it causes to the land.

Containment/Control

During rapid population growth or colonization, managers should abandon efforts to eradicate the plant species and focus on control or containment. If no action is taken to contain the species from spreading, it can eventually become naturalized, occupying the land close to its carrying capacity and replacing local species.

Restoration

At the naturalization phase of the invasion process, it is difficult to devise and implement strategies to manage such a widespread problem species unless substantial amounts of time and money are spent. Usually, attempts at restoration are confined to local areas, such as stands, fields, and occasionally watersheds.

Land managers and management agencies tend to direct resources toward control of weed species that are already major problems, and not much toward the prevention, early detection, and or even early containment of new exotic plants. Most conventional and biological control programs get under-

way only after a particular species is an obvious problem. Understanding the biological and environmental factors that allow for the appearance of an invasive plant species in a habitat will help land managers undertake appropriate action. However, changing prevailing land management regimes, such as grazing or logging practices, may be necessary to avoid the continual reoccurrence of an invasive species episode.

SUMMARY

Plant invasions are influenced by both the biological characteristics of the invasive plant species and the environmental characteristics of the site(s) being invaded. These factors often interact allowing successful invasions to occur. Stages of the invasion process are also influenced by characteristics of biology and environment. Thus, the invasive process can inform land managers about the best time to use tool or tactics that limit plant invasions.

Management activities to prevent invasions, such as quarantines or early detection/eradication, are best informed by environmental factors that relate to site. Restoration of an area already heavily infested by an invasive plant usually requires manipulation of site factors to favor desirable plants while disfavoring the invasive plant species. Management to contain/control an invasive species usually is best informed by the biological characteristics of the species that influence the growth and expansion of the invasive plant population over an area.

LITERATURE CITED

- Alpert, P., E. Bone, and C. Holzapfel. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics* 3(1): 52–66.
- Auld, B.A., and B.G. Coote. 1980. A model of a spreading plant population. *Oikos* 34:287-292.
- Auld, B.A., J. Hosking, and R.E. McFadyen. 1982. Analysis of the spread of tiger pear and parthenium weed. *Australian Weeds* 2:56-60.
- Baker, H.G. 1974. The evolution of weeds. *Annual Review of Ecological Systems* 5:1-24. Baker, H.G. 1986. Patterns of plant invasion in North America. In: H.A. Mooney and J.A. Drake (Eds.), *Ecology of Biological Invasions of North America and Hawaii*. Springer-Verlag, New York, NY, pp. 44-58.
- Baker, H.G. 1995. Aspects of the genecology of weeds. In: A.R. Kruckebert, R.B. Walker, and A.E. Leviton (eds.), *Genecology and Ecogeographic Races*. Pacific Division American Association for the Advancement of Science, San Francisco, CA, pp 189-224.
- Betancourt, J.L., T.R. VanDevender, and P.S. Martin. 1990. Fossil packrat middens: The last 40,000 years of biotic change in the arid west. University of Arizona Press, Tucson, pp. 259-289.
- Burke, M. J., and J.P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* 77(3): 776-790.
- Caswell, H., Lensink, R., Neubert, M.G. 2003. Demography and dispersal: Life table response experiments for invasion speed. *Ecology* 84(8): 1968-1978.
- Chippendale, J.F. 1991. Potential returns to research on rubber vine (*Cryptostegia grandiflora*). M.S. Thesis. University of Queensland, Brisbane.
- Cousens, R., and Mortimer, M. 1995. *Dynamics of Weed Populations*. Cambridge University Press, New York, NY, pp. 21-54.
- Cronk, Q.C.B., and Fuller, J.L. 1995. *Plant Invaders, a 'people and plants' conservation manual*. Chapman and Hall, London, p. 45.
- Crooks, J., and M.E. Soule. 1999. Lag times in population explosions of invasive species: causes and implications. In: O.T. Sandlund, S.J. Schei, and A. Vikens (eds.), *Invasive species and Biodiversity Management*. Kluwer Academic Publishers, The Netherlands, pp. 103-125.
- Darwin, C. 1859. *The Origin of Species by Means of Natural Selection*. Murray, London.
- D'Antonio, C.M., and P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.
- Forcella, F. and S.J. Harvey. 1983. Relative abundance in an alien weed flora. *Oecologia* 59:292-295.
- Forman, R.T.T. 1995. *Land Mosaics, The ecology of landscapes and regions*. Cambridge University Press, New York, pp. 393-397.
- Ghersa, C. M., E. H. Satorre, R. L. Benech Arnold, and M. A. Martínez-Ghersa. 2000. Advances in weed management strategies. *Field Crops Research* 67:95–105.
- Grime, J.P. 1979. *Plant Strategies and Vegetation Processes*. John Wiley & Sons, New York.
- Groves, R.H. 1986. Invasion of Mediterranean ecosystems by weeds. In: B. Dell, A.J.M. Hopkins and B.B. Lamont (eds.), *Resilience in Mediterranean-type Ecosystems*. Junk, Henderson, L. 1991. Alien invasive *Salix* spp. (willows) in the grassland biome of South Africa. *South African Forestry Journal* 157:91-95.
- Hobbs, R.J. 1991. Disturbance a precursor to weed invasion in native vegetation. *Plant Protection Quarterly* 6:99-104.
- Hobbs, R.J., and L. Atkins. 1988. The effect of disturbance and nutrient addition on native and introduced annuals in the Western Australian wheat belt. *Australian Journal of Ecology* 13:171-179.
- Hodkinson, D. J., and K. Thompson. 1997. Plant dispersal: the role of man. *Journal of Applied Ecology* 34:1484–1496.

- Huenneke, L.F., S.P. Hamburg, R. Koide, H.A. Mooney, and P.M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71(2):478-491.
- Humphries, S.E., R.H. Groves, and D.S. Mitchell. 1991. Plant invasions and Australian ecosystems: a status review and management directions. In: *Plant Invasions: The incidence of Environmental Weeds in Australia*. Australian National Parks and Wildlife Service, Canberra, Australia, pp. 1-127.
- Kornas, J. 1990. Plant invasions in Central Europe: historical and ecological perspectives. In: F. di Castri, and A.J. Hansen (eds.), *Biological Invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 19-36.
- Kowarik, I. 1995. Time lags in biological invasions with regard to the success and failure of alien species. In: P. Pysek, K. Prach, M. Rejmanek, and M. Wade (eds.), *Plant Invasions, General Aspects and Special Problems*. SPB Academic Publishers, pp. 15-38.
- Latore, J., P. Gould, and A.M. Mortimer. 1998. Spatial dynamics and critical patch size of annual plant populations. *Journal of Theoretical Biology*: 190(3):277-285.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of the evidence linking diversity and invasibility. *Oikos* 87: 15-26.
- Mack, R.N. 1995. Invading plants: their potential contribution to population biology. In J. White, (Ed.) *Studies in Plant demography*. Academic Press, London, pp. 127-142.
- Mack, R.N., and J.N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. *American Naturalist* 119:757-773.
- Maxwell, B.D., M.V. Wilson, and S.R. Radosevich. 1988. Population modeling approach for evaluating leafy spurge (*Euphorbia esula*) development and control. *Weed Technology* 2:132-138.
- Moody, M.E., and R.N. Mack. 1988. Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* 25:1009-1021.
- Nilson, E.T., and C.H. Muller. 1980. A comparison of the relative naturalization ability of two *Schinis* species in Southern California. *Bulletin of the Torrey Botanical Club* 107:51-56.
- National Resource Conservation Service. 1997. *National Range and Pasture Handbook*: USDA, Natural Resources Conservation Service Grazing Lands Institute, 190-vi-NRPH, September 1997, Washington, D.C.
- National Resource Conservation Service. 1998. *National Forestry Manual*, 190. ftp://ftp-fc.sc.gov.usda.gov/NSSC/National_Forestry_Manual/2002_nfm_complete.pdf
- Panetta, F.D., and N.D. Mitchell. 1991. Homoclimate analysis and the prediction of weediness. *Weed Research* 31:273-284.
- Pickett, S.T.A., and P.S. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, FL.
- Pysek, P. 1997. Clonality and plant invasions: can a trait make a difference? In: H. deKroon, and H. van Groenendael (eds.), *The Ecology and Evolution of Clonal Plants*. Backhuys, Leiden, pp. 405-427.
- Radosevich, S.R., M.M. Stubbs, and C.M. Ghera. 2003. Plant invasions—processes and patterns. *Weed Sci.* 51:254-259.
- Radosevich, S.R., J. Holt, and C.M. Ghera. 1997. *Weed Ecology, Implications for Management*. John Wiley and Sons. New York, NY, pp. 114-160.
- Rejmánek, M. 1999. Invasive plant species and invulnerable ecosystems. In: O.T. Sandlund, P.J. Schei, and A. Vilken (eds.), *Invasive Species and Biodiversity Management*. Kluwer, The Netherlands, pp. 79-102.
- Rejmánek, M. 2000. Invasive plants: approaches and predictions. *Australian Ecology* 25:497-506.
- Richardson, D.M., N. Allsopp, C. D'Antonio, S.J. Milton, and M. Rejmanek. 2000. Plant invasions – the role of mutualisms. *Biological Reviews* 75:65-93.
- Sauer, J.D. 1988. *Plant Migration. The Dynamics of Geographic Patterning in seed Plant Species*. University of California Press, p. 3.

- Silvertown, J.W., and J. Lovett-Doust. 1993. Introduction to Plant Population Biology. Blackwell Scientific Publications, London, pp. 107-115.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* 69(1): 25-46.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78(1): 81-92.
- Watson, A.K. 1985. Integrated management of leafy spurge. In: A.K. Watson (Ed.), *Leafy Spurge*. Weed Science Society of America, Champaign, IL, pp. 93-104.
- Weeda, E.J. 1987. Invasions of vascular plants and mosses into the Netherlands. In: W. Joenje, K. Bakker, and L. Vlijm (eds.), *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Amsterdam. Series C: Biological and Medical Sciences*, pp 19-29.
- Williamson, M. 1996. *Biological invasions*. Chapman & Hall, London, UK.
- Zamora, D.L and D.C. Thill. 1999. Early detection and eradication of new weed infestations. In Sheley, R.L and Petroff, J.K. (eds.), *Biology and Management of Noxious Rangeland Weeds*. Oregon State University Press, Corvallis, OR, pp. 73-84.