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Principles for Ecologically Based Invasive Plant Management

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Land managers have long identified a critical need for a practical and effective framework for designing restoration strategies, especially where invasive plants dominate. A holistic, ecologically based, invasive plant management (EBIPM) framework that integrates ecosystem health assessment, knowledge of ecological processes, and adaptive management into a successional management model has recently been proposed. However, well-defined principles that link ecological processes that need to be repaired to tools and strategies available to managers have been slow to emerge, thus greatly limiting the ability of managers to easily apply EBIPM across a range of restoration scenarios. The broad objective of this article is to synthesize current knowledge of the mechanisms and processes that drive plant community succession into ecological principles for EBIPM. Using the core concepts of successional management that identify site availability, species availability, and species performance as three general drivers of plant community change, we detail key principles that link management tools used in EBIPM to the ecological processes predicted to influence the three general causes of succession. Although we acknowledge that identification of principles in ecology has greatly lagged behind other fields and recognize that identification of ecological principles and the conditions in which they hold are still being developed, we demonstrate how current knowledge and future advances can be used to structure a holistic EBIPM framework that can be applied across a range of restoration scenarios.

Key words: Ecosystem repair, land management, planning, restoration, succession.

Land managers have long identified a need for a practical and effective framework for achieving restoration goals (Cairns 1993; Clewell and Rieger 1997). Accordingly, much research in restoration ecology has focused on developing frameworks and conceptual models linking ecological theory to various restoration approaches for degraded systems (Aronson and LeFloch 1996; King and Hobbs 2006; Westoby et al. 1989; Whisenant 1999). One major area of advancement is centered on the movement toward ecologically based invasive plant management (EBIPM) (Krueger-Mangold et al, 2006; Sheley et al. 2006). The broad goal of this framework is to move management away from strategies focused exclusively on controlling abundant invaders and toward strategies focused on repairing damaged ecological processes that facilitate invasion. Although small plot studies have demonstrated compelling evidence supporting EBIPM as an effective and sustainable approach to managing invasive plants (Mangold and Sheley 2008; Sheley et al. 2009), lack of an easily applied, holistic framework that synthesizes ecological knowledge into a useful format has limited adoption and implementation of EBIPM by land managers.

Development and widespread adoption of a general EBIPM framework require integration of several key components, including (1) methods to assess ecological processes leading to degradation; (2) a conceptual framework, based on ecological principles, to allow managers to identify appropriate tools and strategies that alter ecological processes and mechanisms that allow plant communities to change in a favorable direction; and (3) a method to measure success and to improve management strategies when necessary (Hobbs and Harris 2001; Hobbs and Norton 1996). Advances in ecosystem health assessment and adaptive management have been made, and a general conceptual basis for EBIPM, based on successional management, has been developed (Krueger-Mangold et al. 2006; Morghan et al. 2006; Pyke et al. 2002). However, well-defined principles on which to base application of tools and strategies managers typically use have been slow to emerge, mostly because of the complex nature of biological invasions (Daehler 2003; Williamson and Fitter 1996). To be useful, EBIPM will require that our understanding of the mechanisms and processes influenc-

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Interpretive Summary

Land managers have long identified a critical need for a practical and effective framework to guide the implementation of successful restoration. Using the core concepts of successional management that identify site availability, species availability, and species performance as the three general causes of plant community change, we detail key principles that can link management tools to the ecological processes predicted to influence plant community change.

By integrating ecological principles into a management framework, the framework can be applied across a range of restoration scenarios, allowing mangers to transfer knowledge gained from one situation to another.

ing plant community change be complete enough to begin identifying general principles on which managers can base their decisions (Werner 1999).

The need to develop conceptual frameworks for restoration based on ecological principles has been widely recognized (Hastings et al. 2005; Young et al. 2005). Identifying principles in ecology, however, has greatly lagged behind other fields causing some question about the ability of ecology and associated applied disciplines to become a predictive science (Berryman 2003). Despite these concerns, some subdisciplines in ecology, such as population ecology, have made substantial progress in identifying general principles capable of predicting dynamics of populations under specific sets of conditions (Berryman 2003). In addition, principles associated with disturbance have been described (Dale et al. 2000). Most recently, major advances in understanding evolutionary constraints and trade-offs associated with plant ecological strategies as well as ecosystem characteristics influencing invasibility have emerged, allowing some principles related to invasion to be identified (Stohlgren et al. 1999; Wright et al. 2004). Although the specific sets of conditions in which these various principles hold are only beginning to be understood, advances have been sufficient to start using these results to formulate principles for EBIPM.

A holistic framework for EBIPM has been proposed, but principles to support this framework have not been developed (Figure 1). The broad objective of this article is to synthesize current knowledge of the mechanisms and processes that drive plant community succession into ecological principles for EBIPM. For the purposes of this article, we define ecological principles as fundamental causes that link ecological processes to the relative abundance of desired and invasive species. Therefore, principles identified in this article indicate a relative magnitude and direction of change that a management strategy likely will have on invasive and desired plants. With this definition, we recognize that in many situations we have an incomplete understanding of the conditions in which any particular principle holds. We first briefly outline the proposed holistic EBIPM framework (Figure 1). Under each of the three causes of succession, we then detail key principles that link management tools to ecological processes driving plant community change.

A Holistic Framework for EBIPM and a Need for Principles

The core framework for EBIPM is based on the successional management model developed by Pickett et al. (1987) (Figure 1). This model includes three general causes of succession (site availability, species availability, and species performance), ecological processes that influence these causes and factors that affect ecological processes. The core point of this model is that the ability of managers to guide plant community change in a favorable direction hinges on the ability to modify and repair the appropriate ecological processes that drive the three general causes of succession (Luken 1990; Sheley et al. 2006; Whisenant 1999). This framework integrates assessment and adaptive management efforts with the successional management model. Therefore, this holistic approach incorporates a conceptual model linking drivers of plant community change to specific ecological processes, methods for identifying damaged ecological processes that may be responsible for directing successional patterns in a negative direction, and a formal procedure quantifying the success of various management strategies and making ongoing adjustments to management as needed. However, this current framework provides no general principles allowing mangers to understand how various tools will modify ecological processes. Instead, managers are left to use their own experience and intuition to identify tools and approaches needed to successfully repair damaged processes. To provide managers with a general restoration framework that has some ability to predict outcomes across a suite of scenarios but is practical and easy to implement, the principles that link management tools and strategies to ecological processes must be identified.

Ecological Principles Forming the Conceptual Basis of EBIPM

The successional management framework proposes three general causes of succession and the processes that influence those three causes. In this section, we take an initial step toward synthesizing existing scientific literature and identifying general principles that will allow mangers to link tools commonly used in invasive plant management to ecological processes that managers may want to alter in their efforts to restore weed-infested systems. For each of the three causes of succession, the general ecological processes that influence the causes are described, then principles are outlined that

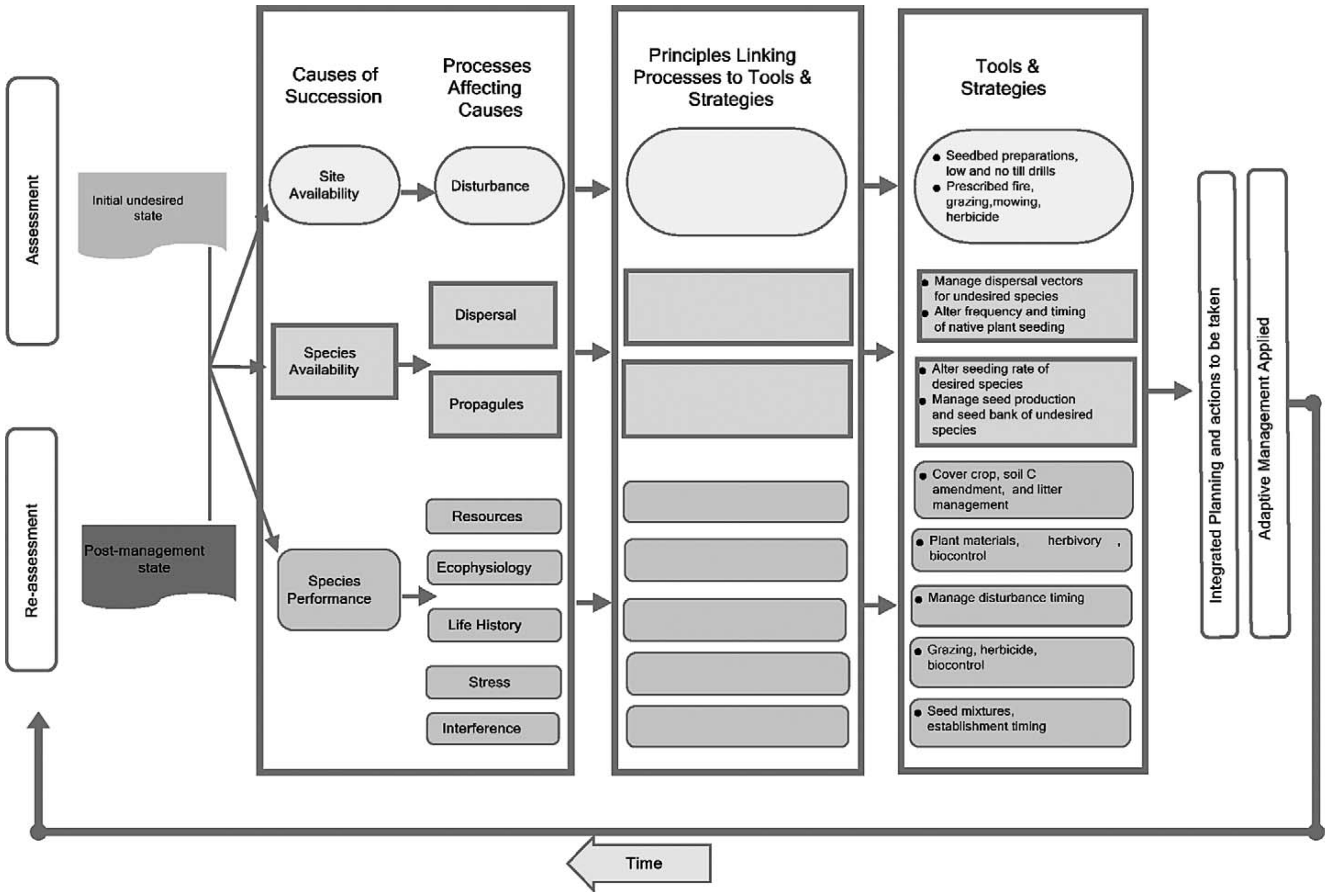

Figure 1. Integration of ecological principles into a holistic framework for ecologically based invasive plant management. This figure illustrates how development and refinement of ecological principles allow managers to identify how various tools and strategies will modify damaged ecological processes, ultimately allowing the underlying causes of invasion to be treated. Framework steps include (1) initial assessment of ecological processes; (2) use of the successional management model, developed by Picket et al. (1987), identification of key ecological process that influence the three general causes of succession; (3) use of principles that link management tools and strategies to ecological processes that need to be repaired; (4) identification of tools and strategies managers can use to repair ecological processes; (5) use of adaptive management procedures to adjust management outcomes; and (6) reassessment of the postmanagement state, which allows continual adjustment of tools and strategies applied. A subset of these tools and strategies are shown. Principles associated with each process are listed in Table 1.

pertain to each ecological process. These principles detailed below are outlined in Table 1.

Site Availability. A sufficient amount of safe sites must be available to incoming propagules for species composition to change. A safe site provides the set of conditions allowing a seed to germinate and a seedling to establish. Such sites can include factors such as soil water content, air and soil temperature, light, soil organic matter, soil texture, density, and identity and distribution of neighboring plants (Harper et al. 1965). Traditionally, plant communities have been classified as being limited by either propagule or safe site availability (Turnbull et al. 2000). Most communities, however, tend to exhibit some degree of both propagule and safe site limitations (Clark et al. 2007). In general, site availability tends to be more limiting in late successional plant communities and in portions of the community with higher vegetative cover (Turnbull et al. 2000). Disturbance is the central ecological process affecting safe site availability and is, therefore, a double-edge sword. Some form of disturbance is natural in all systems and is fundamental to maintaining recruitment windows for newly arriving and established species (Hobbs and Huenneke 1992). On the other hand, disturbance also provides opportunities for invasive plants to establish (Burke and Grime 1996).

Process: Disturbance. Disturbance can be defined as a relatively discrete event in time that changes resource availability or the physical environment by altering the

Table 1. Principles for ecologically based invasive plant management that link tools and strategies managers can use to modify and repair ecological processes underlying the three general causes of succession (Figure 1).

Causes of succession	Processes	Principles linking management tools and strategies to processes
Site availability	Disturbance	• Lower disturbance frequencies favor establishment of desired species compared with higher disturbance frequencies (Noble and Slatyer 1980; Rejmanek and Richardson 1996) • Lower disturbance intensity favors establishment of desired species compared with higher disturbance intensity (Berendse et al. 1992; Davis 2000; Lambers and Poorter 1992) • Smaller-scale disturbances spread through time are less likely to promote growth of invasive plant populations than simultaneous, large-scale disturbances (Benefield et al. 2001; Meyer et al. 2007; Noble and Slatyer 1980)
Species availability	Propagule dispersal	• Increasing frequency of dispersal of desired species and decreasing frequency of dispersal of undesired species can allow plant communities to change in a favorable direction (Sale 1977) • Less-competitive desired species can "win" a safe site from more competitive invasive species by arriving at the safe site first (Egler 1952; Drake 1991; Korner et al. 2008)
	Propagule pressure	• Increasing propagule pressure of desired species and decreasing propagule pressure of undesired species can allow plant communities to change in a favorable direction (Sale 1977; von Holle and Simberloff 2005) • Control of seed production by invasive plants is required to realize benefits of seeding desired species (DiVittorio et al. 2007; Smith and Fretwell 1974; Turnbull et al. 1999) • Damage to vegetative material can have a larger negative effect on seed production by desired plants than by invasive plants (Caldwell et al. 1981; Hempy-Mayer and Pyke 2008; Rogers and Siemann 2005)
Species performance	Resource availability	• Managing environments for low resource availability favors resource conservation over resource capture by plants, favoring desired species over invasive species (Diaz et al. 2004; Fraser and Grime 1999; Wright et al. 2004) • Initial establishment of desired species needs to be successfully managed to realize any benefit of resource management (Chapin 1980; DiVittorio et al. 2007) • Resource availability can be minimized primarily by maximizing biomass production and secondarily by managing for variation in traits such as phenology and root distribution of dominant species (Fargione and Tilman 2005; Grime 1998; Zavaleta and Hulvey 2006) • Resources available to an invader can be minimized by establishing desired species that are functionally similar to an invader (Botkin 1975; Pokorny et al. 2005; Turnbull et al. 2005)
	Ecophysiology	• Managing environments to favor resource conservation over resource capture will favor desired species over invasive species (Coley et al. 1985; Diaz et al. 2004; Lambers and Poorter 1992, Lambers et al. 1998; Leishman et al. 2007; van Aredonk et al. 1997; Wright et al. 2004) • A sufficient amount of abiotic or biotic stress needs to be applied at appropriate times to inhibit performance of invasive species in low nutrient environments (Coley et al. 1985; Lambers et al. 1998)
	Life history	• Less-frequent and less-intense disturbances favor establishment and population growth of desired species (Grime 1977; MacArthur and Wilson 1967; Rejmanek and Richardson 1996) • Establishing desired communities with species having a diverse life history can increase stability (Chesson and Huntly 1997; Grime 1987)
	Stress	• Moderate, prolonged stress favors desired species over invasive species compared with short-duration, intense stress (Leps et al. 1982, MacGillivray et al. 1995, Niinemets et al. 2003) • Desired species with high tissue density are more resistant to stress than species with lower tissue density (Lambers and Poorter 1992; Leishman et al. 2007; Wright et al. 2004)
	Interference	• If priority effects are managed, desired species have a proportionately greater competitive effect on invasive species and a greater ability to respond to competitive pressure of invasive species in low-resource environments compared with high-resource environments (Chapin 1980; Lambers and Poorter 1992; Leishman et al. 2007) • Desired species or functional groups with patterns of resource capture similar to that of the invader have a greater competitive effect per unit of biomass compared with species with less-similar patterns of resource capture (Grime 1998; Dukes 2002; Pokorny et al. 2005)

ecosystem, community, or population structures (Hobbs and Huenneke 1992; Krueger-Mangold et al. 2006). Not all disturbances are the same, differing in type (e.g., grazing, fire, flood, drought), frequency (common or episodic), intensity (low or high), and extent (patch or landscape). Disturbance often kills or damages existing vegetation, decreasing resource uptake by resident vegetation and opening up gaps for new seedlings to establish. Disturbance also increases nutrient-cycling rates (Smithwick et al. 2005). The decrease in the uptake of resources by the resident vegetation, combined with an increase in nutrient cycling, usually results in an increase in resource availability following disturbance (Davis et al. 2000).

Principle: Lower disturbance frequencies favor establishment of desired species compared with higher disturbance frequencies. Many invasive species are characterized by rapid growth, short generation time, and abundant seed production, whereas many desired species are characterized by slow growth and long periods between seed productions, and they tend to invest a relatively lower proportion of their biomass in seed production each year (Noble and Slatyer 1980; Rejmanek and Richardson 1996). Therefore, frequent disturbance will tend to favor invasive species, whereas less-frequent disturbance regimes will tend to favor desired species.

Principle: Lower disturbance intensity favors establishment of desired species compared with higher disturbance intensity. As disturbance intensity increases, nutrient-cycling rates increase, and the ability of resident vegetation to sequester nutrients decreases, increasing nutrient availability (Davis et al. 2000). The rapid growth rate exhibited by most invasive species is favored in nutrient-rich environments (Lambers and Poorter 1992). Therefore, invasion will be directly and positively related to disturbance intensity. Most desired species have traits that increase longevity of root and shoot tissue and, therefore, allow conservation of previously captured resources (Lambers and Poorter 1992). These traits confer a competitive advantage in low-nutrient environments (Berendse et al. 1992). As a result, low disturbance intensity tends to favor desired species to a greater extent than high disturbance intensity.

Principle: Smaller-scale disturbances spread through time are less likely to promote the growth of invasive plant populations than simultaneous, large-scale disturbances are. Plants have a fixed amount of resources to allocate to reproduction (Smith and Fretwell 1974). Thus, each plant species is faced with a trade-off between producing a small amount of large seeds or a large amount of small seeds. Producing a large amount of small seeds is assumed to provide an advantage in terms of colonization, whereas producing a small amount of large seed is assumed to provide an advantage in terms of ability to establish in harsh microsites where competition from neighboring vegetation may be high (Tilman 1994). Most invasives share traits of colonizing species and, thus, tend to produce many small seeds (Rejmanek and Richardson 1996). This strategy is expected to be favored in areas with large-scale disturbances, where population growth is primarily limited by the amount of seed a species can disperse across the landscape (Noble and Slatyer 1980). Likewise, the colonization strategy of invasive species is usually associated with rapid germination and little seed dormancy, allowing invasive plant seed banks to quickly and uniformly respond to a disturbance but leaving little seed carryover in the seed bank (Benefield et al. 2001; Meyer et al. 2007). As a consequence of the greater colonizing ability of most invasive plants compared with desirable plants, minimizing the scale of disturbance and spreading planned disturbances through time will be critical in minimizing the spread of weed populations.

Species Availability. Propagule limitations of desired species usually are present to some degree in all communities and often are pronounced in degraded and weed infested-systems (Clark et al. 2007; Navie et al. 2004). Propagules can include reproductive (e.g., seed) and vegetative components (e.g., rhizomes). Propagule limitations can be due to dispersal limitation, the amount of propagules produced, or both factors. Limitation by propagule numbers occurs when not enough seeds are produced to saturate potential recruitment sites, even if all seeds produced reach a site. Dispersal limitations occur when seeds produced do not reach all potential sites, even though enough seeds are produced to saturate available safe sites. Because dispersal and propagule limitations often co-occur, recruitment of desired and undesired species can be viewed as a probabilistic event (Davis et al. 2000). Therefore, managing plant community change requires managing both the frequency of dispersal and the propagule production of desired and undesired species.

Process: Propagule dispersal. Dispersal is the movement of propagules away from the parent plant or population through time and space (Harper 1977). Dispersal is the first step toward determining whether a new species will penetrate a community. Potential mechanisms of dispersing through space include wind, animals, and hydrologic vectors. A range of seed dormancy and other biochemical mechanisms allow some species to disperse propagules through time (Baskin and Baskin 2001). Most species tend to have dispersal adaptations particularly advantageous for a specific vector (e.g., plumes as adaptations for wind dispersal), but this does not necessarily preclude dispersal by other vectors.

Principle: Increasing the frequency of dispersal by desired species and decreasing the frequency of dispersal by undesired species can allow plant communities to change in a favorable direction. In systems that display some degree of heterogeneity in site availability, successful colonization of a site by a particular species will involve at least some random elements. Lottery models have been used to describe some of these effects. In these models, seeds of species that successfully colonize sites are drawn randomly from a pool of potential species. A particular species has a greater chance of arriving at a site if it disperses more frequently, even if it is an inferior competitor (Sale 1977). Therefore, managers can facilitate plant community change toward a desired state by increasing the dispersal frequency of desired species or by decreasing the dispersal frequency of undesired species.

Principle: Less-competitive desired species can "win" a safe site from more-competitive invasive species by arriving at the safe site first. Competitive hierarchies have been widely demonstrated in plant ecology (Tilman and Wedin 1991), directly questioning how subdominant species can establish in areas where competitive dominants also are dispersing seed. However, even very small differences in the order in which seeds arrive at a site (e.g., weeks) can influence which species establish and, ultimately, the composition of the community (Egler 1952; Korner et al. 2008). In general, the species that arrives first tends to be the most successful (Drake 1991). Because of this "priority effect," in areas where a weak competitor arrives first, it can persist, even when a more competitive species tries to subsequently establish. Therefore, small shifts in dispersal timing that favor early dispersal of desired species and delayed dispersal of undesired species can facilitate plant community change toward a desired state.

Process: Propagule production. Propagule production can include both reproductive and vegetative components, but management often centers on seed production because that is the main way most species colonize heterogeneously dispersed gaps in communities.

Principle: Increasing propagule production of desired species and decreasing propagule production of undesired species can allow plant communities to change in a favorable direction. As outlined in dispersal principles, site availability is heterogeneous in most systems, indicating that, although competitive hierarchies may exist among species, colonization of a site by a particular species will involve at least some random elements. As a result, a particular species will have a greater chance of colonizing a site if that species produces a greater number of propagules than other species (Sale 1977). Therefore, managers can facilitate plant community change toward a desired state by increasing propagule pressure of desired species or decreasing propagule pressure of undesired species (von Holle and Simberloff 2005).

Principle: Control of seed production by invasive plants is required to realize the benefits from seeding desired species. As discussed under the disturbance principles, plants have a fixed amount of resources to allocate to reproduction (Smith and Fretwell 1974), which forces plants to produce a smaller amount of larger seed or a larger amount of smaller seeds. Producing large amount of small seeds is assumed to provide an advantage in terms of colonization, whereas producing a small amount of large seed is assumed to provide an advantage in terms of ability to establish in marginal microsites where environmental stress or competition from neighboring vegetation may be high (Tilman 1994; Turnbull et al. 1999). Although the per-capita ability of seed of desired species to establish may be higher than undesired species, undesired species often produce much more seed per plant than desired species. Even a moderate difference in seed production can overwhelm the per-capita establishment advantage of desired species, acting as an effective filter limiting recruitment of desired species (DiVittorio et al. 2007).

Species Performance. Species performance is associated with a range of ecological processes that determine how a species captures and uses resources to maintain and increase population size. Species performance can be modified by resource supply patterns of the ecosystem (resources); physiological processes that allow a plant to affect and respond to the immediate environment (ecophysiology); the patterns of birth, mortality, and growth of individuals in a population (life history); how a species responds and maintains fitness under harsh abiotic conditions (stress); and how an individual of a species is influenced by its neighbors of different species (interference). Although the ecological processes associated with species performance are varied, and potential interactions among processes can be complex, not all processes necessarily need to be modified. By managing a subset of key processes, either by altering environmental conditions to favor performance of a desired species or by altering the target pool of the desired species to match environmental conditions, it is possible to direct invasive plant–infested communities toward a more desired state.

Process: Resources availability. Resources refer to any item that a plant needs to procure from the environment that is essential for survival (Bloom et al. 1985). Not all resources are limiting, however, so manipulation of any particular resource may not alter species performance. The resources that tend to be the most limiting are light, water, and the soil nutrients, nitrogen (N) and phosphorous (P) (Lambers et al. 1998). Because plants require relatively high quantities of N to support growth compared with the amount of N supplied by most ecosystems, N limitations are fairly ubiquitous in natural systems (Vitousek and Howarth 1991). Although most ecosystems experience some N limitations, water or light limitations also occur, depending on regional climate and weather as well as the canopy structure of the plant community.

Principle: Managing environments for low resource availability favors resource conservation over resource capture by plants, favoring desired species over invasive species. Research on plant ecological strategies based on leaf and root tissue economics have demonstrated a trade-off between construction of tough, long-lived tissue capable of yielding a long return on tissue but at a low rate, or construction of thin, short-lived tissue capable of yielding short returns on tissue but at a high rate (Diaz et al. 2004; Wright et al. 2004). Empirical studies and models suggest construction of short-lived tissue with a high rate of return is beneficial in resource-rich environments, whereas construction of long-lived tissue with a slow rate of return is beneficial in resource-poor environments (Berendse 1994; Berendse and Aerts 1987; Berendse et al. 1992; Fraser and Grime 1999). Not surprisingly, many invasive species are characterized by construction of short-lived tissue, whereas many natives and desirable species are characterized by construction of long-lived tissue (Grotkopp and Rejmanek 2007; James and Drenovsky 2007; Leishman et al. 2007). Managing environments for low resource availability, therefore, should favor performance of desired species over invasive species.

Principle: Initial establishment of desired species needs to be successfully managed to realize any benefit of resource management. The benefits of resource conservation in low resource environments are manifested through time by mechanisms such as nutrient resorption and recycling (Chapin 1980). During the establishment phase, both invasive and desirable plants need to capture the bulk of their resources from the immediate environment. Because these species groups have comparable resource requirements during the establishment phase, low resource availability is not expected to differentially affect species performance of these two groups (James 2008; Ryser and Lambers 1995; van der Werf et al. 1993).

Principle: Resource availability can be minimized primarily by maximizing biomass production and secondarily by managing for variation in traits such as phenology and root distribution of the dominant species. Research examining the effects of species or functional group diversity on resource availability largely has overlooked the importance of how natural variation in species abundance influences resource capture by a particular species or group of species (Zavaleta and Hulvey 2006). Theory and empirical work indicate species biomass is central in determining how much resource a species sequesters (Aarssen 1997; Grime 1998). Species that are more abundant sequester more resources. Although considering the primary importance of abundance, plant communities that have co-dominant species that differ in phenology and root distribution or other traits that influence the pattern of resource capture can sequester more resources than monoculture communities can (Fargione and Tilman 2005; Hooper and Vitousek 1997). This suggests managers can minimize resources available by first managing for biomass and then, subsequently, for variation in traits among potentially dominant species.

Principle: Resources available to an invader can be minimized by establishing the desired species that are functionally similar to an invader. The potential for different species to influence ecological processes and properties in a similar manner because of similar morphological and physiological characteristics has long been recognized (Botkin 1975). From this, researchers have arranged species into functional groups (e.g., based on morphological—shrubs, grasses, forbs, or physiological—C_3, C_4, classifications) and have recognized that functional group composition (i.e., which particular groups are present) and functional identity of the invader are major determinates of invasion and invasion resistance (Symstad 2000; Turnbull et al. 2005). Desired and invasive species within the same functional group tend to have similar patterns of resource capture and use. Therefore, desired species functionally similar to potential invaders will have a disproportionately greater negative effect on resources available to the invader than would be predicted by their biomass alone (Pokorny et al. 2005).

Process: Ecophysiology. Ecophysiology generally encompasses any physiological or morphological mechanism allowing a plant to affect and respond to the immediate environment (Lambers et al. 1998) and, therefore, involves a wide range of processes and attributes. Initially, there was much hope that these traits could be used to identify traits of invaders so that potential new invasions could be predicted (Noble and Slatyer 1980; Rejmanek and Richardson 1996). Unfortunately, identifying common traits was elusive and limited the ability to develop predictions beyond certain families or life forms (Mack et al. 2000). Nevertheless, a few underlying traits and associated principles have emerged that can help identify how systems can be managed to favor desired species.

Principle: Managing environments to favor resource conservation over resource capture favors desired species over invasive species. As outlined under ''Resource Availability,'' one of the unifying traits that distinguish many invasive species from their native counterparts is centered on how they allocate biomass to develop root and shoot systems. Native plants tend to invest in energetically expensive, heavily protected tissue, whereas invasive plants tend to invest in cheaper, poorly protected tissue (Diaz et al. 2004; Wright et al. 2004). These alternative strategies result in a suite of ecophysiological differences among these groups, which, in turn, allows these species groups to be favored in different environments. For example, by constructing cheap, poorly protected tissue, invasive species can create much more root surface and leaf area per unit of biomass allocated to roots and leaves. A high, specific leaf area (SLA) and high, specific root length (SRL) allow these species to rapidly compound the rate of return on root and leaf tissue investment (Lambers and Poorter 1992). Higher photosynthetic capacity and lower respiration rates are associated with a high SLA, and a higher root nutrient uptake rate per the biomass of the roots is associated with a higher SRL (Leishman et al. 2007). Construction of thin, poorly defended root and leaf tissue, however, comes at a cost. A high SLA and SRL is associated with less-lignified tissue and tissue with thinner cell walls (Harris and Wilson 1970; van Arendonk et al. 1997). This makes high SRL and SLA tissue susceptible to environmental stress (e.g., wind, drought) and more susceptible to damage by generalist herbivores (Coley et al. 1985; Lambers et al. 1998). Combined, these factors interact to greatly reduce the longevity of these tissues. In resource poor environments, conservation of previously captured resources, and maintenance of previously constructed tissue may be more important than capturing new resources and developing new tissue. Consequently, the high SLA and SRL and associated traits that characterize some of the core ecophysiological advantages invasive species have in high resource environments should be disadvantageous in low resource environments.

Principle: A sufficient amount of abiotic or biotic stress needs to be applied at appropriate times to inhibit performance of invasive species in low nutrient environments. As outlined above, nutrient conservation should be as important as nutrient capture in low nutrient environments. Although a trade-off between SLA and tissue longevity has been described, resource conservation can also be achieved by using resources efficiently. Producing thinner leaves (higher SLA) means invasive plants can allocate less N to each unit of leaf area to maintain similar levels of photosynthesis, compared with species with lower SLA (Osone et al. 2008). This may allow invasive plants to achieve greater N use efficiency and to maintain greater growth than native plants do in low N soils (Funk and Vitousek 2007; James 2008). As outlined above, a high SLA comes at a cost in terms of tolerance to abiotic and biotic stress. To ensure low-nutrient environments disproportionately affect invasive populations more than they affect desired species, these stresses need to occur at a magnitude and time that ensure the invasive species incurs a cost associated with having a high SLA.

Process: Life history. Life history describes patterns of birth, mortality, and growth of an individual in a population as it passes from seed to adulthood. As outlined under Site Availability, plants allocate a limited amount of resources to reproduction so plants are faced with an inevitable trade-off between producing many small seeds or fewer, larger seeds. In most cases, a trade-off between seed size and establishment success in unfavorable environments can be demonstrated (Harper 1970; Rejmanek and Richardson 1996; Turnbull et al. 1999). Natural selection in a particular habitat favors the life-history strategy that optimizes the number and size of seeds produced. There are two broad approaches to describing variation in life history: categorical approaches (e.g., r selection, K-selection, or ecological strategies) (Grime 1977; MacArthur and Wilson 1967), which classify life history based on selection forces, and demographic approaches, which consider plant life span and size in plant reproduction (e.g., annual, biennial, perennial).

Principle: Less-frequent and less-intense disturbances favor establishment and population growth of desired species. Population growth rates are mainly determined by the chance of an individual surviving to reproductive age multiplied by their reproductive output if they do survive (Gurevitch et al. 2002). A common trait of many invasive plant species is a short juvenile period and, in perennial plants, a short period between large seed crops (Rejmanek and Richardson 1996). These traits reflect an R strategy, a ruderal strategy, under the categorical approach to life history, and allow rapid population growth (Grime 1977; MacArthur and Wilson 1967). This life history strategy is most beneficial when survival of adult plants is much lower than survival of juvenile plants (Charnov and Schaffer 1973). Conversely, when survival of adult plants is much higher than the survival of juvenile plants, life history traits of most invader plants are not favored. Disturbance frequency and intensity are major factors influencing plant survival. Less-frequent and less-intense disturbances tend to favor the life history characteristics of desired species.

Process: Stress. Stress can be generally defined as any condition that limits plant growth (Grime 1977). Because conditions rarely are completely optimal for growth in natural systems, stress levels tend to range along a continuum from mild to severe. Although not all forms of stress are induced by disturbance, most forms of disturbance induce some degree of stress with the magnitude depending on disturbance type, intensity, and frequency as well as the stress tolerance of the particular plant species. Therefore, although disturbance may be used as a process to alter site availability, disturbance can also be applied in various ways to induce stress on undesired species. As outlined earlier, plants need to balance resources to support tissue maintenance, new growth, and reproduction (Bloom et al. 1985). Any physical or physiological damage to a plant during vegetative growth ultimately means less energy is available to support new growth and reproduction.

Principle: Moderate, prolonged stress favors desired species over invasive species compared with short-duration, intense stress. Stress tolerance at the community and species levels includes resistance, the ability of a community or species to avoid changes in production or population size when exposed to stress, and resilience, the ability of a community or species to recover back to initial levels following stress (Leps et al. 1982). The ability of a species or plant community to resist stress is negatively correlated with intrinsic growth rate (MacGillivray et al. 1995). In addition, there is a negative correlation between resistance and resilience (Leps et al. 1982). Most invasive species have a high, intrinsic growth rate and greater physiological plasticity than desired species have (Grotkopp and Rejmanek 2007; James and Drenovsky 2007; Niinemets et al. 2003). Therefore, it is expected that the invasive species group will have higher resilience and be favored under short but intense stress regimes. On the other hand, moderate, prolonged stress should favor the greater stress resistance of desired species.

Process: Interference. Interference refers to the reduction of fitness of neighboring plants from various mechanisms, including competition, allelopathy, resource availability, and other trophic interactions (Pickett et al. 1987). Interference is the broadest and most difficult of the processes to quantify and the processes for which principles appear to be the least developed.

Principle: Desired species or functional groups with patterns of resource capture similar to the invader species have a greater competitive effect per unit of biomass compared with species with fewer similar patterns of resource capture. Resource sequestration by a species is broadly related to species abundance, per unit rate of resource uptake and loss, and the duration of resource uptake (Grime 1998). Differences in rooting depth and phenology, as well as root and leaf physiology and morphology, are important drivers of species specific uptake patterns. Species that are more similar in these traits have more comparable patterns of resource capture than species that are less similar in these traits. Although competition for belowground resources is expected to be size-symmetric, with larger plants expected to acquire proportionately more resources than smaller plants, native species with resource-capture traits functionally similar to those of invader species have a greater negative effect on resource capture by invader species compared with native species with fewer similar traits (Dukes 2002; Pokorny et al. 2005).

Synthesis and Conclusion

The need to extract general ecological principles and use them to formulate frameworks that allow practitioners to predict the outcomes of alternative management strategies to guide restoration efforts has been widely acknowledged (Cairns 1993; Clewell and Rieger 1997; Hobbs and Norton 1996). Although there have been recent valuable efforts to develop unifying frameworks that predict patterns of biological invasion as well as efforts to integrate various conceptual models of ecosystem degradation and repair (Barney and Whitlow 2008; Catford et al. 2009; King and Hobbs 2006), a complete decision-making process for land managers has not emerged. In this article, we have demonstrated how ecological principles can be incorporated into a holistic EBIPM framework that includes the necessary steps to assess management needs, formulate management strategies, identify appropriate management tools and options, and quantify and adjust management outcomes for invasive plants. Clearly, these principles do not apply to every invasion scenario, but the ecological theory and basis used to develop these principles identify the conditions in which these principles are likely to hold. For example, much of the ecological theory and research suggests species with high relative growth rate (RGR) and short generation times will be favored under conditions of high disturbance intensity, particularly when intense disturbances are frequent. If the invasive species of concern exhibits higher RGR and shorter generation times than the native species a manager wishes to reestablish, the principles associated with disturbance can indicate how a manager may use various tools to apply disturbance in a manner that would favor desired species and not favor the weeds. In this case the differences in RGR among invasive and desired species would indicate to the manager that use of a low intensity disturbance to create a safe site (e.g., by using a harrow or no-till drill), as opposed to a more intense disturbance, which might create more safe sites but provide invasive species with too much advantage. As managers use the framework of successional management to determine what processes they need to repair, the principles developed here provide the basis and rationale for determining how to use the available tools most appropriately for a specific situation. By examining the theory and basis for each principle, it is also possible to identify the conditions in which the principle will be unlikely to hold.

This initial effort recognizes that identification of ecological principles and the conditions in which they hold are still being developed, and it is expected that this general framework will be expanded, modified, and improved. Nevertheless, this effort shows the critical need for basic and applied ecology to jointly work on development of general principles that allow restoration and other land management activities to move away from recurring agronomic inputs, designed on a site-by-site basis, and to move toward sustainable, ecologically based strategies that can be easily applied to a range of restoration scenarios.

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