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Invited Review

Restoration Ecology and Invasive Plants in the Semiarid West

Cynthia S. Brown, Val. J. Anderson, Victor P. Claassen, Mark E. Stannard, Linda M. Wilson, Sheryl Y. Atkinson, James E. Bromberg, Thomas A. Grant III, and Marques D. Munis*

Invasive plants are a common problem in the management and restoration of degraded lands in the semiarid western United States, but are often not the primary focus of restoration ecologists. Likewise, restoring native vegetation has not been a major concern of weed scientists. But trends in the literature demonstrate increasing overlap of these fields, and greater collaboration between them can lead to improved efficacy of restoration efforts. Succession and ecosystem development are the products of complex interactions of abiotic and biotic factors. Our greatest restoration and invasive plant management successes should result when we take advantage of these natural processes. Recent shifts in management objectives have generated approaches to directing plant community development that utilize species that are strong competitors with invasive species as a bridge to the establishment of native perennial vegetation. Soil water and nutrient characteristics and their interactions can affect desired and undesired plant species differentially and may be manipulated to favor establishment and persistence of desired perennial plant communities. Selection of appropriate plant materials is also essential. Species assemblages that suppress or exclude invaders and competitive plant materials that are well adapted to restoration site conditions are important keys to success. We provide guidelines for restoration based on the fundamental ecological principles underlying succession. Knowledge of the complex interactions among the biotic and abiotic factors that affect successional processes and ecosystem development, and increased collaboration between weed scientists and restoration ecologists hold promise for improving restoration success and invasive species management.

Key words: Remediation, rehabilitation, succession, community assembly, revegetation, ecosystem processes, assisted succession, succession management.

Competition from invasive plants is a primary limitation to the success of semiarid land restoration in the western United States (Allen 1995). Conversely, the competitive ability of native vegetation established through restoration activities can reduce the proliferation of invasive plants (e.g., Bakker and Wilson 2004; Floyd et al. 2006). Here we assess critical issues that face restoration of ecosystems in the western United States with respect to invasive plants. First, we review the past association of weed science and restoration ecology, define terms to provide a basis for discussing restoration and invasive plants, and describe the history of restoration and invasive plant management in the West. We provide ecological conceptual underpinnings for restoration and invasive plant management, and discuss principles of utilizing successional processes to reach restoration goals. We next present important considerations of soil characteristics that influence the relative success of invasive and native species, and suggest management activities to favor native perennials. Finally, we provide information to assist selection of appropriate

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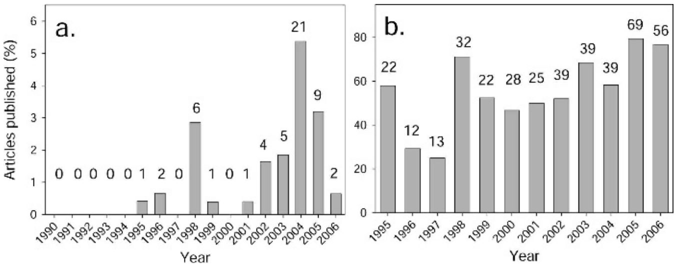

Figure 1. (a) Percentage of articles published in *Weed Science* and *Weed Technology* from 1990 to 2006 that included the terms restoration, revegetation, reclamation, rehabilitation, or remediation. (b) Percentage of articles published in *Restoration Ecology* from 1995 and 2006 that included the terms weed, invasion, nonnative, exotic, alien, adventive, introduced, and their variants. Above each bar is the number of articles with the terms published in that year.

plant materials for restoration projects. Although a great deal of research has been published in recent years on the ecology of invasive plants, the information has not been well integrated into management and restoration (D'Antonio and Meyerson 2002). With this review, we wish to provide a basis from which weed scientists and land managers can incorporate principles of ecology into their research and management programs.

Weed Science and Restoration Converge. We quantified the overlap of the disciplines of restoration and weed science by evaluating the use of terms in the U.S. journals in these topic areas. First, we searched for terms associated with restoration activities (restoration, revegetation, reclamation, rehabilitation and remediation, and their variants) in titles, keywords, and abstracts in the weed science journals *Weed Science* and *Weed Technology* between 1990 and 2006. We found a general increase in the frequency of the terms over time, but there was a great deal of variation from year to year. A peak in 2004 was due to the special issue of *Weed Technology* on invasive plants comprising papers from the Invasive Plants in Managed and Natural Systems conference (Fort Lauderdale, FL, November 2003) (Figure 1a). Similarly, although less dramatic, topics related to invasive plants have increased in the restoration literature. We searched the journal *Restoration Ecology* for articles using the words weed, invasion, invasive, nonnative, exotic, alien, adventive, introduced, and their variants in titles, keywords, and abstracts between 1995 and 2006. We found an increase in the number and a trend toward higher percentages over time of articles using these terms (Figure 1b). Increasing overlap of weed science and restoration speaks to the need for better collaboration and integration of the principles of both fields to more efficiently and effectively restore ecosystem structure and function.

A Review of Terminology. There is fairly good consensus that restoration involves reestablishment of the structure and function of an ecosystem to a historical or idealized state that is resilient, self-assembling, self-sustaining, and integrated into the surrounding landscape (Allen 1995; Bradshaw 1997; SERI 2004). The Society for Ecological Restoration International Primer (SERI 2004) provides nine criteria for ecological restoration and recognizes that reclamation, rehabilitation, and mitigation, the latter referring to activities intended to compensate for environmental degradation, may have much in common with or meet the criteria for ecological restoration. Like restoration, rehabilitation focuses on reestablishing a previous condition; however, the goals and strategies differ from restoration in that rehabilitation emphasizes repairing "ecosystem processes, productivity and services," (SERI 2004, p. 12) without emphasizing reestablishing the species composition of the historical state. Reclamation is used in reference to utilitarian purposes such as soil stabilization, public safety, or aesthetics (SERI 2004).

The terminology of invasive plants and weeds is complex and terms are not consistently defined (Davis and Thompson 2000, Pyšek 1995). To avoid confusion, here we provide the definitions we will use. We use "invasive" to refer to species that are not native to North America, are experiencing range expansion, and have a large impact in the introduced range. These are the true invaders described by Davis and Thompson (2000). We use the term "weed" to refer to species that are nonnative, but seem to have minimal effects on ecosystem processes. They include species recognized as common agricultural weeds that occur in disturbed areas and early-seral communities. These are the novel, noninvasive colonizers of Davis and Thompson (2000). We rely on the U.S. Department of Agriculture (USDA) Plants Database (USDA NRCS 2008) for provenance of species and refer to those from North America as "native" and those from other regions as "nonnative" without connotations regarding impacts or range expansion. We use "local" to refer to plants from a particular habitat within a specific region, and "nonlocal" to refer to plants that do not meet those criteria.

The Need for Restoration and Invasive Plant Management: An Historical Context

Plant communities that have evolved under a particular set of abiotic and biotic conditions have also developed a level of resilience to the disturbances that are characteristic of the system including fire, drought, erosion, and herbivory, among others. When external forces are applied that change the frequency or intensity of these natural disturbances or introduce new disturbances, plant communities may be subject to invasion. Examples of disturbance-triggered shifts abound, especially in the history of the colonization of the semiarid western states by European settlers. Great herds of livestock increased grazing pressures by orders of magnitude above historical norms. Fire frequency was reduced by fire suppression efforts of settlers. These changes in disturbance along with effects of drought drove a change in many western rangelands to decrease herbaceous understory species as less palatable woody species (sagebrush [*Artemisia* spp.] and juniper [*Juniperus* spp.]) thrived. The loss of the herbaceous layer caused extensive soil erosion from already shallow soils on sloping landscapes, which decreased site productivity potentials.

Another outside force that followed settlement, but can be attributed to it, was the introduction of invasive plant species. Some were introduced as ornamentals and subsequently escaped cultivation. Others were accidentally introduced as contaminants in seed shipments and other products and have expanded their range from where they first established. Many of these latter species were well adapted to the wet winters and dry summers of the western United States. Species such as cheatgrass (downy brome, *Bromus tectorum* L.), medusahead [*Taeniatherum caput-medusae* (L.) Nevski], halogeton [*Halogeton glomeratus* (Bieberstein) C.A. Meyer], and Russian thistle (*Salsola kali* L.) found their way into shrub interspaces and understories as native perennial grasses and forbs succumbed to increased grazing pressures. The early-season annual invaders have relatively short active growing periods in which they produce abundant biomass and seed. Following seed dispersal, these plants die, providing a fine, continuous fuel bed between woody species. This continuity increases the area susceptible to fire ignitions and the size of fire perimeters. Fires in recent years have been catastrophic in size and intensity (Westerling 2006), which has proven devastating to native perennial vegetation. These large fires decrease competition from perennials and enable aggressive regeneration from an abundant annual seed bank. Initial natural regeneration of native plants may also occur; however, these are often subdued by the aggressive nature of early-season competition from the annuals and then further compromised by subsequent fires induced again by annual plant materials. These cyclic events have changed historical fire frequencies that previously ranged from 30 to 50 yr in sagebrush steppe communities to as few as 3 to 5 yr (Whisenant 1990). This self-perpetuating cycle is often associated with increased soil erosion and subsequent loss of productivity potential. As a result, vast areas across the western United States now exist in an alternative stable state dominated by invasive annuals that preclude succession to the original plant species and types.

In the mid-20th century, land managers turned to a number of aggressive nonnative perennial species to reclaim degraded lands. Invaded plant communities are often unstable, have low plant diversity, and are less functional than the intact, native perennial communities they displaced (Davison and Smith 2005). Wildlife habitat, livestock grazing, and simple aesthetics were common drivers for action to return these sites to a more preferred condition. As a result, millions of hectares of western lands were converted to crested wheatgrass [*Agropyron cristatum* (L.) Gaertner] and other related species such as Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski], and desert wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult.] that were aggressive in the seedling stage and, once established, could competitively displace invasive annuals (D'Antonio and Vitousek 1992; Hansen and Wilson 2006). Large-scale seeding of these nonnative perennials was acceptable when livestock production coupled with soil stability were the primary land management goals.

During the latter part of the 20th century and extending to the present, recognition of and demand for uses of public lands beyond livestock grazing has created a paradigm shift from reclamation to restoration (Lesica and DeLuca 1996). New federal policies directed the planting of native species for restoration of Western rangelands. However, efforts to shift from highly disturbed conditions with extensive infestations of invasive annuals to diverse, native plant communities have met with limited success (Allen 1995; Monson and McArthur 1995). Some sites have lost their potential to sustain historic plant communities because of disturbance and subsequent soil erosion. Many native perennial species are unable to establish in the presence of the more aggressive invading annual species (Harris 1967; Wilson et al. 2004) even when viable seed and conditions are acceptable for natural regeneration. Early-season resource preemption and strong competition of annual invaders have been suggested as possible reasons for the poor success rate (Dyer et al. 1996; Dyer and Rice 1999; Harris 1967; Holmes and Rice 1996; Kulmatiski et al. 2006; Tausch et al. 1995). Where there has been success with reseeding native species immediately following burning, the seeding rates are often much higher than required for crested wheatgrass and other similar nonnative species and at prices many times that of the nonnative perennials (Thompson et al. 2002).

Ecological Foundations for Restoration and Management of Invasive Plants

Abiotic and biotic environmental factors influence plant communities and their invaders throughout successional development and can be influenced by management actions. As succession proceeds, the environment serves as a filter at the community and ecosystem level, similar to the effects of natural selection on populations (Keddy 1992; Temperton et al. 2004). The plant community at a site persists because the species there have endured the filter of the abiotic environment, including climate, nutrient, and

Table 1. Three causes of succession and the associated interactions, processes, or conditions that can be influenced by management actions.[a]

General causes of succession	Management components
1. Site availability	1. Designed disturbance
2. Differential species availability	2. Controlled colonization
3. Differential species performance	3. Controlled species performance

[a] Modified from Pickett et al. (1987) and Luken (1990).

disturbance regimes. Any new species introduced to a site for restoration, and those that arrive unintentionally, must also withstand this abiotic filter. The plant community interacts with other biotic components of the ecosystem, such as herbivores, mutualists, and soil biota. These additional biotic elements are also the products of the abiotic screening process. When a new species arrives, whether it be an invasive plant or one intentionally introduced for restoration purposes, it is subjected to the same abiotic screening as the resident organisms plus interactions with the biological elements. We must keep this complexity in mind, and remember that the filters change as succession proceeds and communities and ecosystems develop over time. Nevertheless, we can manipulate some of these factors through our management decisions and activities to favor the species that we desire.

Facilitating ecosystem development and successional processes, which can take from decades to centuries when unassisted (Dobson et al. 1997; Prach et al. 2007), is a primary goal of reclamation and restoration. Disturbed habitats are typically first colonized by annual plant species with propagules that are easily dispersed by wind, water, or animals (Bazzaz 1996; Walker and del Moral 2003) or that reside in the soil seed bank. Midseral stages that follow are often dominated by clonal, perennial species (Bazzaz 1996). In semiarid regions of the West that do not sustain forests, late-successional communities near the end of the developmental trajectory are dominated by perennial grasses and shrubs, although mesquite (*Prosopis* spp.) or piñon (*Pinus* spp.)–juniper woodlands occur in some regions.

Pickett et al. (1987) developed a comprehensive conceptual model of succession that encompasses most approaches to restoration and invasive plant management, and has served as a cornerstone of these areas of study (e.g., Luken 1990; Sheley and Krueger-Mangold 2003, Walker and del Moral 2003; Walker et al. 2007). Three causes of succession and corresponding components of management that contribute to the causes are the basis for this mechanistic model (Table 1). ''Site availability'' is the first cause of succession. Restoration efforts are initiated by disturbances that create open niches for establishment of desired species, or eliminate them for invasive species. The disturbances that initiate succession may be accidental (e.g., wildfire, flood) or intentional (i.e., designed disturbance such as control of invasive species, prescribed fire, or cultivation). Disturbances vary in type, size, dispersion, severity, and timing (Luken 1990). ''Differential species availability'' is the second cause of succession, and is most influenced by the propagule pool and initial species composition of the site (Luken 1990). To control colonization, propagules of desired species may be introduced, while those of invasive species may be reduced or eliminated through control measures (i.e., controlled colonization). ''Differential species performance'' is the third cause of succession. It is influenced by the ecophysiology and life histories of the species involved, environmental stress, and interactions among biotic components of the system including competition for resources, allelopathy, herbivory, and mutualisms (Luken 1990, Pickett et al. 1987). This cause of succession can be manipulated through targeted control of invasive species with herbicides or activities that more subtly shift the competitive balance to favor native species such as increasing or decreasing the availability of nutrients and water (i.e., controlled species performance). Management activities may affect multiple causes of succession simultaneously. For example, tillage may be a designed disturbance that increases site availability, whereas it controls colonization and species performance by reducing seed production and uprooting of resident invasive plants and weeds, respectively.

Invasive plants can cause changes that breach ecological thresholds (Briske et al. 2006), altering successional trajectories and causing systems to enter alternative stable states that are resistant to restoration efforts (Suding et al. 2004; Suding and Gross 2006). Ecological thresholds can be crossed when invasive species change ecosystem function through their effects on microbial communities (Belnap and Philips 2001; Hawkes et al. 2005, 2006; Kourtev et al. 2003), soil water (Kulmatiski et al. 2006), nutrient cycling (Ley and D'Antonio 1998; Sperry et al. 2006; Vitousek et al. 1987), or fire frequency (D'Antonio and Vitousek 1992). Invasion-caused alternative stable states have been demonstrated in shrub steppe communities in north-central Washington (Kulmatiski et al. 2006), piñon–

juniper communities in the southwestern corner of Colorado (Floyd et al. 2006), and shrub communities in southern California (Keeley et al. 2005; Stylinski and Allen 1999). We propose that it is possible to initiate a transition from an undesirable stable state to one that has the structural and functional attributes of the predisturbance or preinvasion ecosystem by applying the conceptual model of Pickett et al. (1987).

Utilizing Successional Processes to Achieve Management Objectives. Given the goals of land managers to restore native plant diversity and curb the ever-increasing invasion of nonnative annuals, the procedural questions of how to make the conversion is central to current management discussions. Restoration efforts commonly include seeding of mid- or late-seral species in an effort to accelerate succession (e.g., Baer et al. 2002; Bugg et al. 1997; Sheley and Carpinelli 2005), but this may not be successful if the soil conditions are more suitable for early-seral species (Kardol et al. 2006; Kulmatiski et al. 2006), or if highly competitive invasive plants are present (Dyer et al. 1996; Wilson et al. 2004). These mid- or late-seral species are often planted after designed disturbances (sensu Pickett et al. 1987) such as prescribed fire (e.g., Masters and Nissen 1997), cultivation (e.g., Baer et al. 2002; Bugg et al. 1997), or control of invasive plants (e.g., Ambrose and Wilson 2003; Cox and Anderson 2004; Masters and Nissen 1997; Wilson et al. 2004) to increase site availability (sensu Pickett et al. 1987) (Figure 2a).

One possible solution may be to combine earlier strategies of reclamation using nonnative perennials with a subsequent infusion with native plant species. This approach was termed "assisted succession" by Cox and Anderson (2004) and subsequently referred to as a "bridging plant community" by Pellant and Lysne (2005). The approach utilizes seeding of nonnative perennial plants to recapture the site from invasive annual plants and then requires perturbation of the nonnative perennial community to open niches (i.e., increased site availability sensu Pickett et al. 1987) for the insertion of native species (i.e., increased species availability sensu Pickett et al. 1987) (Figure 2b). Nonnative perennials such as crested wheatgrass have demonstrated their ability to establish and out-compete the invasive annuals to their near extirpation on a site (D'Antonio and Vitousek 1992). On Western rangelands this site recapture represents a shift back to a former perennial state of resource.

Once a site is recaptured to a perennial cover, niche opening (i.e., increased site availability sensu Pickett et al. 1987) can most effectively be achieved through the use of mechanical or herbicide treatments. The niche opening treatments are designed to weaken the existing community's hold on site resources by reducing the density and health of these plants, while at the same time facilitating the establishment of seeded native species (Mangold and

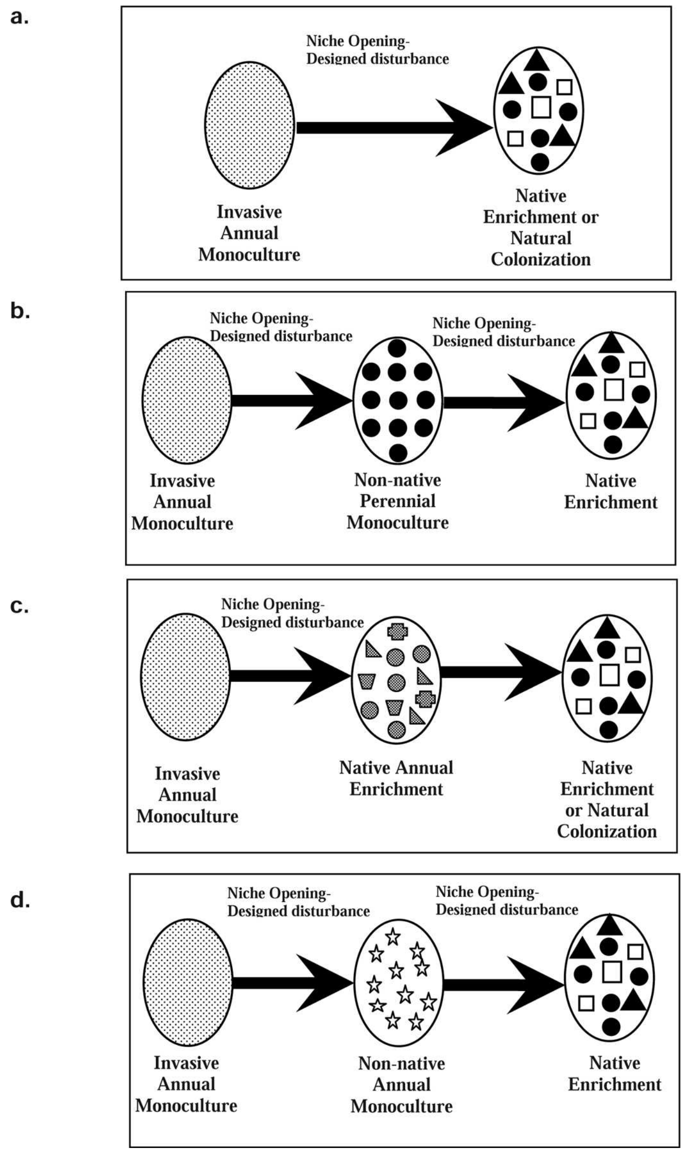

Figure 2. Assisted succession from (a) invasive annual to native perennial dominants, (b) invasive annual to nonnative perennial to native perennial dominants, (c) invasive annual to native annual to native perennial dominants, and (d) invasive annual to nonnative annual to native perennial dominants using principles of succession management (Picket et al. 1987).

Fansler 2007). Using more aggressive nonnative plants as surrogates for early colonizers creates a fire-resistant vegetative cover that can suppress invasive annuals. Unfortunately, they also provide resistance to the recovery of native perennials (Ambrose and Wilson 2003; Waldron et al. 2005). The proximity of populations of annual invaders poses a risk to the success of this approach. Thus, significant buffers should be left in place around restoration treatments to preempt reinvasion.

Cox and Anderson (2004) demonstrated the feasibility of the assisted succession approach. They compared perturbation treatments (herbicides and tilling or harrowing) and subsequent seeding of native grasses and shrubs (drill-seeding, broadcasting, or broadcasting followed by a drag cover) in a cheatgrass-dominated community and in a crested wheatgrass–dominated community that had been recovered from cheatgrass invasion. The niche opening treatments and subsequent seeding had little effect on establishment of native species in the cheatgrass-dominated sites (no plants survived 2 yr), whereas successful openings and significant recruitment (up to as many as 10 native grasses and two native shrubs per meter square) occurred in the crested wheatgrass sites. Most of the native grasses succumbed to 5 yr of severe drought that followed the study, but the native shrubs survived and were reproducing in the crested wheatgrass sites with no encroachment of invasive plants or weeds 9 yr posttreatment. In contrast, the treated cheatgrass sites remained monocultures of cheatgrass.

Another approach to succession management is to plant native annual species after disturbance such as fire, cultivation, or invader control (Figure 2c). Native annuals may be good competitors against invasive annual species. Recent studies have shown that species from one functional group can most suppress species from the same functional group (Bakker and Wilson 2004; Dukes 2001; Fargione et al. 2003; Pokorny et al. 2005; Sheley and Carpinelli 2005). A functional group is a set of species that are similar in one or more physiological, morphological, or phenological traits, or in other characteristics of importance in a given system (Brown 2004). Both native and nonnative annual species are adapted to early-seral conditions and generally have faster growth and establishment than their perennial counterparts. Annual species can also foster successional development by stabilizing soil and increasing soil organic matter and nutrients (Whisenant 1999). Early-successional species are often less dependent on mycorrhizal fungi than late-successional species (e.g., Allen and Allen 1984, 1988; Wilson and Hartnett 1998; Rowe et al. 2007), which makes them especially well suited for disturbed sites.

The success of this approach will likely depend on addition of seed of native annual species (i.e., to increase species availability sensu Pickett et al. 1987) because forbs are often seed-limited. For example, Seabloom et al. (2003) found that establishment of native annual forbs was most restricted by seed availability in a Southern California grassland, and Keeley et al. (2006) found that regeneration of herbaceous annual species depended on dormant seed banks rather than dispersal from unburned areas in California chaparral and sage shrub communities.

Similar outcomes may be achieved with nonnative annual species such as wheat (*Triticum aestivum* L.), mustards (*Brassica* spp.), and annual medics (*Medicago* spp.), which establish well and can be easily eliminated (Figure 2d). Nonnative annuals have the same advantages as native annuals, but are unlikely to persist because of poor adaptation to wildland conditions. However, the potential for these species to become invasive or affect the genetic structure of local native species (described below) must be considered.

Soil–Plant Relationships in Restoration and Invasive Plant Management

Soil resources are among the many factors that influence the relative success of invasive plants and desired native species in restoration and rehabilitation projects. Soil resources directly influence causes of succession such as site availability and differential species performance (sensu Pickett et al. 1987). Site availability is affected by the susceptibility and response of soil resources to disturbance, whereas species performance is influenced by interactions between the availability of water and nutrients and the differing resource requirements of plant species. Succession is essentially a ''plant-by-plant'' replacement process, with significant neighborhood interactions that are often derived from soil-related factors (Pickett et al.1987). If we are to direct succession, we must identify management actions that alter causes of succession (Table 1) to favor desired species relative to invasive species. This knowledge can be applied to assess the restoration potential of sites and choose management methods that will take advantage of the differences among species and promote restoration success. To that end, here we consider soil resource characteristics and differential responses of native and invasive species to them.

Numerous abiotic and biotic factors other than those we present affect the relative success of invasive and desired native species. However, a comprehensive treatment of all aspects of ecosystems that influence succession and restoration success is beyond the scope of this review. Therefore, we discuss the factors that (1) have strong direct effects on plant establishment and growth, (2) affect plant functional groups differentially, and (3) may be manipulated by management actions. They are factors that are most likely to produce change when altered, and can be utilized to tip the competitive balance to favor desired species.

Water Availability and Use. Plants that colonize and persist in semiarid habitats require different amounts of water and extract it from different depths and at different times of the growing season. We can make use of the differences in these characteristics between native and invasive species to reach our restoration goals.

Amount of Soil Water Use. Disturbances that reduce soil volume, root access, or water holding capacity (e.g., erosion, compaction, or loss of organic matter) favor early-season annuals over perennials. This is because annual plants that senesce in the early summer require less water than perennials that are at least partially active through the dry summer season. Soil water use of annual grasses is about half that of perennial grasses (Borman et al. 1992; Cline et al. 1977) or annual forbs (Borman et al. 1992). If soil volume or water holding capacity has been compromised, native perennial establishment is unlikely to be successful until the conditions are mitigated. Depending on the circumstances, soil volume may be increased by deep ripping as described below, or by creating a dry mulch to reduce evaporation. The mulch may be a layer of litter created with mowing, or a layer of dry soil created with surface tillage, which occludes pores through which water can evaporate. However, growth of annual invaders is often also improved with tillage, thus, vigorous control of annual seed production for a few years (e.g., using mowing, burning, or herbicides) followed by spot treatments as needed (Young and Claassen 2008) can help reduce invader populations while native perennials are most vulnerable.

Depth of Rooting and Water Use. The rooting depths of invasive species and the desired plant community may differ, which can be exploited to facilitate attaining restoration objectives. The roots of invasive annual grasses are concentrated in the top 0.3 m of soil (Cline et al. 1977; Dyer and Rice 1999). Many perennial grass species extract water from depths of 1 to 2 m (Brown and Thompson 1965; Cline et al. 1977; Dyer and Rice 1999), and shrubs often utilize water from deeper soil layers (Inouye 2006). In the shortgrass steppe of northeastern Colorado, grasses and herbaceous vegetation utilized shallow soil moisture recharged from rain, trees utilized deeper groundwater to 1.8 m, and shrubs appeared to have access to both sources of moisture (Dodd et al. 1998). Velvet mesquite (*Prosopis velutina* Woot.) trees in Arizona used soil water to depths of 3 m (Cable 1977).

Differences in rooting depths between invasive and native perennial species can be exploited for improved restoration success. Reestablishment of deep-rooted species should be attempted on soils that are sufficient to allow their typical rooting behavior, thus providing the best opportunity for their survival. In addition, established deep-rooted species in deep soils can reduce site availability (sensu Pickett et al. 1987) for deep-rooted invaders such as yellow starthistle (*Centaurea solstitialis* L.) (Enloe et al. 2004) and diffuse knapweed (*Centaurea diffusa* Lam.) (Kulmatiski et al. 2006). If soil depth has been compromised because of compaction, which can be caused by construction, traffic, or soil-formed hard pans, mechanical ripping may be necessary prior to seeding to increase the soil volume accessible to plant roots. Soil compaction can also be reduced by planting deep-rooted forbs, which typically have thicker roots than grasses and can form deep, continuous pores for water infiltration, steadily improving availability of subsurface moisture on compacted substrates.

Seasonality of Water Use. Interaction between timing of water availability and differential timing of water use by invasive species and desired native species can be exploited to favor the latter (i.e., differential species performance). Late-season nonnative invasive plants in the winter-wet, summer-dry climate of California (yellow starthistle) (Enloe et al. 2004; Young et al. 2008) and in central Washington state (diffuse knapweed) (Kulmatiski et al. 2006) used water late into the summer. Invasive annual grasses used soil water early in the season (Enloe et al. 2004; Kulmatiski et al. 2006), and the timing of perennial grass water use was intermediate (Enloe et al. 2004). Enloe et al. (2004) and Kulmatiski et al. (2006) found deep-rooted nonnative and native perennial grass species, respectively, competed most directly with late-season annual forb invaders (yellow starthistle and diffuse knapweed, respectively).

Temporal patterns of plant water use provide explanations for the failure of native grassland restoration efforts when annual grass or forb invaders are present, and suggest strategies to improve restoration success. Early-season competition for water is a primary obstacle to native perennial species seedling survival (Dyer and Rice 1999; Holmes and Rice 1996; Kulmatiski et al. 2006; Piemeisel 1951; Tausch et al. 1995). Furthermore, residual late-season moisture that early-season invaders leave behind in deeper horizons (Dyer and Rice 1999; Holmes and Rice 1996) can be used by late-season invaders while native perennial grasses are dormant (Enloe et al. 2004; Kulmatiski et al. 2006; Young et al. 2008).

Knowledge of differential timing of soil water use of invaders and native species can be used to improve native perennial establishment. Survival may be improved by providing roots access to water below the root zones of early-season invasive species (Kulmatiski et al. 2006). This may be accomplished by (1) planting desired species as transplants to give their roots a head start toward deeper horizons; (2) removing annual invaders to reduce competition during the critical establishment period; (3) providing irrigation at times when competition for water is greatest until roots of native species can grow below those of early-season annual species (Kulmatiski et al. 2006); and (4) conducting restoration activities during the most suitable seasons and (5) during years with above-normal spring precipitation.

Nitrogen Availability and Use. Second in importance to water in the western United States, plant-available nitrogen (N) has a strong influence on plant growth and interspecific competition. Details of the impact of nutrient availability on invasion by annual species are reviewed by Norton et al. (2004a, 2004b). Native shrub-steppe nutrient cycling systems are characterized as being "tight," with conservative cycling of N and little surplus or loss. In contrast, agronomic cropping systems and systems invaded by annual grasses are characterized as being ''leaky'' with pulsed nutrient releases and surpluses of inorganic N available for uptake by fast-growing species.

In general, transition from dominance of perennial to annual species leads to larger, rapidly available pools of inorganic N (nitrate and ammonium) and depletion of stabilized, organic-matter N pools. The inorganic N can be leached deep below the root zone into local watersheds (Lewis et al. 2006), or it can provide a resource for invasive plant growth. Where atmospheric N deposition from internal combustion is common, N availability and uptake can increase by 10 to 50% of annual plant requirements under normal conditions (Weiss 1999).

Altered cycling of N with disturbance from annual plant invasion occurs because these species alter carbon (C) cycling, producing increased levels of easily decomposable litter and subsequent accumulation of nitrate in the soil profile (Sperry et al. 2006). C and N cycles are closely interconnected because microbes either take up (immobilize) N as they utilize C to build biomass during population growth, or they release (mineralize) N during population declines after decomposable C substrates are depleted. For example, cheatgrass invasion speeds up decomposition, and in the long term, decreases total C content in soil and increases N loss from the system (Lewis et al. 2006). Booth and Vogel (2003) compared N levels in big sagebrush– and squirreltail [*Elymus elymoides* (Raf.) Swezey]–dominated communities with N levels in cheatgrass-dominated communities. The invaded annual sites had greater N mineralization and nitrification rates, higher ammonium and nitrate consumption rates, and an accumulation of nitrate during summer followed by rapid uptake and depletion in a seasonal nutrient pulse.

N availability can be reduced to suppress invasive species and provide a window of opportunity for native perennials. Amending soils with readily decomposable carbon such as sucrose (e.g., McLendon and Redente 1992; Paschke et al. 2000; Young et al. 1995, 1998) or more recalcitrant forms of carbon such as sawdust, straw, or grass mulch (e.g., Corbin and D'Antonio 2004; Zink and Allen 1998) will temporarily reduce available N and can reduce annual plant density. Even if it does not decrease growth of invasive annual grasses, C addition can reduce the competitive suppression of perennials until they are well established and less vulnerable to competition from shallow-rooted invaders (Corbin and D'Antonio 2004). For the vast areas of invaded rangeland in the semiarid West, other, larger-scale approaches to reducing N levels are needed. Methods to remove N that can be applied on the field-scale include grazing (Weiss 1999) and mowing with removal of aboveground biomass from the site (Maron and Jeffries 2001). A more systemic approach may be to utilize plant species that produce litter with slower rates of decomposition. As these more complex tissues degrade, N is sequestered for longer periods of time. Big sagebrush communities, for example, have high N immobilization potential associated with shrubs, but not grasses (Smith et al. 1994), which generally have litter that decomposes more rapidly than shrubs.

The presence of established plants that will compete directly with invaders for resources is an important deterrent. Whether the most limiting resource to plant growth is water or N, direct competition between species with phenologies, root distributions, and resource requirements similar to invasive species can suppress the invaders (Bakker and Wilson 2004; Fargione et al. 2003). Resistance of crested wheatgrass to invasion of cheatgrass (Cox and Anderson 2004) and resistance of native fields to invasion by tap-rooted nonnatives (Kulmatiski et al. 2006) provide evidence that this principle can be utilized to maintain stable plant communities and further restoration goals.

Plant Materials for Restoration and Invasive Plant Management

In the initial phases of a restoration project, the site potential must be assessed (Jones and Johnson 1998). This includes the edaphic conditions, topography, climate, disturbance regime, and availability of native, nonnative, and invasive species propagules at the site. To evaluate the site potential, the USDA Natural Resources Conservation Service (NRCS) Ecological Site Information System houses ecological site descriptions for each state and includes climax species lists and ecological dynamics models (Table 2).

Selecting Plant Materials. Plant selection will impact whether the goals of a restoration project are met. Unsuitable or improper plant materials can cause catastrophic failures, waste tremendous amounts of time and money, and reduce the credibility of the restoration practitioner. The species to be planted in a restoration project should be selected from the community species pool (sensu Zobel et al. 1998), i.e., the set of species representing the target community. These species will likely be best adapted to the abiotic and biotic conditions of the site. As described above, highly eroded sites that are shallow to bedrock are not suitable for species that require deep soils, and sites frequently burned will prove inhospitable for many desirable woody species.

When appropriate for the seral stage of the site and goals of the restoration project, planting lists should include comparable species richness to the target plant community and species from the same functional groups as invaders on or near the restoration site. Evidence is mounting that diverse plant communities with species from different functional groups can reduce the growth of invasive plants (Bakker and Wilson 2004; Dukes 2001; Fargione et al. 2003; Pokorny et al. 2005; Sheley and Carpinelli 2005).

Table 2. Websites with information useful for planning restoration projects.

Site name and description[a]	URL
USDA Plants Database Provides standardized information about the vascular plants and lower plants of the United States and its territories. It includes names, characteristics, distributional data, images, Web links, and references.	http://plants.usda.gov
The USDA NRCS Ecological Site Information System houses ecological site descriptions for each state and includes climax species lists and ecological dynamics models.	http://esis.sc.egov.usda.gov/
VegSpec is a Web-based revegetation planning tool. VegSpec uses soil, plant, and climate data to create a list of potential revegetation species that are adapted and appropriate for the planting purposes.	http://vegspec.sc.egov.usda.gov
The USDA Forest Service Fire Effects Information System houses information on the biology and ecology of approximately 900 plant species.	http://www.fs.fed.us/database/feis/index.html
The USDA NRCS Plant Materials Program houses information on plant releases, revegetation, seed production, and species attributes.	http://plant-materials.nrcs.usda.gov/
The Tarleton State University, Department of Agribusiness, Agronomy, Horticulture, and Range Management Website houses plant images and descriptions of North American range types.	http://www.tarleton.edu/~range/
The Native Plant Network houses the *Native Plants Journal* as well as propagation protocols of many native plants.	http://www.nativeplantnetwork.org/
The Association of Official Seed Certifying Agencies brochure describes procedures for collecting, growing, and labeling native seeds.	http://www.aosca.org/aoscanativeplantbrochure.pdf
Calflora provides information on wild California plants for conservation, education, and appreciation.	http://www.calflora.org/
The University of Texas at Austin Ladybird Johnson Wildflower Center Network allows users to search for native plant information by plant raits or names, browse through a collection of 17,000 native plant images, and pose plant questions to a resident horticulturalist.	http://www.wildflower.org/
The Iowa Living Roadway Website promotes the implementation of integrated roadside vegetation management activities—including the preservation, establishment, and maintenance of native vegetation—along Iowa's roadsides.	http://www.iowalivingroadway.com/
The Rangeland Technology Equipment Council's Revegetation Equipment Catalog Website is a comprehensive list of implements used for revegetation.	http://reveg-catalog.tamu.edu/
The Center for Invasive Species Management's Restoration Resource Database provides resources on restoration, particularly relating to invasive species.	http://www.weedcenter.org/restoration/restoration.html
The California Invasive Plant Council aims to protect California wildlands from invasive plants through restoration, research, and education.	http://www.cal-ipc.org/

[a] Abbreviations: USDA, U.S. Department of Agriculture; NRCS, Natural Resources Conservation Service.

Different functional groups have their greatest effects on different resources (Brown 2004; Davies et al. 2007; Hooper and Vitousek 1998). Some studies have shown that more functionally diverse communities utilize resources more completely than less-diverse communities (Davies et al. 2007), and are less prone to invasion through this decreased niche availability (Dukes 2001; Fargione et al. 2003; Pokorny et al. 2005; Sheley and Carpinelli 2005).

Once the list of species to be planted has been developed, the appropriate genetic material must be selected. The genetic issues of restoration are well reviewed by Hufford and Mazer (2003), Lesica and Allendorf (1999), and McKay et al. (2005). It is often thought that genetically local, native species are the best plant materials to restore a site (Hufford and Mazer 2003; Knapp and Rice 1996; Lesica and Allendorf 1999; McKay et al. 2005). Local genotypes have evolved to the disturbance, soil, and climatic conditions of the site, whereas nonlocal genotypes may not persist if their traits are not well suited to the environment (Knapp and Rice 1994, 1996; Lesica and

Allendorf 1999; McKay et al. 2005; Millar and Libby 1989). Moreover, introducing genetically nonlocal plants can contaminate the gene pool of local populations (Lesica and Allendorf 1999; Rogers and Montalvo 2004) by introducing maladapted genotypes (i.e., increasing genetic load), disrupting coadapted gene complexes, or eliminating locally adapted genotypes through genetic swamping (i.e., overwhelming local genotypes by numerical or adaptive superiority of introduced genotypes) (Hufford and Mazer 2003; McKay et al. 2005). Nonlocal genotypes might reduce the growth and persistence of the local vegetation through competition (Allen et al. 2001; Humphrey and Schupp 2002), which is more likely if the genetic material has undergone selection for traits enabling quick establishment and growth (Lesica and Allendorf 1999).

Alternatively, transitional early- or midseral plant communities that modify the environment and make the site more hospitable for late-seral vegetation have been advocated (Jones 1998; Thompson et al. 2002). As described above, succession management with native or nonnative annual, or nonnative perennial transitional species can be a valuable approach when highly competitive invasive annuals are present. However, the likelihood of successful establishment and subsequent conversion to a community dominated by late-seral native species must be considered in light of potential harmful effects of the transitional species. First, it may be difficult to eliminate the transitional species and replace them with desired natives (Ambrose and Wilson 2003). Second, although nonnative species may be unlikely to hybridize with local native species, there is some risk that hybridization of nonnative species with closely related natives will create novel combinations of genes. Issues associated with hybridization are discussed in Ellstrand and Schierenbeck (2000) and Hufford and Mazer (2003). As with native species that have undergone artificial selection, introduction of nonnative genotypes can result in loss of local genetic variation through genetic swamping, increased genetic load, superior competitive ability, or disruption of coadapted gene complexes (Ellstrand and Schierenbeck 2000; Hufford and Mazer 2003; McKay et al. 2005). This risk can be minimized by selecting species that are selfing and have low dispersal capabilities (Lesica and Allendorf 1999), or are not closely related to species in the local species pool.

Finally, even though a nonnative species has not been previously invasive, its population growth may simply be in a lag phase prior to exponential population increase, which is a typical pattern for invasive species (Mack et al. 2000; Sakai et al. 2001). The nonnative transitional species may spread to relatively pristine natural areas and out-compete local species or ecotypes when it enters a phase of exponential population growth after overcoming density-dependent limits to reproduction, eliminating deleterious alleles that constrain growth (i.e., reducing genetic load), undergoing local adaptation (Mack et al. 2000; Sakai et al. 2001), or experiencing favorable changes in the environment (e.g., climate change or arrival of a mutualist). Selecting species that have low dispersal capabilities can reduce this risk (Lesica and Allendorf 1999).

Types of Revegetation Plant Materials. There are three general types of revegetation plant materials: (1) collections, (2) contract productions, and (3) commercially available seed or plants. Collections made in the wild (referred to as Generation zero or G0 germplasms) are advocated by many restoration ecologists because they preserve much of the genetic diversity within the population (Lesica and Allendorf 1999; Richards et al. 1998; Rogers and Montalvo 2004). However, the volume of plant material needed to restore a site often exceeds what can be directly collected, and overcollection that compromises the survival of wild populations must be avoided.

Contract production is commonly used to increase the volume of seed available for a species. Growers acquire G0 seed or plants from the contracting agent and grow this plant material for seed, which is Generation 1, or G1. In some cases a second generation (G2) is needed to increase the volume of seed further. Issues of inadvertently selecting for traits that differ from the G0 seed become greater with each generation grown. For example, the simple act of swathing will affect genetic diversity because phenotypes with seed structures that readily shatter and fall from the plant before harvest will be lost, and phenotypes with seed structures that are less prone to shattering will be retained. This trait, i.e., low seed-structure shatter, may be amplified in future generations. Furthermore, producing seed of a population in an environment unlike its origin can result in loss of some phenotypes and amplify the occurrence of others. Finally, the commercial market supplies the vast majority of the revegetation plant material. For example, the Washington State Department of Agriculture certified over 3,440 ha (8,500 ac) of seed production of revegetation plant materials in 2005 (Washington State Department of Agriculture 2005), which resulted in over 1.8 million kg (4 million lb) of seed. Most of this seed was publicly developed varieties and the remainder was prevarietal releases.

Plant Varieties, Cultivars and Prevarietal Selections Explained. Traditional plant germplasm development produces "varieties" that exhibit distinct, uniform, and stable characteristics (Young et al. 2003). Varieties, also known as "cultivars," are developed by intense selection of plant populations for desirable attributes. Desirable attributes such as rapid emergence may occur in the natural germplasm and no further selection pressure need be applied to the variety. Sometimes the attributes are enhanced by purposeful genetic manipulation and artificial selection to create a variety (Young et al. 2003).

Traditional plant germplasm development methodologies that select for superior traits are largely not appropriate for developing restoration plant materials (Young et al. 2003), which has resulted in the development of an alternative approach to plant material improvement. Cultivars of native plants are less appropriate for many restoration projects because the genetic diversity of the original wild collection (G0 germplasm) has been manipulated purposely or accidentally.

The Association of Official Seed Certifying Agencies created the ''Pre-Variety Germplasm'' procedure, which facilitates the development of plant material for restoration (Young et al. 2003). The ''Pre-Variety'' approach created procedures for labeling, increasing, and marketing seed of native plants destined for the restoration market. Three new classes of seed were created: source identified, selected, and tested. Seed classified as ''source identified'' is unevaluated germplasm and identified only to the geographic origin of the parental stock. It has undergone no purposeful genetic manipulation and the number of generations is usually restricted to prevent accidental manipulation. Source identified seed is the most sought after class of seed by restoration practitioners. ''Selected'' class seed is germplasm that exhibits promising traits based upon comparison plantings of other populations or individuals within a population. Selected class seed is somewhat less desirable than source identified seed because the promising traits might influence plant community development. For example, if plants from the selected class seed have the trait of very tall growth, then this may increase shading and change the dynamics of the plant community. ''Tested'' class seed is germplasm in which the progeny of the stock germplasm exhibit promising traits and infers that the traits are heritable. As expected, tested class seed is less desirable for plant community restoration than selected class seed because the traits are not only strongly expressed, but very likely to persist for many generations.

A Basis for Selecting Plants to Manage for Succession. Lesica and Allendorf (1999) asserted that the interaction of the degree and size of disturbance can be used to select the most appropriate type of germplasm for restoration plantings. They indicated that it is especially important to use local genotypes when restoration sites are large, requiring that a great deal of seed be applied, and have not undergone disturbance that radically alters the environment (i.e., local germplasm is likely still well adapted to the site conditions) (Lesica and Allendorf 1999). Under these conditions, the risk of genetic swamping of local gene pools would be high and no survival advantage would be gained should nonlocal genotypes be used.

Cultivars and nonnative species are more appropriate for sites that are small and highly disturbed (Lesica and Allendorf 1999). We suggest that sites heavily occupied by invasive species are also appropriate for use of cultivars and nonnative species. These improved natives and nonnatives are good alternatives under these conditions because local genotypes may be unlikely to flourish in a postinvasion competitive environment, especially following severe disturbance or if the ongoing disturbance regime differs from that of their evolutionary history. Planting genotypes that are introduced or have undergone selection on small sites where little seed is applied limits the risk of genetic swamping (Lesica and Allendorf 1999). If sites are large and have undergone severe disturbance, Lesica and Allendorf (1999) recommended introducing mixtures of genotypes with high genetic variation to increase the likelihood of rapid evolution to the new conditions.

Genetic appropriateness is very important, but seed availability, budget constraints, and relative competitive ability of plant materials must be considered as well. Poor seed-production years, lack of available labor to collect seed, and large commercial purchases by government agencies limit seed supplies. Availability of some valuable restoration species may be limited because of difficulty of production or previous low demand for the seed. The ''best'' plant material might exceed budget limitations, which necessitates compromises such as reducing the size of the seeded area. We propose the following guidelines to balance the considerations suggested by Lesica and Allenorf (1999) with seed expense and availability. (1) The best option is to use local mid- and late-seral germplasm on sites that have high potential of success (i.e., good soil conditions, low populations of invasive species, and minimal external disturbances). Availability of sufficient seed and its cost are challenges of this approach. (2) For sites that have been severely altered by disturbance, but invasive plants are not a primary concern, plant early-seral native species to facilitate ecosystem development. Allow natural recolonization of mid- and late-seral species from nearby native plants, or supplement these seed sources with locally derived germplasm. The shift to late-seral species will usually occur without applying a designed disturbance. Availability and expense of seed of early-seral native species will likely be the primary limitations of this approach. (3) For large sites (i.e., greater than 8 ha [20 ac]) that have been heavily disturbed or invaded and are devoid of native plants, use nonnative transitional species (Figures 2b and 2d). Apply planned disturbances to increase site availability for reintroduction of local native perennial species in subsequent years. The perennial species should be a mixture of genotypes with a great deal of genetic variation (Lesica and Allendorf 1999). The second phase may be applied to small sections of the total area sequentially as the appropriate plant materials become available through seed increase or collections, or both. The initial expense of this approach is likely to be lower than the first two approaches described. However, its limitations are associated with possible negative effects on local native species. To minimize these, choose species that are unlikely to hybridize with or swamp the gene pools of native species, and select species that are unlikely to persist at the site for long periods.

Plant Material and Other Restoration Resources. Lists of suitable revegetation species can be developed using VEGSPEC, a Web-based revegetation planning tool that uses soil, plant, and climate data to identify potential revegetation species that are adapted and appropriate for the planting purposes (Table 2). The USDA Plants Database; the USDA Forest Service Fire Effects Information System; the USDA NRCS Plant Materials Program; the Tarleton State University Department of Agribusiness, Agronomy, Horticulture and Range Management; and the University of Texas at Austin Ladybird Johnson Wildflower Center Network websites provide descriptions of important site and species characteristics (Table 2). There are many additional sources of information to assist those initiating restoration projects while combating invasive species, some of which are listed and described in Table 2.

Invasive Plant and Restoration Research Needs

Restoration is a complex process that is further complicated by invasive plants. More-sophisticated methods to selectively control invasive plants while promoting the establishment of desired species are needed to overcome this primary obstacle to restoration success. This end may be achieved through the formulation of herbicides with precise selectivity, or manipulation of the abiotic or biotic environment in ways that favor native over invasive species. This may include applying soil amendments, irrigating, fertilizing, promoting beneficial microbial communities, or selecting suitable plant species, among other activities. We should continue to expand and apply our knowledge of trophic interactions, such as those among native and invasive plants and pollinators, herbivores, and microbes, to selectively encourage the establishment and proliferation of desired species. We can even learn to use the traits of invasive plants to our advantage. For example, some weeds or invasive plants may play a valuable role in establishment of native species, e.g., Russian thistle can serve as a nurse plant (Allen 1995). Collaboration between weed scientists and restoration ecologists can rapidly improve our success at controlling invasive plants and achieving our restoration objectives. In particular, such partnerships can work to identify susceptibility and tolerance of native species to new herbicide chemistries, and study the long-term effects on ecosystems of using herbicides in restoration projects. Much progress will be made when weed science and restoration ecology researchers and practitioners work together using fundamental ecological principles and technological advances to address these and the many other challenges that remain.

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