Lessons from primary succession for restoration of severely damaged habitats

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Abstract

Questions: How can studies of primary plant succession increase the effectiveness of restoration activities? Can restoration methods be improved to contribute to our understanding of succession?

Results: Successional studies benefit restoration in six areas: site amelioration, development of community structure, nutrient dynamics, species life history traits, species interactions, and modeling of transitions and trajectories. Primary succession provides valuable lessons for understanding temporal dynamics through direct, long-term observations on severely disturbed habitats. These lessons assist restoration efforts on infertile or even toxic substrates. Restoration that uses scientific protocols (e.g., control treatments and peer-reviewed publications) can offer insights into successional processes.

Conclusions: A century of studying successional dynamics has provided modern restoration activities with many useful lessons that are not being fully utilized.

Keywords: Disturbance; Life history; Models; Nutrients; Retrogressive succession; Species interactions; Trajectory.

Introduction

Succession, the study of species change over time, is a fundamental concept of ecology (McIntosh 1999). It addresses ecosystem dynamics both during and beyond the life span of organisms. Formal studies of plant succession have been conducted since 1895 (Warming 1895) and much has been learned about how ecosystems respond to a dynamic physical environment (Pickett & White 1985), how species colonize and interact (Glenn-Lewin et al. 1992), and how communities assemble and change (Temperton et al. 2004). Applying these lessons to practical needs is urgent and risky – urgent because land managers need immediate guidance, risky because focusing any scientific pursuit strictly on applicability of results can impede serendipitous discovery. One beneficial application of successional lessons is to guide ecological restoration (sensu lato, Aronson et al. 1993), which is essentially the purposeful manipulation of succession (Bradshaw & Chadwick 1980; Walker et al. 2007a). Restoration practices benefit from successional discoveries in at least six areas: site amelioration, development of community structure, nutrient dynamics, species life history traits, species interactions, and modeling the transitions between successional stages and how those stages fit together into trajectories. Scientific approaches to restoration also can clarify successional processes and improve the predictability of succession, thus leading to reciprocal benefits between the two fields.

Primary succession is species change on substrates where the disturbance has left a scant biological legacy (Clements 1916). Many classic studies of plant succession have been conducted on primary seres (successional sequences). These include dunes in Denmark (Warming 1895), Michigan, USA (Cowles 1901), and Australia (Coaldrake 1962); volcanoes in Indonesia (Ernst 1908), Alaska, USA (Griggs 1933), and Hawaii, USA (Eggler 1971); and glacial moraines in Alaska, USA (Cooper 1923) and New Zealand (Stevens & Walker 1970). Primary succession is integral to any thorough examination of temporal dynamics for several reasons. First, valuable long-term studies have been conducted at some of the study sites listed above and on many other primary seres (Walker & del Moral 2003). Direct observation over time is always preferred over single measurements along the landscape (chronosequence) where assumptions of similar development among differently-aged plots are problematic (Fastie 1995). Second, primary seres provide a contrast to studies of secondary succes-

sion that occur on more fertile and stable substrates (e.g., old field succession; Cramer & Hobbs 2007). Third, in many severely disrupted ecosystems, particularly those dominated by long-lived organisms such as trees, shifts in vegetative composition are slow (hundreds to thousands of years). Primary succession is an important approach to these long-term processes and helps to link successional processes with even longer processes such as soil formation and development (Wardle et al. 2004). Finally, primary succession provides the most appropriate tools for restoring heavily damaged systems of both natural and anthropogenic origin (del Moral et al. 2007). Ecosystems highly disrupted by human activities can be unstable, infertile, or even toxic. Lessons from primary succession, initially developed on naturally disturbed surfaces with spontaneous recovery, are often relevant for restoration (directed recovery) of such anthropogenic disturbances.

In this paper, we highlight six ways that successional studies in severely disturbed habitats have contributed to the development of ecological principles and help to clarify the goals of ecological restoration. The coverage of such a broad range of topics cannot be comprehensive, but we illustrate each topic with a few examples. We also briefly examine how restoration can help advance the understanding of succession. Our aim is to illustrate the usefulness of recognizing the tight, mutually beneficial links between succession and restoration.

Site Amelioration

Studies of primary succession describe and attempt to explain how plant, animal, and soil communities respond in the aftermath of severe disturbances (Walker 1999a). Inevitably, this involves evaluating the attributes of the original disturbance (magnitude, severity) and of any subsequent occurrences (frequency) and explaining the amelioration of the initial physical conditions by both abiotic and biotic processes (Walker 1999b). Restoration can use this information to accelerate the amelioration of harsh conditions (Table 1). However, restoration must be placed in a human context. Prediction, assessment, and mitigation of natural disasters have been increasingly emphasized as human populations expand and more human lives are at risk. Historically, humans relied more on avoidance (Oliver-Smith & Hoffman 1999) but now disasters are analyzed by geologists, engineers, and sociologists for their actual or potential impact on humans.

Table 1. Examples of restoration tactics to address problems at crucial stages of the restoration process.

Restoration topic	Goal	Tactics
Establishment	Ameliorate stress	Create safe sites to enhance survival Install fences to trap seeds Install perches to enhance dispersal Appropriate fertilization Dense stocking rates to create 'nurse plant effect' by mutual protection
Carbon accumulation	Accelerate development	Surface preparations (e.g., mulch, safe sites) Direct planting of mature individuals Stabilize erosion (short-lived cover plants) Limit grazing (e.g., fencing, thorny shrubs)
Nutrient dynamics	Increase availability	Adjust fertility by: use of N-fixing species; adding carbon (e.g., sawdust) to immobilize excessive nutrients; add phosphorus and organic matter in later stages to provide nutrient retention
Life history	Enhance diversity	Consider local species pools (i.e., donors) and any seed bank Modify site for mix of growth forms planned Select species based on its weakest link (e.g., seedling survival or competitive ability, not its adult characteristics)
Species interactions	Self-sustaining species	Limit competition from nutrient-responsive species through planned disturbances Include shade-tolerant species and N-fixers

Biologists have long incorporated the impact of natural disturbances on populations of all organisms, including humans. Now humans utilize at least 30% of all global net primary productivity (Vitousek et al. 1986), with that value reaching 100% in some regions (Foley et al. 2007). Because we have profoundly affected all of Earth's ecosystems (Steffen et al. 2007), humans now trigger, enhance, or are otherwise involved in disturbances in a positive feedback loop that not only increases disturbances but also increases human risk (Fig. 1; Keys 2000; Diamond 2005; del Moral & Walker 2007). One way to break this cycle is through changes in human behaviors that contribute to disturbance, for without such changes, restoration of severely damaged habitats may be only temporary. For example, stabilization of landslides triggered by road cutting ultimately means that road construction should not continue unabated. However, lessons of natural recovery gleaned from successional studies can increase the effectiveness of restoration of severely damaged habitats (Reice 2001; del Moral & Walker 2007), and, at best, also inform policy and land management
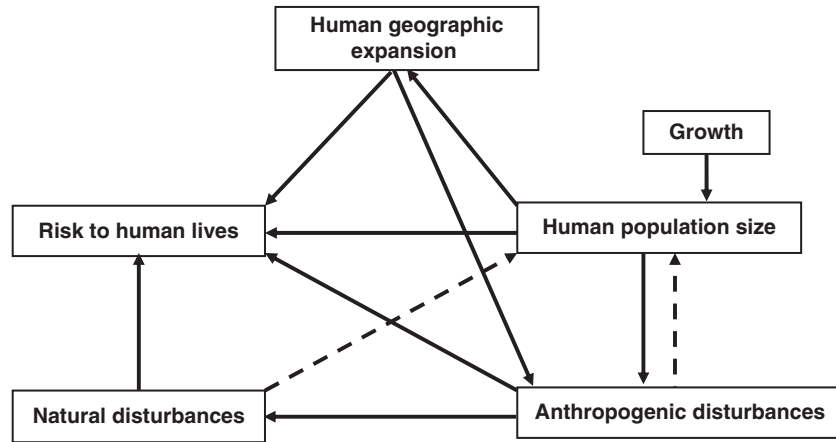
Fig. 1. Human population growth leads to geographic expansion and both of these changes increase anthropogenic disturbances (e.g., agriculture, logging, urbanization) that precipitate and intensify natural disturbances (e.g., dune expansion, floods, landslides). Human lives are then increasingly at risk from the direct effects of larger population size and geographic expansion and indirectly through increased disturbance (both anthropogenic and natural). Disturbances also kill people, but not enough to offset rapid population growth. Solid lines indicate a positive influence, dashed lines a negative influence. Modified from del Moral & Walker (2007).

about the ecological consequences of some human activities. For example, successful restoration of Puerto Rican landslides involves a thorough grasp of plant life histories and species interactions but also an understanding of how soil stability is best achieved (through either physical or biotic manipulation; Walker et al. 1996; Shiels et al. 2008). Coupling ecological and engineering tools with appropriate land use will maximize recovery from specific disturbances at both local and landscape levels.

Accumulation of Carbon and Development of Community Structure

The sequential development of different plant communities after severe disturbances remains an intriguing mystery, despite a century of examination. How communities assemble is so complex that there is little agreement on even general patterns, although carbon certainly accumulates and community structure becomes more complex. Primary succession is often less predictable than secondary succession (Turner et al. 1997; Fukami et al. 2005). Early in primary succession, recurrent (but stochastic) disturbances are likely, and safe sites that are both fertile and stable enough for establishment are rare (Walker et al. 2006). Nonetheless, any guidelines from successional observations or experiments can help achieve the usual restoration goals of increased plant cover and biodiversity and their corollaries (e.g., more shade, leaf litter, moderated

surface temperatures, reduced erosion, and increased animal activity).

Carbon accumulation is not continuous even in successional systems that are left undisturbed. Following a progressive accumulation of carbon and nutrients, many primary seres undergo a retrogressive phase where carbon and often phosphorus decline (Walker et al. 2001; Wardle et al. 2004). Restoration strategies will differ between these two phases, with recovery of biomass likely to be much more difficult during retrogression than progression (Walker & Reddell 2007), especially when thresholds of deterioration (e.g., loss of carbon or community structure) have been passed that require extra effort to reverse (Whisenant 1999; Hobbs & Harris 2001). Although retrogression is commonly viewed as occurring only after many centuries of gradual accumulation of carbon and community structure, shorter-term losses also alter successional dynamics and subsequent restoration efforts (Walker & del Moral 2008). These losses can arguably be considered retrogression (Fig. 2). For example, frost damage reduced dominance by a shrub on a 100-year-old volcanic surface in New Zealand and thereby delayed succession (Walker et al. 2003). Ongoing disturbances such as fires and flooding (Reice 2001), landslides (Walker et al. 1996) and invasions (Vitousek et al. 1987), or novel disturbances such as vehicle tracks (Bolling & Walker 2002) can reduce carbon accumulation and cause retrogression, as long as they are not so severe as to reset the sere. Indeed, any disturbed landscape
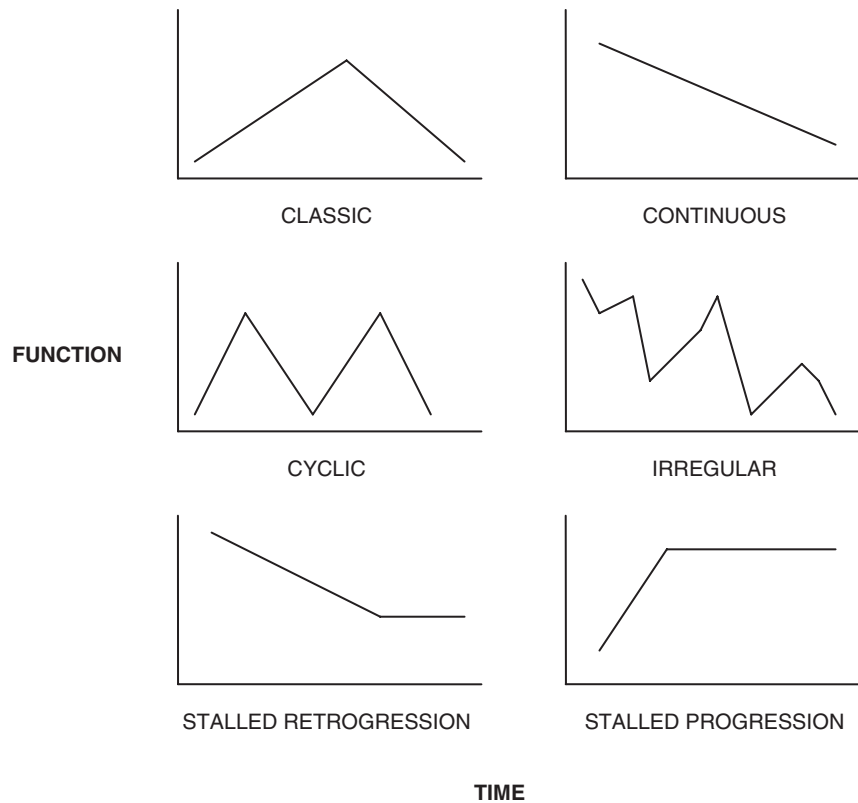
Fig. 2. Possible patterns for retrogressive change during succession based on a single ecosystem function (e.g., biomass, nutrient pool). The classic pattern involves a long build-up phase (longer in primary than secondary succession) followed by a long decline. Other possible patterns include continuous decline, regular or irregular alternating periods of progressive and retrogressive change, or even a stalled retrogression (analogous to arrested or stalled progression). The time scales may differ among the patterns (e.g., the classic pattern may involve centuries, the cyclic pattern only decades).

may have patches of both progressive and retrogressive change.

Restoration efforts to accelerate the accumulation of carbon and structure can involve direct carbon inputs through mulching or transplanting (Table 1). Such efforts, especially the use of fast-growing ground cover, might help stabilize the surface but the introduction of species that produce dense swards or thickets often can make establishment of natives and development of subsequent stages difficult (see 'Species interactions'). Revegetation with grass species on construction sites in the Alaskan tundra, for example, delayed establishment by native plants (Densmore 1992). Other restoration efforts attempt to skip successional stages and introduce large, late-successional vegetation directly. This is most effective in stable and fertile habitats where the transplants are initially protected from competition (Whisenant 2005). Planting young shrubs or trees can act as mutual protection from physical stress, eliminate competition from other species, and limit grazing effects (Bradshaw & Chadwick 1980).

Nutrient Dynamics

The accumulation of nutrients in primary seres that are initially very infertile is a critical determinant of successional pathways and an issue with implications for restoration. In many infertile seres, the almost universal increase in nitrogen is largely due to microbial nitrogen fixation, particularly when fixation occurs symbiotically with vascular plants (Van Cleve et al. 1971; Walker 1993). Common limits to nitrogen fixation include available phosphorus and moisture (Sprent 1987). Therefore, vascular plants with nitrogen fixing symbionts (hereafter called 'nitrogen-fixers') are more successful invaders of habitats with some initial soil development than of recently exposed, highly infertile sites (Uliassi & Ruess 2002). Subsequent successional dynamics (exactly which plant species follow the nitrogen-fixers) depend on the density, life form, and longevity of the nitrogen-fixer, its impact on seed dispersal and microclimate, and its historical role in the community (Vitousek et al. 1987; Walker & del Moral 2003). Unlike nitrogen,

phosphorus levels typically decline through primary succession as labile forms are leached or immobilized (Walker & Syers 1976; Vitousek & Farrington 1997); the balance between nitrogen and phosphorus levels in both soils and plants affects and is impacted by successional processes (Sterner & Elser 2002).

There are several implications of nutrient dynamics for restoration. First, primary seres occur under initially infertile conditions, so fertilization may impede rather than aid restoration (del Moral et al. 2007). This can happen when too much fertilizer favors fast-growing weeds over slow-growing natives, when nutrient ratios become altered, or when either of these effects leads to different successional trajectories. The utilization of nitrogen-fixers may provide an optimum nutrient balance, but there can be unintended consequences such as the inhibition of succession. For example, the herbaceous nitrogen-fixer *Lupinus nootkatensis* was widely planted in Iceland to restore forests in areas of severe soil erosion but had negative impacts on native legumes and small shrubs where it formed thick mats (Aradottir 2004). A common method for restoring favorably low nutrient levels is the addition of a carbon source such as sawdust or mulch in order to immobilize available nutrients in soil microbes (Blumenthal et al. 2003). Such additions frequently counteract invasive species as well (Alpert & Maron 2000). Second, highly variable spatial patterns in soil nutrients are common so restoration efforts must account for them (Walker & del Moral 2003). Steep nutrient gradients, often at very small scales as found around desert shrubs (Bolling & Walker 2002) or in sand dunes (Grootjans et al. 1998), suggest that careful soil analyses would help most restoration efforts. Finally, when retrogressive conditions exist due, for example, to long-term salt accumulation or nutrient leaching, these conditions must be ameliorated before progressive succession can be established. Vegetation can be used to improve freshwater retention and organic matter accumulation (Walker & Reddell 2007). However, inappropriate additions of vegetation or fertilizers can trigger new shifts in trajectories and changes in the balance between progressive and retrogressive change (Fig. 2). Ultimately, no restoration effort can ignore nutrient dynamics. Indeed, a successful (self-maintaining) restored ecosystem will have at least a semblance of the original nutrient cycles. These cycles are best reestablished indirectly via restoration of plant and soil fauna communities; fertilizers should be used only sparingly (Table 1).

Species Life Histories

One important lesson from successional studies is that each species has a range of responses to the environment, depending on its life history stage (seed, seedling, juvenile, and reproductive adult) and whether the plant is colonizing, establishing, growing, or senescent (Grubb 1977). How species respond differentially to disturbances is particularly accentuated in the inhospitable environments of early primary succession (Bruno 2000; Levine 2000; see 'Site amelioration'). Species interactions such as facilitation and competition within a successional community also vary by life history stage. For example, nitrogen-fixing shrubs on a volcano in New Zealand (Walker et al. 2003) and a glacial moraine in Alaska (Chapin et al. 1994) both inhibited and facilitated subsequent species and these effects varied by life-history stage and successional stage. In both cases, the shrubs inhibited germination and establishment but had a net positive effect because of the large increase in organic matter and the facilitation of growth of the later successional species.

A thorough knowledge of the life-history stages of the plants used in any restoration effort is clearly helpful. Huberty et al. (1998) found that nitrogen additions improved overall growth, but did not cause displacement of one growth form by another even though individual species were affected differently. Details at the species level concerning traits such as dispersal ability, germination requirements, growth rates, life spans, and functional types can help plan the best approach (Table 1). When these details are unknown, one must rely on known life histories of closely related species, but often with unfortunate results (Simmons et al. 2007). When recovery is allowed to proceed spontaneously, the results are unpredictable and they are satisfactory only under special conditions (Prach & Pyšek 2001).

Dispersal and physical stresses limit establishment and growth of plants in early primary succession. Overcoming these obstacles is central to any acceleration (restoration) of recovery processes. Direct introduction of propagules can offset dispersal limitations, especially when disturbed areas are large, or when propagules are limited in number or when the species are poor dispersers. Successful introductions depend on knowledge of the most favorable microsite conditions for each species. Slight differences in topography or substrate can improve microclimates for germination and survival (del Moral & Deardorff 1976). For instance, gravel-covered microsites on Mauna Kea volcano in Hawaii provided optimal conditions for seed

germination and transplanted seedling survival of the rare silversword (*Agyroxiphium sandwicense*; Walker & Powell 1999a). However, the presence of woody vegetation favored seed germination but inhibited seedling growth, so each restoration approach had both advantages and disadvantages. Attempts at direct introductions often fail due to a lack of understanding of the tolerances of the target species in each life stage. Indirect methods of introductions can allow for the sorting of various natural processes. For example, artificial perches were successful in attracting birds and hence seeds of many forest trees to Puerto Rican landslides (Shiels & Walker 2003), but few seeds germinated, in part because they were inhibited by dense vegetation dominated by wind-dispersed grasses. Further, indirect means can be spatially constrained, or can allow the introduction of undesirable species. Dispersal, germination, and early seedling survival are stages during which a particular species may have subtly different environmental optima (Brooker & Callaghan 1998; Levine 2000).

Models of succession demonstrate that seed dispersal usually dictates trajectories in early succession and can be more important than resource availability (Martineau & Saugier 2007). Studies of spontaneous succession in the Czech Republic demonstrated that pioneer communities were highly heterogeneous and determined by dispersal availability, while, after several years, soil properties imposed a deterministic structure on the vegetation (Lepš et al. 2000). This study suggested that the course of restoration would be affected first by the appropriate selection of species and then by proper preparation of the soil. Dispersal limitations (Rehounkova & Prach 2006) can create unpredictable trajectories, so planning for restoration starts with knowledge of the dispersal potential of the surrounding vegetation. Sowing desirable species is nearly always required if any control of early restoration is needed. Lepš et al. (2007), in a large-scale study in five European countries, demonstrated that sowing different seed mixtures over existing vegetation markedly altered successional trajectories. Spontaneously recovering control plots were more diverse, but the least productive. This study demonstrated that proper sowing regimes result in highly productive communities within which undesirable species (i.e., weeds) were suppressed. Experimental work in a successional context that couples both scientific and restoration goals will be most productive in discovering and ameliorating the dispersal limitations for each life history stage of each species of concern (Walker & del Moral 2003).

Many seeds reach a site without germinating (Wood & del Moral 1987), so understanding germination requirements is crucial for successful restoration. Seeds can persist in a seed bank, only to germinate years later, perhaps following a major disturbance such as fire (Willis & Read 2007). This hidden pool of colonists can adversely affect planned trajectories, so the seed bank should be considered carefully. Conditions for successful seed germination include not just specific microsite requirements (e.g., safe-sites; Jones & del Moral 2005), but also proper pre-germination conditions (Satterthwaite 2007). Sowing seeds that require stratification requires quite different timing from agricultural species that lack dormancy. Many species require scarification (Pugnaire et al. 2006) or heat treatments. These pre-conditions are often difficult to apply, but stratification (cold, wet, dark conditions) or treatment with hormones (e.g., gibberellins) can be effective substitutes. In contrast, unforeseen natural disturbances can alter succession. In Panama, fire inhibited seed germination of many species, leading to competitive dominance by a few pioneer species (Hooper et al. 2004). Slow germinating species may be at a substantial disadvantage when sown with rapidly emerging species, so phased planting or sowing may be required. Differential longevity also affects trajectories (Connell & Slatyer 1977) and determines competitive dominance in many types of vegetation (Schippers & Kroptt 2001).

The fate of viable and potent seeds is rarely considered when succession is being investigated, yet seed predation can seriously alter or arrest succession. When Barbera et al. (2006) explored reasons for arrested succession in degraded Mediterranean scrublands now dominated by perennial tussock grasses, they found that the former dominant oak species suffered very high predation rates. Arrested succession occurred even before potential dominants could establish. Alternatively, various forms of facilitation can promote successional transitions. *Trema micrantha*, a pioneer of Brazilian rain forests, facilitated the invasion of other forest trees in a highly fragmented system (Rodrigues et al. 2004). This pattern is repeated in habitats as diverse as dry European woodlands (Kunstler et al. 2007) and open North African savannas (Aerts et al. 2006).

Once plants are established, they still must face competitive threats from other species, so the competitive abilities of species must be considered. Often, functional types (sensu Grime 2001) can be used to assess longer-term competitive ability and

success. Caccianiga et al. (2006) demonstrated that functional types shifted during primary succession on an alpine glacier foreland, from ruderal to stress-tolerant species. Erschbamer (2007) provided experimental confirmation for differential responses among species in a similar habitat. Purely pioneer or ruderal species, common to young glacier forelands, were less able to adapt to increasing temperatures when compared to competitive, stress-tolerant species. Her results suggested that more plastic or tolerant species should be preferred in restoration projects to ensure greater success under changing conditions.

Herbivory can have various impacts on vegetation dynamics (Horsley et al. 2003; Graaf et al. 2007) and can arrest, retard or accelerate succession, depending on circumstances (Walker & del Moral 2003). Invertebrate herbivory can impact successional trajectories by impeding or facilitating plant establishment (Brown & Gange 1992; Bach 1994) but is most likely to affect species change in later stages of succession (Walker & Chapin 1987). Periodic insect outbreaks, especially those that reduce the viability of one dominant species (Fagan et al. 2005), are most likely to occur in favorable habitats and represent the biggest influence of invertebrate herbivory on succession (Walker & del Moral 2003). The influence of vertebrate herbivory, in contrast, generally declines over successional time, as multiple, better-defended plant parts mature. Vertebrates are also more likely to impact species change in favorable than unfavorable habitats (Walker & del Moral 2003). Restoration activities must first evaluate conditions for the particular case, then decide to either factor in herbivory by establishing species that resist grazing (or mixing them with more vulnerable ones) or consider the exclusion of herbivores (del Moral et al. 2007). Herbivory also impacts succession indirectly through alterations of nutrient dynamics (Wardle & Peltzer 2007).

Life-history characteristics of species planned for use in restoration programs are rarely considered in detail, yet they are crucial. Many projects have failed due to inattention to such details. Failing detailed knowledge, functional group classifications based on available information can be useful to enhance the prospects for success. Attention must be paid to the likely pool of beneficial and detrimental species, germination requirements (both physiological and physical), responsiveness to fertility levels, the ability to tolerate herbivory and disease, competitive abilities, and the ability of the species to protect and facilitate other desirable species.

Species Interactions

As the physical stability and fertility of a primary sere increase, the impact of biotic interactions on succession increases. Although complex, these interactions have been categorized into those that are facilitative, inhibitory or neutral (Connell & Slatyer 1977), and they can impact all stages of succession (Walker & Chapin 1987) and each life history stage of the dominant species (Walker et al. 2003). The balance between facilitative and inhibitory interactions often varies along environmental gradients, and facilitation tends to increase with environmental stress (Callaway & Walker 1997; Brooker & Callaghan 1998). However, this generalization may not be universally applicable (Maestre et al. 2005). Any species interaction will be described differently, depending on the perspective chosen. A positive outcome for one species can be negative for another. In a successional context, facilitative interactions tend to promote succession and the order of species replacement while inhibitory interactions tend to arrest the rate of change (McCook 1994; Walker et al. 2003). Successful restoration clearly must addresses species interactions that impact successional trajectories.

Nitrogen-fixers (see 'Nutrient dynamics') have the potential to facilitate primary succession by adding nitrogen to developing soils (del Moral & Rozzell 2005). However, a comparison of five primary seres where the impact of woody nitrogen-fixers has been examined showed little or no impact on the arrival of subsequent species, mostly negative effects on their germination, and a mixed impact on growth (Table 2). The net effect on growth (whether positive or negative) was not explained by the amount or increase in nitrogen (Table 2). The two seres where the nitrogen-fixer had a net negative effect on the growth of subsequent species had either the highest or lowest increase in nitrogen. Net negative effects were generally due to root competition, while soil nitrogen increases usually benefited growth of subsequent species in pot experiments. The net negative effect of the Hawaiian nitrogen-fixer *Myrica* (an invasive species) on *Metrosideros* (the native) summarizes a complex set of both positive and negative impacts of different environmental effects of *Myrica* on various life stages of *Metrosideros* (Table 3). The net effect of a nitrogen-fixer is dependent on many variables, including its growth form, density, and impact on soil phosphorus or water (Walker & Vitousek 1991; Walker & del Moral 2003; Aradottir 2004).

Table 2. Effects of woody vascular plants with nitrogen-fixing symbionts ('nitrogen-fixer') on the arrival, germination, and growth of the subsequent woody species and on soil nitrogen in five different successional sequences.

Site	Habitat	Nitrogen-fixer	Subsequent species	Arrival	Germination	Growth	N Before	N During	Increase
Hawaii	Volcano	*Myrica*	*Metrosideros*	Neutral	Negative	Negative	2	13	6.5
New Zealand	Volcano	*Coriaria*	*Griselinia*	Positive	No data	Positive	15	78	5.2
New Zealand	Floodplain	*Carmichaelia*	*Griselinia*	Neutral	No data	Positive	22	106	4.8
Alaska	Floodplain	*Alnus*	*Picea*	Neutral	Negative	Negative	40	110	2.7
Alaska	Moraine	*Alnus*	*Picea*	Neutral	Negative	Positive	4	22	5.5

References: Hawaii: Vitousek & Walker (1989), Walker & Vitousek (1991); New Zealand volcano: Walker et al. (2003); New Zealand floodplain: Bellingham et al. (2001); Alaska floodplain: Walker et al. (1986), Walker & Chapin (1986); Alaska moraine: Chapin et al. (1994). Soil nitrogen levels are shown for before the nitrogen-fixer was present ('N Before') and during its dominance at each site ('N During') (total nitrogen in g/m^2 except for Hawaii: available nitrogen in $\mu g/g$). Increase in soil nitrogen was calculated as N During/N Before.

Table 3. Effects of the invasive *Myrica* tree on the native *Metrosideros* tree in Volcanoes National Park, Hawaii, USA. Responses in parentheses are non-significant trends. Modified from Walker & del Moral (2003).

Metrosideros life Stage	*Myrica* factor	Effect of *Myrica* on *Metrosideros*
Germination	Litter	Negative
	Shade	Positive
	Leaf leachate	(Negative)
Seedling growth	Litter	(Positive)
	Shade	(Negative)
	Roots	Negative
	Soils	Positive
Seedling survivorship	Shade	Positive
	Roots	Negative
	Soil	Neutral
Tree growth		Neutral

Data from Vitousek & Walker (1989) and Walker & Vitousek (1991).

Humans consider restoration successful when the newly established community has several native species that interact and where succession eventually occurs with minimal additional input. Many restoration efforts fail when a single species dominates the resources and is long-lived or self-replacing. These arrested seres occur when the dominant species forms a mat (e.g., bryophytes), sward (grasses), or thicket (shrubs) that impedes growth of other species through reduction of light or nutrients (Walker & del Moral 2003). Sometimes arresting succession is desirable in order to build up nutrients. For example, the climbing ferns (Gleicheniaceae) that dominate disturbed areas such as burns, landslides or road edges in the tropics delay forest succession by shading out forest trees (Walker 1994; Slocum et al. 2004) but also reduce soil erosion through extensive rhizomes and accumulate large amounts of organic matter (Russell et al. 1998). Removal of fern mats does not necessarily result in rapid tree colonization because initially infertile or unstable conditions may persist (Slocum et al. 2006).

Similarly, facilitating succession may not be the goal where intermediate stages are themselves desirable. They may be productive, support characteristic species, produce valuable commodities, or provide other services such as low maintenance power line corridors (Niering et al. 1986; De Blois et al. 2004). Clarity about restoration goals is essential, whether the goals are to decrease erosion, increase biodiversity, favor a specific successional pathway, or promote flexibility in a community to respond to a variety of scenarios (Hobbs et al. 2007).

Modeling of Transitions and Trajectories

Models help to clarify the successional role of each of the above processes (response to disturbance, carbon accumulation, nutrient dynamics, species life histories, species interactions). Each process is influential in how one community undergoes the transition to a new community and how these transitions combine to form complex trajectories. Most restoration activities focus on only one or two of these processes and rarely address their integration into longer-term trajectories, spatial consequences at the landscape level (van Diggelen 2006), or whether those trajectories are in a progressive or retrogressive phase (Fig. 2).

Ecological models have recently been incorporated into the nascent development of restoration theory (Temperton et al. 2004; van Andel & Aronson 2006; Walker et al. 2007b; Suding & Hobbs 2008) and some of these models address succession. However, the lack of predictability about the details of successional trajectories makes predicting the consequences of a given set of restoration actions difficult. Two paths hold promise, however, in linking successional models to restoration activities. These are the modeling of restoration effects on immediate transition dynamics and the

modeling of broader landscape impacts. Good examples of both approaches come from detailed research on progressive and retrogressive succession and restoration of fens in northwestern Europe (Schrautzer et al. 2007) and of arid lands in Australia (Walker & Reddell 2007). Other modeling approaches use simulations (Schippers & Kroptt 2001), functional type, or process-based approaches (Martineau & Saugier 2007).

How Restoration Can Help Explain Succession

Ecological restoration developed as a practical, goal-driven activity on lands disturbed by humans and has only recently started assembling a set of fundamental principles. Succession has its foundations in observations about natural ecosystems and a well-developed body of theory. Yet, better linkage between these disciplines is inevitable because restoration is essentially managed succession. Restoration activities that follow scientific protocols such as hypothesis testing, un-manipulated controls, and peer-reviewed publication of results can provide practical tests of successional principles. For example, revegetation of a short mining road in southern Nevada involved ripping the entire road but sowing native seeds on only half of its length. This simple procedure allowed a comparison of natural colonization vs. sowing on ripped surfaces (Walker & Powell 1999b). A more thorough investigation could have involved a factorial design to evaluate the benefits of ripping or various watering, fertilizing or planting regimes. In addition, when such a design is developed to test questions about gaps in our understanding of desert succession, real progress can be made. Finally, tying local, site-specific studies into systematic suites of experiments across environmental gradients will allow tests of broader generalizations – a benefit to both the theorist (how representative is one study of successional principles?) and the practitioner (can lessons learned somewhere else apply to my particular project?). A merger is overdue and would benefit both fields, with succession providing the conceptual background and restoration providing the practical tests (Walker et al. 2007b).

Conclusions

The principles developed from studies of primary succession underpin practical efforts to restore heavily damaged habitats. Successional studies have examined how plants respond to disturbance, how plant communities grow by accumulating carbon and developing spatial structure, how nutrients flow between soils and plants, how species colonize, establish, grow and interact, and how all of these interactions produce transitions between communities and eventually create complex trajectories. This basic understanding of vegetation change is a phenomenally rich source of ideas for planning restoration programs. Unfortunately, it has not yet been adequately tapped by practitioners of restoration (Walker et al. 2007a), despite the pioneering work of Bradshaw and colleagues (Bradshaw & Chadwick 1980; Bradshaw 1983, 1987, 1996). In turn, restoration programs have a great potential to help elucidate successional principles. Facilitating the mutual exchange of information will help both succession and restoration to reach their respective goals of understanding and manipulating vegetation change.

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