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# Old Fields

*Dynamics and Restoration of  
Abandoned Farmland*

*Edited by*

Viki A. Cramer and Richard J. Hobbs

SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL



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*Succession on the Piedmont of  
New Jersey and Its Implications  
for Ecological Restoration*

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AND STEWARD T. A. PICKETT

The revegetation of disturbed ground through succession is one of the most fundamental processes studied by plant ecologists. In fact, the early history of plant ecology was dominated by attempts to understand the dynamic nature of vegetation through studying succession (e.g., the work of Cowles, Clements, Gleason). In a modern context, the manipulation of succession represents a dynamic approach to the creation and management of restored systems (Luken 1990). Vegetation development during restoration is analogous to successional dynamics and can benefit directly from the integration of successional theory into restoration ecology. Frederick Clements was an early champion of utilizing natural processes in restoration. His perspective, from "Ecology in the Public Service," is summarized in this statement:

From the very nature of the climax and succession, development is immediately resumed when the disturbing cause ceases, and in this fact lies the basic principle of all restoration or rehabilitation. (1949a)

Our perspective on succession, and on vegetation dynamics in general, is a hierarchical one (Pickett et al. 1987; Pickett and Cadenasso 2005). This perspective recognizes three separate coarse-scale drivers of ecological change that revolve around variation in (1) site availability, (2) species availability, and (3) species performance. Within each of these major categories are nested specific determinants of community structure and composition. For example, landscape connectivity may alter species availability (Haddad et al. 2003), and herbivory may alter relative species performance. Successional dynamics are driven by changes in one or more of these variants. Similarly, ecological restoration depends on the manipulation of these independent causes of change. We define succession as the change in species composition

or community architecture of a site over time (Pickett and Cadenasso 2005). This broad definition avoids some of the debate associated with narrower definitions and can encompass the variety of outcomes and dynamics suggested by the hierarchical perspective. Here we present data from a long-term experimental study of succession, specifically focusing on drivers of successional change and their application to restoration.

### History of the Buell–Small Succession Study

In 1958, Murray Buell, Helen Buell, and John Small initiated an experimental study of succession at the Hutcheson Memorial Forest Center (HMFC), New Jersey, USA. This site ( $40^{\circ}30' N$ ,  $74^{\circ}34' W$ ) is located within the piedmont of the Mid-Atlantic region and is operated by Rutgers University. The study had two main objectives (Pickett et al. 2001): (1) determine whether space-for-time substitution gives a reliable account of the successional dynamics of the area, and (2) determine whether Egler's (1954) initial floristic composition hypothesis of succession merited support. Space-for-time substitution studies were commonly used to infer long-term successional dynamics within a short study period (Pickett 1989) but had not been specifically tested for accuracy of prediction.

The ten fields of the Buell–Small Succession Study (BSS) range in size from 0.4 to 1.0 ha. Eight of these fields are along the edge of an old-growth forest, while the remaining two are separated from the old growth by the other fields (figure 8.1). Beginning in 1958, fields were abandoned as pairs in alternate years until 1966. The experimental structure of the study generated fields that differed in season of abandonment (fall or spring), final crop (hay

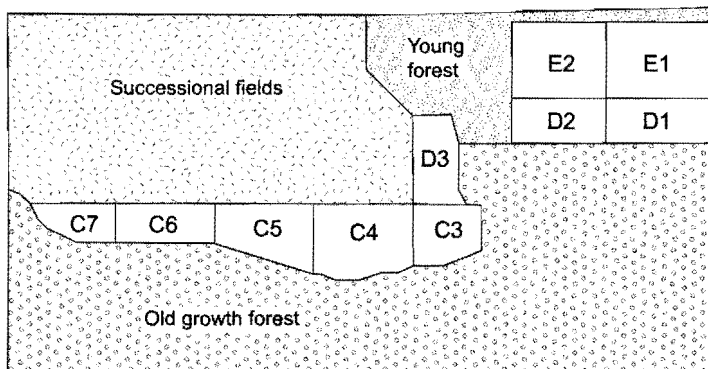


FIGURE 8.1. Map of the Hutcheson Memorial Forest, Rutgers University, showing locations of the Buell–Small Succession Study (BSS) fields.

field or row crops—sorghum and soybeans), and soil treatment at abandonment (plowed or vegetation left intact). Within each of ten fields, forty-eight plots were arranged in a regular pattern that varied with the shape of the field. At each sampling, the percentage cover of all species present was visually estimated in each permanently marked  $0.5 \times 2.0$  m plot. Data collection occurred every year, after the release from agriculture, until 1979, when sampling switched to alternate years, though 2005.

### Site History and Conditions

The area surrounding the HMFC was farmed continuously since 1701, when Dutch farmers settled the region. The Piedmont region of central New Jersey is characterized by soils derived from Triassic red shales that tend to dry out in late summer and are not very fertile (Ugolini 1964). However, the Mettler's Farm, which became the HMFC, was reputed to be well managed and relatively fertile (Pickett et al. 2001). Records indicate that cow manure was applied to the fields regularly, but that in 1963 amendments shifted to chemical fertilizers.

The climate of the area is characterized as mesic continental. The mean annual temperature is  $11.5^{\circ}\text{C}$ , with average daily high temperatures of  $-1.2^{\circ}\text{C}$  in January and  $23.7^{\circ}\text{C}$  in July. Annual rainfall averages 1,180 mm and is evenly distributed throughout the year. Monthly precipitation ranges from an average of 76 mm in February to 123 mm in July. While average site conditions are mesic, fluctuations in rainfall combined with the tendency of the soil to dry out have resulted in periods of drought that have influenced plant growth and vegetation dynamics (Buell et al. 1961; Small 1961; Bartha et al. 2003).

### Target Community Composition

The old-growth forest of HMFC is a mixed-oak deciduous forest. When originally described, upland areas were dominated by three oak species, *Quercus alba*, *Q. velutina*, and *Q. rubra*, which accounted for nearly half of the stems and more than half of the basal area (Monk 1961b). Other species present included, in order of abundance, *Carya ovalis*, *Fraxinus americana*, and *Acer rubrum*. The understory of the upland was described as having a nearly continuous subcanopy of *Cornus florida* and a shrub layer dominated by *Viburnum acerifolium* (Monk 1957). Lowland portions of the site were dominated by a canopy of *Acer rubrum*, *Fraxinus americana*, and *Nyssa sylvatica*, with a shrub layer composed largely of *Lindera benzoin* and

*Viburnum dentatum*. The understory also supported a diversity of herbaceous species (Monk 1957; Monk 1961b; Frei and Fairbrothers 1963; Davison and Forman 1982).

Though the forest is referred to as old growth, it is dynamic and has experienced variation over time. Before European settlement, frequent surface fires occurred at roughly ten-year intervals (Buell et al. 1954). Fires were set by the indigenous people of the area until shortly after European colonization, with the last fire occurring in 1711 (Buell et al. 1954). The disturbance regime of the forest also includes periodical damage by severe winds that accompany hurricanes. The most recent of these was in 1950 and resulted in 299 trees being blown down (Frei and Fairbrothers 1963). Contemporary challenges to the forest include high deer (*Odocoileus virginiana*) densities and the persistent invasion of several exotic plants.

Tree regeneration is remarkably low at the site, particularly for oaks and hickories (*Carya* spp.). However, *Acer saccharum* and *Fagus grandifolia*, both characteristic of mesic forests, and the exotic *Acer platanoides* still appear to regenerate. This suggests that the forest may be transitioning from an oak-dominated forest to a more mesic forest type (Monk 1961a). The once dominant *Viburnum acerifolium* understory has also declined steadily over time (Davison and Forman 1982). These changes in forest composition may be related to increased deer density or the loss of fire from the system. In 1973 an outbreak of gypsy moths (*Lymantria dispar*) led to widespread oak defoliation and a resulting increase in light-demanding species in the subcanopy and understory (Moulding 1977; Davison and Forman 1982). The herbaceous understory of the forest has also been severely altered, first by grazing pressure from deer, then from apparent displacement by the exotic grass *Microstegium vimineum*, which has formed a nearly continuous carpet throughout much of the old-growth forest.

### Successional Trends Over Time

The successional patterns of the Buell–Small Succession Study (BSS) represent a straightforward progression of life-forms from short-lived herbaceous species to longer-lived woody species (figure 8.2). Annuals, such as *Ambrosia artemisiifolia*, *Bromus* spp., and *Erigeron annuus*, are abundant only the first one or two years after abandonment. Biennials and short-lived perennials, such as *Aster pilosus*, *Daucus carota*, and *Verbascum blattaria*, quickly replace these annuals but are in turn displaced by longer-lived perennials, such as *Calystegia sepium*, *Fragaria virginiana*, and *Solidago* spp. Shrubs and lianas dominate the system approximately fifteen to thirty years postabandon-

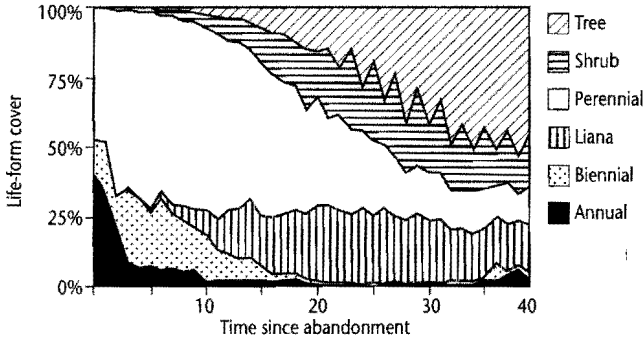


FIGURE 8.2. Change in plant life-forms over forty years of succession expressed as a percentage of total plant cover. Data are summed across all ten BSS fields.

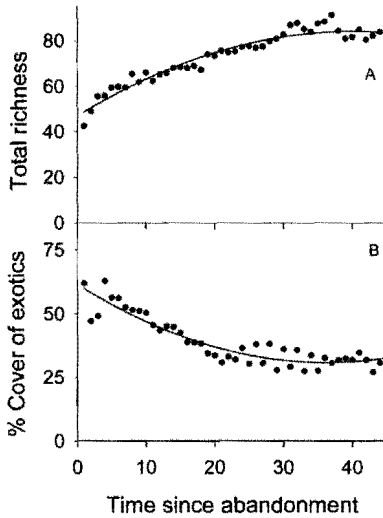


FIGURE 8.3. Successional change in (a) the total number of species, and (b) the percentage cover of exotic species, averaged across the ten BSS fields.

ment. The vast majority of these two life-forms is made up of two exotics, *Lonicera japonica* (liana) and *Rosa multiflora* (shrub). Native lianas common in the site include *Parthenocissus quinquefolia*, *Toxicodendron radicans*, and *Vitis* spp.; native shrubs include several species of *Cornus*, *Rhus*, and *Rubus*. Tree cover begins to dominate the site thirty years postabandonment and consists of native taxa such as *Acer* spp., *Juniperus virginiana*, *Quercus* spp., and *Cornus florida*.

While the number of species occurring in each 1 m<sup>2</sup> permanent sampling plot has not changed over time (Meiners et al. 2002), the total number of species in each field has continued to increase over time (figure 8.3a). This

suggests that the number of species that can coexist at small spatial scales is limited. Plot richness averaged twelve to thirteen species during the first thirty-five years of succession (Meiners et al. 2002), which is well within the range of species richness documented for a variety of herbaceous communities at the 1 m<sup>2</sup> scale (Gross et al. 2000). Compositional variation among plots leads to a much larger species pool across each field, and this pool becomes larger as succession proceeds. Clearly, successional communities do not become closed to new species as envisioned by Egler (1954). However, most common species become established relatively early in succession, as predicted.

After forty years of succession, it appears that the total richness of the BSS fields may be beginning to decline slightly. If this trend continues, the BSS may provide support for the intermediate disturbance hypothesis, which predicts maximum diversity at intermediate stages of succession, when the community contains a mix of early- and late-successional species (Loucks 1970; Connell 1978). As succession proceeds past this maximum, early-successional species are selectively lost from the community because they depend on disturbance or high resource availability for persistence (Bazzaz 1996). Though greatly reduced in abundance, most early-successional species have persisted as occasional occupants of small openings in the canopy or have appeared as a pulse following droughts. It is likely that at least some of the species that have disappeared from one or more of the BSS fields persist in the plots as dormant seeds and may reappear if the proper conditions arise. The occasional reappearance of *Ambrosia artemisiifolia* is an example of this kind of dynamic.

Exotic species are important components of successional systems worldwide (Inouye et al. 1987; Rejmánek 1989; Bastl et al. 1997). This is largely due to the dependence of many exotic species on disturbance for establishment. As many of the exotic species that occur early in succession are agricultural weeds, it is not surprising that the cover of exotic species starts high but becomes proportionately lower as succession proceeds (figure 8.3b). Exotic taxa are also disproportionately represented in early-successional life-forms. Exotics make up 53% of both annual and biennial species, 29% of perennials, 28% of shrubs, 21% of lianas, and 19% of trees. Because trees and other woody taxa dominate the later stages of succession, the decline in exotic cover over time may be partially driven by a lack of suitable species within the local pool rather than an inherent advantage to being native. Furthermore, most of the exotic tree species in the BSS are shade intolerant and limited to open areas.



## Repeatability of Successional Sequences

Central to the utility of successional processes in restoration is whether succession is predictable in space and time. If succession leads to variable endpoints, then the outcome of a restoration may also be variable. We can directly address the predictability of succession in time by comparing the BSS data to a space-for-time substitution study conducted within the same area (Bard 1952). We can also examine the consistency of successional dynamics across the ten BSS fields to address the predictability of succession in space.

Gily Bard's thesis work (directed by Murray Buell) described successional patterns from the Piedmont of New Jersey by sampling twenty-six sites of various ages and inferring successional transitions from one stage to the next (a chronosequence approach). Because all study areas occurred within 8 km of the old-growth forest of the HMFC and used similar sampling methodology (1 m<sup>2</sup> vegetation plots), Bard's study provides an excellent comparison for the experimental BSS data. The general transition of life-forms that Bard described is repeated in the BSS data (figure 8.2). However, there are some significant departures that illustrate the inherent variability of successional systems.

Bard's (1952) chronosequence study describes the perennial C4 grass *Schizachyrium scoparium* as one of the major stages of succession, dominating vegetation for nearly thirty years. However, this species is relatively unimportant within the BSS fields. At its peak, it never occurred in more than 20% of the plots and rarely made up more than 50% of the cover of any individual plot. The relative unimportance of this species in succession at HMFC may be caused by two factors. First, seeds of *S. scoparium* may not have arrived in sufficient numbers because of the landscape position of the fields (Pickett 1983). Bordered on one side by old-growth forests and the other by active and recently abandoned farmland, few reproductive individuals of this species were likely within dispersal range. Second, the lack of *S. scoparium* in the BSS fields may reflect local site conditions. In other successional systems, *S. scoparium* is often associated with infertile sites (Billings 1938). Though the soils of the area are often nutrient poor (Ugolini 1964), the farm that became the BSS was considered relatively fertile. Preexisting site conditions may have placed *S. scoparium* at a competitive disadvantage to species adapted to exploit abundant soil resources.

The second significant deviation from Bard's successional projection is the abundance of shrubs and lianas. Both of these life-forms were found in low abundance in Bard's study (Bard 1952). Within the BSS, shrubs and lianas dominated the middle stages of succession (figure 8.2), though the

majority of this cover consisted of two exotic invaders, *Lonicera japonica* and *Rosa multiflora*. Both of these species were present in Bard's chronosequence, but only in minimal amounts. The initiation of the BSS study coincided with the expansion of these species in the landscape and reflects a change in regional species pools. Together, these two relative newcomers to the local flora have dramatically altered succession by changing the structure of midsuccessional communities. Both of these species lead to decreases in local species richness through the inhibition of plant establishment (Meiners et al. 2001; Yurkonis and Meiners 2004). These recent invasions highlight the dynamic nature of local and regional species pools and the potential for rapid changes in successional trajectories in response to invasion.

The composition and dynamics of fields within the BSS also show dramatic spatial variability, though this depends on the scale of observation. The abundance of life-forms is much more predictable across the site than the abundance of any individual species, though there is considerable variation among life-forms. Annuals and biennials tend to vary dramatically among fields, probably reflecting the variation in abandonment conditions. In contrast, the cover of perennials, lianas, shrubs, and trees is quite repeatable among fields over the first forty years of succession. The lack of predictability for individual species probably reflects dispersal limitation that generates spatial variation for even the most abundant species. When a species first appears in the successional community, it is very patchy, leading to great variation among fields. As species spread and increase in cover, this among-field variation decreases. Interestingly, when a species begins to decline, it also does so in a patchy manner, generating higher among-field variability again.

Fields also differ in the timing and rate of tree colonization, though all have eventually become tree dominated. Fields in the lowland portions of the site developed into forests dominated by *Acer rubrum*, mirroring the composition of the lowland old-growth forest. Fields located within the upland have developed a more diverse canopy, including *Quercus* spp., *Carya* spp., *Cornus florida*, and *Fraxinus americana*. Compositionally, tree species vary dramatically among fields with little convergence over time. For example, the largest-seeded species at the site, *Juglans nigra*, is abundant in only one of the ten fields. This probably reflects dispersal limitation and suggests that a mature individual may have been near that field at the time of abandonment.

The difficulties in predicting successional outcomes and trajectories described here have several implications for restoration:

- The past may not be the key to the future. Looking to the surrounding landscape for indications of what may be expected in a successional

system is a critical first step, but may not reflect what will occur within a restoration. Variation in site conditions may lead to different transitional community types and potentially different successional trajectories. Furthermore, target communities may themselves be dynamic, responding to contemporary biotic and abiotic influences.

- Identify local species pools. These pools will determine the species that are available within the regenerating community, wanted and unwanted alike. Desired species that are not within the surrounding landscape may need to be added to the species pool. Likewise, heavily invaded landscapes are likely to generate heavily invaded successional systems. While the landscape surrounding a restoration often cannot be altered, management of invasive species can be included in restoration.
- Variation is natural. While spatial heterogeneity is often great within successional systems, compositional heterogeneity becomes an issue only when it involves missing life-forms or species characteristic of late-successional stages. This condition may represent problems within the site that are likely to persist without active remediation. Early-successional species are typically transient and so will need to be managed only if they are of conservation value.

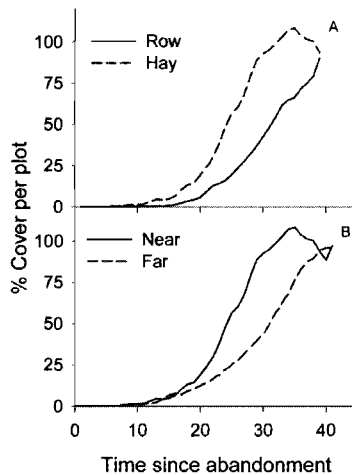
### Factors Affecting Tree Regeneration

Because succession in the BSS is leading to a closed-canopy forest, this study has relevance to the restoration of forested systems. Factors that regulate the establishment and growth of trees may have the most direct impact on the rate of succession and potentially the success of a restoration. Tree regeneration at HMFC has been reviewed elsewhere (Myster 1993), but it is worth revisiting specifically from a restoration perspective. This key transition evokes several of the important drivers of succession (Pickett et al. 1987), which are evident in the BSS.

The experimental variation in agricultural history led initially to differences in the vegetation composition and rate of succession among fields (Myster and Pickett 1990). Fields that differed in agricultural treatments—row crops versus hay fields—exhibit the greatest variation in community structure and dynamics. Hay fields, planted in *Dactylis glomerata*, had distinctly different vegetation dynamics for the first eight years after abandonment (Myster and Pickett 1990). Because competition for water between tree seedlings and grasses has been proposed as a major limitation to tree establishment in herbaceous communities (Davis et al. 1998), agricultural history

may be expected to influence tree regeneration. However, a comparison of the rate of increase in tree cover between row crops and hay fields does not suggest that grasses inhibit trees within the BSS (figure 8.4). Hay fields actually appear to be colonized more quickly, though this may be related to the small size of the hay fields relative to the row crop fields. However, some portions of the row crop fields have remained open for more than forty years, suggesting dispersal is not the sole limiting factor. In general, grasses are relatively unimportant in this system and do not persist. While herbaceous community composition and dynamics were strongly affected by agricultural history, tree regeneration appears to have been unaffected.

A clear driver of the rate and composition of tree regeneration is the proximity of fields to seed sources. Trees colonized fields adjacent to the old-growth forest much more quickly than those separated from the forest by another field (figure 8.4). There are also compositional differences in these fields. Fields adjacent to the old-growth forest supported a more diverse forest canopy that contains wind-, bird-, and mammal-dispersed species. The isolated fields became dominated by *Juniperus virginiana*, a bird-dispersed conifer, and have remained so for more than forty years. Fields adjacent to the forest were colonized early by *J. virginiana*, but these have largely been displaced by more shade-tolerant tree species (Quinn and Meiners 2004). Succession to deciduous forest has been slowed in the isolated fields by the



**FIGURE 8.4.** Influence of previous agricultural treatment (a) and proximity to seed source (b) on the rate of tree colonization of BSS fields. See figure 8.1; data plotted in panel (a) are from hay (C6 and C7) and row crop (C4 and C5) fields adjacent to the old-growth forest. Data plotted in panel (b) are from hay fields adjacent to (C6 and C7), and isolated from (E1 and E2), the old-growth forest.

relative inability of later-successional tree species to colonize the fields, and they have remained dominated by *J. virginiana*. Dispersal limitation can also be seen within fields as tree seedling densities initially declined with distance from the forest edge (Myster and Pickett 1992). This spatial pattern disappeared as the fields become structurally more complex (McDonnell and Stiles 1983; McDonnell 1986), bringing more vertebrate-dispersed species into the fields (Myster and Pickett 1992).

Though not directly assessed in the BSS, herbivory on tree seedlings has been extensively studied at HMFC. Seedlings of palatable trees tend to be clustered closer to the forest edge than nonpalatable species, suggesting that herbivores limit the establishment of these species within fields (Myster and Pickett 1992). Overall, mammalian herbivores severely limit the survival and growth of trees (Myster and McCarthy 1989; McCarthy 1994; Meiners et al. 2000; Cadenasso et al. 2002). Invertebrates have also been shown to regulate tree establishment (Facelli 1994; Meiners et al. 2000), but these tend to be more important in the regeneration of small-seeded trees (Myster and McCarthy 1989). In addition, seed predators consume large portions of the seeds dispersed into successional areas of HMFC (McCarthy 1994; Manson and Stiles 1998; Meiners and LoGiudice 2003), potentially limiting recruitment (DeSteven 1991; Gill and Marks 1991).

Despite the overall impact of herbivory on tree regeneration, there is considerable spatial variability in the intensity of herbivore activity. This spatial variation may be driven by large, landscape-level features or local heterogeneity in the environment. For example, leaf litter is heterogeneously deposited within successional areas (Facelli and Carson 1991). Insect herbivores concentrate their activity in areas containing leaf litter (Facelli 1994), compounding the direct impacts of litter on seedling emergence (Myster 1994). At larger spatial scales, seed predators respond to the presence of forest edges, generating heterogeneity in predation pressure (Myster and McCarthy 1989; Manson and Stiles 1998; Meiners and LoGiudice 2003). In addition to spatial variation, there may be considerable temporal variation in herbivore activity (Manson and Stiles 1998; McCormick and Meiners 2000; Meiners et al. 2000). Taken together, this variation may generate temporal and spatial refugia that allow tree regeneration to occur periodically. For example, seed predator activity varies dramatically among years and is concentrated close to forest edges. Seeds dispersed away from the edge in years with low predation risk would have a much greater chance of establishment than seeds produced in other years or dispersed to other locations.

The observations of patterns and the experimental assessment of processes in the transition between herb and shrub dominance to the establishment

and dominance by trees in the BSS yield insights for restoration. Management directives for the restoration of forested systems include the following:

- Tree regeneration appears independent of site history. Within the BSS, the influences of past agricultural treatments had little influence on tree regeneration. This appears contradictory to many studies that find residual effects of past land use. In systems where agricultural history generates persistent variation in vegetation or where grasses dominate, competition with herbaceous vegetation may become limiting to tree regeneration.
- Dispersal limits establishment. Trees are overall the poorest dispersers in a sere and may require the most direct intervention to ensure adequate regeneration. This is particularly true for species with poor dispersal ability in fragmented systems or for large sites. Lack of propagules from late-successional tree species may arrest succession at an earlier stage.
- Herbivory is a rate-limiting process. The density of herbivores at HMFC clearly limits tree regeneration. Sites with high densities of seed predators or herbivores may require protection of seeds and seedlings or the management of herbivores to ensure adequate and timely regeneration. Temporal and spatial heterogeneity in herbivore activity may provide opportunities for establishment in an otherwise hostile environment.

## Exotic Species Invasions

Exotic species are common in both successional and restored communities and are often problematic (Walker and Smith 1997; Parker et al. 1999; Byers et al. 2002). From a successional perspective, species invasions become a problem only if they inhibit or alter successional trajectories or if they alter the composition of the target community. In most successional systems, and most plant communities in general, there are relatively few exotic species that warrant concern and potentially require management. Within the BSS, 117 exotic species have been recorded, compared to 216 native species. Of these invaders, only 12 became abundant enough to examine for impacts on the richness of local (1 m<sup>2</sup>) communities. Of those, the invasions of only 4—*Elytrigia repens*, *Trifolium pratense*, *Lonicera japonica*, and *Rosa multiflora*—depressed richness (Meiners et al. 2001; Yurkonis and Meiners 2004). However, abundance of an invader does not necessarily lead to impacts on community structure. *Hieracium caespitosum*, a perennial invader that

peaked ten years after abandonment, had no impacts on richness despite covering an average 30% of each plot at its peak.

Most of the exotic species recorded within the BSS are short-lived species associated with agriculture and do not represent serious management concerns. As successional communities develop, these exotic species naturally leave the system. *Elytrigia repens* and *Trifolium pratense* become successional dominants for very brief periods. The two most abundant exotics at the site, *Lonicera japonica* and *Rosa multiflora*, also decline with tree canopy closure. These two species are considered to be regionally problematic management concerns. However, in this site they did not prevent the trees that are slowly shading them out from establishing. Fields abandoned when these invaders had become more prevalent in the landscape may have become invaded sufficiently to inhibit tree regeneration, requiring intervention.

Currently, two exotic species appear to be management concerns within the BSS: *Alliaria petiolata* and *Microstegium vimineum*. Both of these are invaders of forested systems (Cavers et al. 1979; Gibson et al. 2002). As such, they have the potential to alter the composition of the target community. Both of these species have spread throughout the forested portions of the BSS fields. *Alliaria petiolata* exudes chemicals with antifungal activity that reduces the ability of competing plants to acquire nutrients (Roberts and Anderson 2005). It appears to reduce the diversity of the herbaceous understory and can cover large areas quickly (McCarthy 1997). Likewise, *Microstegium vimineum* forms a thick continuous layer that reduces the diversity and cover of understory herbs (unpublished data).

Because these species are both (1) likely to persist and (2) have considerable impacts on the community, they represent serious management concerns. Any species that meets both of those criteria should be considered a management concern, while species meeting only one will have minimal or only transient effects. Based on information from other sites, it appears that several other species meet these criteria, though they have not yet become abundant in the BSS fields. These include *Acer platanoides*, *Berberis thunbergii*, *Lonicera maackii*, and *Rubus phoenoclasius*.

The directives from the BSS for the management of exotic species in restoration are clear:

- They're not all bad. The vast majority of exotic species, even those that become abundant, have no effects on the plant community and represent little to no threat to the successional development of the site.
- Be patient. Most invaders, because they are adapted to open and disturbed habitats, tend to disappear from systems as the successional

sorting of life-forms and species progresses. Management to remove early-successional invaders may hasten their decline, but should be considered a low priority. However, if management introduces new disturbed sites in an area, it may in fact prolong their occupancy.

- Focus management efforts wisely. Management of exotic species invasions should focus on species that inhibit key successional transitions (e.g., tree regeneration), or that can both persist and have an impact on the target community. Management of taxa that do not meet these criteria may provide aesthetic benefits but should not improve the ecological function or ultimate success of the restoration.

## Conclusion

Successional dynamics are the result of a complex suite of processes that interact to generate spatial and temporal heterogeneity. Knowledge of the primary processes that influence succession can help land managers effectively manipulate systems toward restoration. The Buell–Small Succession Study data suggest several major implications for restoration: (1) Dispersal appears to be a primary driver of restoration success, as it has the potential to regulate the availability of both late-successional and exotic species. (2) Site history clearly controls early-successional community dynamics but may not have persistent impacts. (3) Exotic species of early-successional stages are relatively nonproblematic, while exotics that persist within the target community have the potential to dramatically impact the system. Finally, (4) herbivory, particularly on the seeds or seedlings of trees, may limit the rate of canopy closure and the success of forest restorations. The applicability of these restoration lessons for other sites must be assessed based on the similarity of target communities and successional drivers. By placing site-specific factors appropriately in the framework of site availability, species availability, and species performance, managers should be able to successfully manage and enhance successional communities. The necessary linkage between successional processes and remediation was affirmed by Clements:

Nature's cooperation is essential to the success of the many present endeavors to undo man's destructiveness. Since this cannot be compelled, it must be won by understanding and insight. (1949b)

## Acknowledgments

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## REFERENCES

- Bard, G. E. 1952. Secondary succession on the piedmont of New Jersey. *Ecological Monographs* 22:195–215.
- Bartha, S., S. J. Meiners, S. T. A. Pickett, and M. L. Cadenasso. 2003. Plant colonization windows in a mesic old field succession. *Applied Vegetation Science* 6:205–12.
- Bastl, M., P. Kocir, K. Prach, and P. Pyšek. 1997. The effect of successional age and disturbance on the establishment of alien plants in man-made sites: An experimental approach. In *Plant invasions: Studies from North America and Europe*, ed. J. H. Brock, 191–201. Backhuys, Leiden, The Netherlands.
- Bazzaz, F. A. 1996. *Plants in changing environments*. Cambridge University Press, Cambridge, UK.
- Billings, W. 1938. The structure and development of old field shortleaf pine stands and certain associated physical properties of soil. *Ecological Monographs* 8:437–500.
- Buell, M. F., H. F. Buell, and J. A. Small. 1954. Fire in the history of Mettler's woods. *Bulletin of the Torrey Botanical Club* 81:253–55.
- Buell, M. F., H. F. Buell, J. A. Small, and C. D. Monk. 1961. Drought effect on radial growth of trees in the William L. Hutcheson Memorial Forest. *Bulletin of the Torrey Botanical Club* 88:176–80.
- Byers, J. E., S. Reichard, J. M. Randall, I. M. Parker, C. S. Smith, W. M. Lonsdale, I. A. E. Atkinson, T. R. Seastedt, M. Williamson, E. Chornesky, and D. Hayes. 2002. Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* 16:630–40.
- Cadenasso, M. L., S. T. A. Pickett, and P. J. Morin. 2002. Experimental test of the role of mammalian herbivores on old field succession: Community structure and seedling survival. *Journal of the Torrey Botanical Society* 129:228–37.
- Cavers, P. B., M. I. Heagy, and R. F. Kokron. 1979. The biology of Canadian weeds. 35. *Alliaria petiolata* (M. Bieb) Cavara and Grande. *Canadian Journal of Plant Science* 59:217–29.
- Clements, F. E. 1949a. Ecology in the public service. In *Dynamics of vegetation*, ed. B. W. Allred and E. S. Clements, 246–78. H. W. Wilson, New York.
- . 1949b. Plant succession and human problems. In *Dynamics of vegetation*, ed. B. W. Allred and E. S. Clements, 1–21. H. W. Wilson, New York.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–10.
- Davis, M. A., K. J. Wragge, and P. B. Reich. 1998. Competition between tree seedlings and herbaceous vegetation: Support for a theory of resource supply and demand. *Journal of Ecology* 86:652–61.
- Davison, S. E., and R. Forman. 1982. Herb and shrub dynamics in a mature oak forest: A thirty-year study. *Bulletin of the Torrey Botanical Club* 109:64–73.

- DeSteven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: Seedling emergence. *Ecology* 72:1066–75.
- Egler, F. E. 1954. Vegetation science concepts. 1. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio* 4:412–17.
- Facelli, J. M. 1994. Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology* 75:1727–35.
- Facelli, J. M., and W. P. Carson. 1991. Heterogeneity of plant litter accumulation in successional communities. *Bulletin of the Torrey Botanical Club* 118:62–66.
- Frei, K. R., and D. E. Fairbrothers. 1963. Floristic study of the William L. Hutcheson Memorial Forest (New Jersey). *Bulletin of the Torrey Botanical Club* 90:338–55.
- Gibson, D. J., G. Spyreas, and J. Benedict. 2002. Life history of *Microstegium vimineum* (Poaceae), an invasive grass in southern Illinois. *Journal of the Torrey Botanical Society* 129:207–19.
- Gill, D. S., and P. L. Marks. 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecological Monographs* 61:183–205.
- Gross, K. L., M. R. Willig, L. Gough, R. Inouye, and S. B. Cox. 2000. Patterns of species density and productivity at different spatial scales in herbaceous plant communities. *Oikos* 89:417–27.
- Haddad, N. M., D. R. Browne, A. Cunningham, B. J. Danielson, D. J. Levey, S. Sargent, and T. Spira. 2003. Corridor use by diverse taxa. *Ecology* 84:609–15.
- Inouye, R. S., N. J. Huntly, D. Tilman, J. R. Tester, M. Stillwell, and K. C. Zinnel. 1987. Old-field succession on a Minnesota sand plain. *Ecology* 68:12–26.
- Loucks, O. 1970. Evolution of diversity, efficiency, and community stability. *American Zoologist* 10:17–25.
- Luken, J. O. 1990. *Directing ecological succession*. Chapman and Hall, London.
- Manson, R. H., and E. W. Stiles. 1998. Links between microhabitat preferences and seed predation by small mammals in old fields. *Oikos* 82:37–50.
- McCarthy, B. C. 1994. Experimental studies of hickory recruitment in a wooded hedgerow and forest. *Bulletin of the Torrey Botanical Club* 121:240–50.
- . 1997. Response of a forest understory community to experimental removal of an invasive nonindigenous plant (*Alliaria petiolata*, Brassicaceae). In *Assessment and management of plant invasions*, ed. J. O. Luken, 117–30. Springer, New York.
- McCormick, J. T., and S. J. Meiners. 2000. Season and distance from forest–old field edge affect seed predation by white-footed mice. *Northeastern Naturalist* 7:7–16.
- McDonnell, M. J. 1986. Old field vegetation height and the dispersal pattern of bird-disseminated woody plants. *Bulletin of the Torrey Botanical Club* 113:6–11.
- McDonnell, M. J., and E. W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56:109–16.
- Meiners, S. J., S. N. Handel, and S. T. A. Pickett. 2000. Tree seedling establishment under insect herbivory: Edge effects and inter-annual variation. *Plant Ecology* 151:161–70.
- Meiners, S. J., and K. LoGiudice. 2003. Temporal consistency in the spatial pattern of seed predation across a forest–old field edge. *Plant Ecology* 168:45–55.
- Meiners, S. J., S. T. A. Pickett, and M. L. Cadenasso. 2001. Effects of plant invasions on the species richness of abandoned agricultural land. *Ecography* 24:633–44.
- . 2002. Exotic plant invasions over 40 years of old field succession: Community patterns and associations. *Ecography* 25:215–23.
- Monk, C. D. 1957. Plant communities of the Hutcheson Memorial Forest based on shrub distribution. *Bulletin of the Torrey Botanical Club* 84:198–218.

- . 1961a. Past and present influences on reproduction in the William L. Hutcheson Memorial Forest, New Jersey. *Bulletin of the Torrey Botanical Club* 88:167–75.
- . 1961b. The vegetation of the William L. Hutcheson Memorial Forest, New Jersey. *Bulletin of the Torrey Botanical Club* 88:156–66.
- Moulding, J. 1977. The progression of a gypsy moth invasion of a mature oak forest in New Jersey. *William L. Hutcheson Memorial Forest Bulletin* 4:5–11.
- Myster, R. W. 1993. Tree invasion and establishment in old fields at Hutcheson Memorial Forest. *Botanical Review* 59:251–72.
- . 1994. Contrasting litter effects on old field tree germination and emergence. *Vegetatio* 114:169–74.
- Myster, R. W., and B. C. McCarthy. 1989. Effects of herbivory and competition on survival of *Carya tomentosa* (Juglandaceae) seedlings. *Oikos* 56:145–48.
- Myster, R. W., and S. T. A. Pickett. 1990. Initial conditions, history, and successional pathways in ten contrasting old fields. *American Midland Naturalist* 124:231–38.
- . 1992. Effect of palatability and dispersal mode on spatial patterns of trees in old fields. *Bulletin of the Torrey Botanical Club* 119:145–51.
- Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson et al. 1999. Impact: Toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1:3–19.
- Pickett, S. T. A. 1983. The absence of an *Andropogon* stage in old-field succession at the Hutcheson Memorial Forest. *Bulletin of the Torrey Botanical Club* 110:533–35.
- . 1989. Space-for-time substitutions as an alternative to long-term studies. In *Long-term studies in ecology*, ed. G. E. Likens, 110–35. Springer-Verlag, New York.
- Pickett, S. T. A., and M. L. Cadenasso. 2005. Vegetation dynamics. In *Vegetation ecology*, ed. E. van der Maarel, 172–98. Blackwell, Malden, MA.
- Pickett, S. T. A., M. L. Cadenasso, and S. Bartha. 2001. Implications from the Buell-Small succession study for vegetation restoration. *Applied Vegetation Science* 4:41–52.
- Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms, and pathways of succession. *Botanical Review* 53:335–71.
- Quinn, J., and S. J. Meiners. 2004. Growth rates, survivorship, and sex ratios of *Juniperus virginiana* on the New Jersey piedmont from 1963 to 2000. *Journal of the Torrey Botanical Society* 131:187–94.
- Rejmánek, M. 1989. Invasibility of plant communities. In *Biological invasions: A global perspective*, ed. J. A. Drake, 369–88. John Wiley and Sons, Chichester, UK.
- Roberts, K. J., and R. C. Anderson. 2005. Effect of garlic mustard [*Alliaria petiolata* (Beib, Cavara and Grande)] extracts on plants and arbuscular mycorrhizal (AM) fungi. *American Midland Naturalist* 146:146–52.
- Small, J. A. 1961. Drought response in William L. Hutcheson Memorial Forest, 1957. *Bulletin of the Torrey Botanical Club* 88:180–83.
- Ugolini, F. 1964. Soil development on the red beds of New Jersey. *William L. Hutcheson Memorial Forest Bulletin* 2:1–34.
- Walker, L. R., and S. D. Smith. 1997. Impacts of invasive plants on community and ecosystem properties. In *Assessment and management of plant invasions*, ed. J. O. Luken, 69–86. Springer, New York.
- Yurkonis, K. A., and S. J. Meiners. 2004. Invasion impacts species turnover in a successional system. *Ecology Letters* 7:764–69.