Applied Vegetation Science 12: 3–8,
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The success of succession: a symposium commemorating the 50th anniversary of the Buell-Small Succession Study

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Abstract

Motivation: The Buell-Small Succession Study (BSS) is the longest running study of post agricultural succession in North America. To honor this program, a symposium at the Ecological Society of America meetings was organized to explore the state of succession theory and its contribution to the field of ecology and its application to restoration. The BSS was originally motivated by two controversies in the literature during the 1950's. The first was between a community versus and individual basis of secondary succession. The second was the validity of the Initial Floristic Composition hypothesis.

Location: Hutcheson Memorial Forest, Somerset, New Jersey, USA

Methods: Vegetation composition and cover has been continuously quantified in permanent plots established in 10 old fields.

Continued Research Motivation: The rich data set has documented population and community dynamics and the spatio-temporal controls and historical contingencies that influence those dynamics. The regulation of community dynamics continues to be a line of inquiry as does the application of results to restoration and understanding the dynamics of non-native species.

Conclusions: Long term vegetation studies are uncommon in ecology yet they are uniquely valuable for understanding system dynamics – particularly if the studies capture periodic events or system shifts such as droughts and invasions by non-native species. Resilient long term studies, of which the BSS is an example, maintain methods and data structure while allowing motivating questions to evolve along side advancements in the theoretical and conceptual realms of the field. Succession continues to serve as a basic tenet of ecology which is demonstrated by the papers making up this special issue.

The year 2006 marks the 50th anniversary of the Buell-Small Succession Study (BSS) at the Hutcheson Memorial Forest in Somerset, New Jersey. The BSS is the longest continuous study of post-agricultural succession in North America. It serves not only as a model for the development of succession theory in ecology, but also as a demonstration of the importance of long term research for understanding ecological dynamics. The BSS research on ecological succession was initially motivated by the need to test a theoretical debate occurring in the field of ecology in the 1950s. Theory continues to motivate the BSS. Over the course of the past 50 years the old field system itself has changed and so has the landscape context of the site. This has created continuing opportunities for scientific inquiry.

To honor the BSS program, the scientists who initiated it, and the legion of Rutgers University students that have sampled the site each year, a symposium at the Ecological Society of America Annual Meetings of 2007 in San Jose, California was organized by the current leaders of the BSS (Meiners, Pickett, Cadenasso, and Morin). The charge of the symposium was to explore how the theory of ecological succession has progressed, articulate what we have learned through the application of our knowledge to restoration, and synthesize the field to arrive at generalizations applicable across systems and scales. The collection of papers to follow developed from this symposium. Because the BSS provided the motivation for the symposium and many contemporary plant ecologists have contributed to this study, we briefly review the history of the BSS and its contribution to understanding secondary successional dynamics.

Motivation for the Buell-Small Succession Study

Plant community succession is one of the most ubiquitous of ecological processes. The change in structure and species composition of assemblages of plants after physical disturbances, or after release from agricultural management, has been used to generate and test many foundational concepts and theories of ecology. Indeed, the founding of the science of ecology in the United States is closely associated with studies of succession (Cowles 1899; Clements 1916; Cooper 1926).

Succession is a central tenet of ecology. Fundamental to the understanding of succession is the need to know what the patterns of community change through time actually are. All else – the understanding of mechanisms, the prediction of trends, the use of succession by managers – depends on a sound knowledge of the patterns of change. In the early days of ecology, the only method available to discover the patterns of community change through time was to compare sites of different ages since disturbance or abandonment. This method, called either space-for-time substitution or chronosequence, assumes that the different sites are subject to the same conditions and have the same species available to them. If this crucial assumption is not met, the patterns may reflect permanent differences between the sites or other ecological processes rather than successional change (Johnson & Miyanishi 2008).

Studies of successional change have been classified into primary and secondary successions. Primary succession refers to the vegetation development on newly available land such as that formed by sediment deposition or that exposed by glacial retreat (Walker & del Moral 2003). An assumption underlying primary succession is that the site contains no biological legacy. In contrast, secondary succession assumes a legacy from a past plant community and focuses on the replacement of vegetation following a disturbance. Though this distinction between primary and secondary successions exists in the literature, theoretical advancement of the field has emphasized that the line between these two views are blurred (Glenn-Lewin & van der Maarel 1992) and that they represent two ends of a succession continuum established by differential resources available at the site and differential species available to colonize the site (Pickett & Cadenasso 2005). In this paper, and the papers to follow, the discussion of succession focuses more towards the secondary succession end of the continuum.

Fig. 1. John Small, Helen Buell, and Murray Buell (left to right) at the entrance of the Hutcheson Memorial Forest, home to the Buell-Small Succession Study. Photo taken in December 1963. Courtesy of Norma Reiners.

In 1958, Murray Buell, Helen Buell, and John Small (Fig. 1) established a long term secondary successional study using a series of abandoned agricultural fields in the Piedmont region of New Jersey, USA (40°30′N, 74°34′). Murray Fife Buell was Professor of Botany at Rutgers, and he earned his Ph.D. under the great plant ecologist, William S. Cooper at the University of Minnesota. Helen Foote Buell earned her Ph.D. in phycology at the University of Minnesota. Although Dr. Helen Buell was not a member of the Rutgers faculty, she was an important member of the intellectual community in botany and ecology, and contributed significantly to the training of students and to research. Dr. John Alvin Small was a botanist on the faculty at Douglass College who earned his Ph.D. at Rutgers with M.F. Buell.

At around the time that the BSS was established, several controversies existed in the literature about how succession took place. One controversy dealt with the nature of the plant community. At one extreme, tightly unified communities were assumed to be the basis of succession (Clements 1916), while at the other, the individual – but interacting – species populations were assumed to be the basis of succession (Gleason 1926). By examining permanent plots through time, the BSS could show whether communities came and went as wholes, or whether populations rose and fell through time based on their individual properties and capacities for interaction.

A second, more subtle, controversy seems to have been the primary motivator of the BSS initiative. Frank E. Egler (1954) had proposed that many of the species that would come to predominate in later successional communities were in fact present right from the start. His Initial Floristic Composition hypothesis was in opposition to the dominant assumption that species arrived in succession in order of their dominance. Egler's hypothesis apparently seemed unreasonable to the Buells and Small based on their experience. The only sure way to tell, however, was to look at permanent plots through time. This was the design the BSS adopted. Buell and colleagues were also concerned with testing chronosequence-based inferences obtained near the BSS site (Bard 1952) by monitoring individual fields through time.

Since its inception, the study has continued uninterrupted. Murray Buell worked on the study until his death in 1975. John Small worked on the project until his death in 1977. Helen Buell worked on the project until the mid 1980s, but enthusiastically continued to share her energy and knowledge until she died in 1995. Dr. Steward T.A. Pickett, who joined the faculty of Rutgers in 1977, began to work on the project in the summer of 1978. Dr. Mary Cadenasso corrected and standardized the long term BSS data, facilitating the use and sharing of this data with other researchers. Since 2002, Dr. Scott J. Meiners has assumed the leadership role. His Ph.D., earned at Rutgers University, used the fields and forests of HMF.

Key Research and Insights from the BSS

Initial work by Pickett and collaborators focused on documenting population dynamics over time (Pickett 1982; Rankin & Pickett 1989), differences among species (Myster & Pickett 1988), the dynamics of species interactions (Myster & Pickett 1988, 1992a) and spatio-temporal controls on tree regeneration (Rankin & Pickett 1989; Myster & Pickett 1992b). Community level work described changes in community attributes (Pickett 1982), influences of historical contingencies on community dynamics (Myster & Pickett 1990) and the rate of succession (Myster & Pickett 1994). These analyses formed the basis for much of the work which has followed.

The BSS data continues to be valuable for research. Current program researchers have specifically focused on (1) regulation of community dynamics (2) application of successional information to ecological restoration and (3) the ecology of non-native species. Constraints to local species assemblages (Bartha et al. 2000) and the influence of drought and other periodic stressors on community dynamics have been quantified (Bartha et al. 2003; Yurkonis & Meiners 2006). During the herbaceous stages of succession, species richness at the plot scale (1 m^2) stabilizes at the same level as that reported for grassland systems in general (Gross et al. 2000), suggesting that local controls on richness are common among many communities (Meiners et al. 2002). Periodic events, such as drought, may lead to major transitions in community composition that are synchronous among fields (Bartha et al. 2003). However, understory plant communities recovered from drought within a few years, regaining much of the pre-drought structure (Yurkonis & Meiners 2006). As the processes and stresses included in these studies occur in all plant communities, results should be applicable to a wide range of ecological systems.

Practical application of the BSS data has largely focused on using successional understanding to guide restoration practices (Pickett et al. 2001; Bartha et al. 2003; Meiners et al. 2007). Results from these studies provide critical information to practitioners by (1) identifying opportunities for restoration intervention, (2) providing information to determine management priorities, and (3) setting realistic limits to the ability of unassisted successional transitions that must occur for system recovery.

The primary focus of current BSS research is on the comparison of native and non-native plant invasions. Early work documented the general pattern of non-native species through succession (Meiners et al. 2002) and found that most non-native species declined in relative cover with time since abandonment. The diversity-invasion relationship was explored from both the direction of regulation of invasion by local diversity (Meiners et al. 2004) and of impacts of non-native species on local diversity (Meiners et al. 2001; Yurkonis & Meiners 2004). The detailed nature of the BSS data has not only allowed documentation of broad changes in community structure through time, but has also facilitated detailed analysis of individual species dynamics. Colonization by non-native species responded individualistically to naturally occurring gradients of richness. Some species' invasions responded positively to richness while others responded negatively or not at all (Meiners et al. 2004). In the same suite of species, increasing cover of the non-native invaders often leads to local decreases in species richness. Mechanistically, these changes were almost entirely driven by a reduction in colonization rates within heavily invaded plots, while extinction rates remained unchanged (Yurkonis & Meiners 2004). Because diversity may be both a cause and a consequence of local invasion patterns, a conceptual framework was developed which explored the complexity of the diversity-invasion relationship (Meiners & Cadenasso 2005).

A related research theme is to determine whether a systematic difference between native and non-native species explains the relative success of invading species. In general, the spread of native and non-native species is constrained by the same suite of community controllers (Meiners et al. 2004). An analysis of a large suite of species within the BSS found no differences in population dynamics between native and non-native plant species (Meiners 2007). Ongoing work is expanding this research to investigate the invasions of regionally problematic species such as *Rosa multiflora* (Banasiak & Meiners, in press), *Microstegium vimineum* (Cadenasso, unpubl. data) and several liana species (Ladwig L. M., unpubl. data).

Success of Succession

The BSS sampling continues to be motivated by ecological theory. The two controversies that originally inspired the study have in some ways been solved as a result of the BSS, other permanent plot studies in forests and fields, and judicious use of certain chronosequences and experiments. Consequently, contemporary succession theory incorporates aspects of the extremes of the controversies by recognizing when each of the patterns or processes occur. However, far from obviating the need to continue long-term, permanent plot studies of succession, new motivating questions have emerged that are appropriately examined by the BSS and other such studies. Questions that now rise to the top of the list of motivations for the study include those concerning (1) patterns of species assembly and assortment in time and space, (2) the role of functional groups in succession, (3) the place and significance of invasive exotic species in mid- and late-successional communities, (4) how species life histories and morphologies relate to their invasion and persistence, (5) the role of episodic events in succession, and (6) the influence of interannual and decadal climate variation on successional trajectories.

Succession continues to serve as a basic tenet of ecology that can inform ecological restoration efforts and, in turn, can be advanced through scientific understandings gained from the study of restoration efforts. The papers making up this special issue and presented during the symposium at ESA, demonstrate why succession remains a successful area of study within ecology. Pickett et al. (2009) present a mature framework of succession theory. This framework is broad and inclusive of systems and scales and has been built from a rich body of empirical studies. Though Clements is frequently remembered as promoting plant community dynamics as analogous to an organism, Pickett et al. (2009) indicate that Clements' multicausal view of succession forms the foundation of the contemporary succession framework. Fowler & Simmons (2009) reinforce the utility of a succession perspective in understanding vegetation dynamics in a Texas savanna. These systems are frequently described using state-and-transition models which implies alternative stable states. Though this view is useful for some research questions, a directional successional perspective may better reflect current reality and better inform restoration efforts in these systems. Fowler & Simmons (2009) illustrate this argument using examples at two scales within their system – the landscape scale succession from savanna to woodland and two examples at the finer scale within the herbaceous component of the system.

A multi-mechanistic view of succession is the basis of papers by Meiners et al. (2009) and Reynolds & Haubensak (2009). Analysis of long term permanent plot studies inform Meiners et al.'s (2009) conclusion that in successional systems all species play the role of colonizer whether the species is native or non-native. They suggest that knowing the life history information of the species is of more value than focusing on the species place of origin. In fact, vegetation research may be biased by the focus on particularly successful non-native invaders. Reynolds & Haubensak (2009) take the discussion to the underground component of the system and review the literature to evaluate conceptual models addressing the influence of soil characteristics on successional dynamics. Their review found that conceptual models for the influence of soil fertility, heterogeneity, and microbes were not supported by the empirical research and suggest that in fact considering these factors together may lend the most insight.

This richness of successional mechanisms provides many tools for restoration and management of vegetation communities. Restoration is frequently considered as the test bed for ecological theory. Walker & del Moral (2009), however, argue that though the literature contains many lessons for restoration, those lessons are not being fully exploited. They highlight six ways that insights from successional studies can advance the goals of ecological restoration and how lessons from restoration efforts can, in turn, improve the theoretical richness of succession. Because successional trajectories are so obviously dynamic, they provide a powerful stage for disentangling the web of interactions that characterizes communities and ecosystems. In fact applying what we have learned to restoration efforts provides an ideal test of theory and aids in the search for generalizations in successional dynamics across systems and scales.

Acknowledgements. We are greatful for the creativity and foresight of Murray and Helen Buell and John Small in establishing this critical study that has proven through time its importance to the ecological understanding of succession dynamics. The study has been able to continue with support from the Hutcheson Memorial Forest Center, administered by Rutgers University, and the many graduate students in the Ecology and Evolutionary Biology program that have conducted the sampling of the fields each year. In particular, we thank Ted Stiles for his years of stewardship and work towards conserving open space in central New Jersey. The manuscript was improved by the constructive comments of S.T. Jackson. Support from the National Science Foundation (DEB-0424605) through the LTREB program is greatly appreciated.

References

Banasiak, S.E. & Meiners, S.J. in press Long-term dynamics of *Rosa multiflora* in a successional system. *Biological Invasions*. DOI: 1007/s10530-008-9226-1.

Bard, G.E. 1952. Secondary succession on the Piedmont of New Jersey. *Ecological Monographs* 22: 195–215.

Bartha, S., Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. 2003. Plant colonization windows in a mesic old field succession. *Applied Vegetation Science* 6: 205–212.

Bartha, S., Pickett, S.T.A. & Cadenasso, M.L. 2000. Limitations to species coexistence in secondary succession. In: White, P.J., Mucina, L. & Leps, J. (eds.) Vegetation science in retrospect and perspective. Proceedings 41st IAVS symposium. pp. 55–58. Opulus Press, Uppsala.

Clements, F.E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington, Washington.

Cooper, W.S. 1926. The fundamentals of vegetation change. *Ecology* 7: 391–413.

Cowles, H.C. 1899. The ecological relations of the vegetation on the sand dune of Lake Michigan. *Botanical Gazette* 27: 95–117, 167.

Egler, F.E. 1954. Vegetation science concepts. I: initial floristic composition, a factor in old-field vegetation development. *Vegetatio* 4: 412–417.

Fowler, N.L. & Simmons, M.T. 2009. Savanna dynamics in central Texas: just succession? *Applied Vegetation Science* 12: 23–31.

Gleason, H.A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53: 7–26.

Glenn-Lewin, D.C. & van der Maarel, E. 1992. Patterns and processes of vegetation dynamics. In: Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (eds.) Plant succession: theory and prediction. pp. 11–59. Chapman & Hall, New York.

Gross, K.L., Willig, M.R., Gough, L., Inouye, R. & Cox, S.B. 2000. Patterns of species density and productivity at different spatial scales in herbaceous plant communities. *Oikos* 89: 417–427.

Johnson, E.A. & Miyanishi, K. 2008. Testing the assumptions of chronosequences in succession. *Ecology Letters* 11: 419–431.

Meiners, S.J. 2007. Native and exotic plant species exhibit similar population dynamics during succession. *Ecology* 88: 1098–1104.

Meiners, S.J. & Cadenasso, M.L. 2005. The relationship between diversity and exotic plants: cause or consequence of invasion? In: Inderjit (ed.) Invasive plants: ecological and agricultural aspects. pp. 97–114. Birkhuser, Basel.

Meiners, S.J., Cadenasso, M.L. & Pickett, S.T.A. 2004. Beyond biodiversity: individualistic controls of invasion in a self-assembled community. *Ecology Letters* 7: 121–126.

Meiners, S.J., Cadenasso, M.L. & Pickett, S.T.A. 2007. Succession on the Piedmont of New Jersey and its implications for ecological restoration. In: Cramer, V.A. & Hobbs, R.J. (eds.) Old fields: dynamics and restoration of abandoned farmland. pp. 145–161. Island Press, Washington, DC.

Meiners, S.J., Rye, T.A. & Klass, J.R. 2009. On a level field: the utility of studying native and non-native species in successional systems. *Applied Vegeation Science* 12: 45–53.

Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. 2001. Effects of plant invasions on the species richness of abandoned agricultural land. *Ecography* 24: 633–644.

Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. 2002. Exotic plant invasion over 40 years of old field succession: community patterns and associations. *Ecography* 25: 215–223.

Myster, R.W. & Pickett, S.T.A. 1988. Individualistic patterns of annuals and biennials in early successional oldfields. *Vegetatio* 78: 53–60.

Myster, R.W. & Pickett, S.T.A. 1990. Initial conditions, history and successional pathways in ten contrasting old fields. *American Midland Naturalist* 124: 231–238.

Myster, R.W. & Pickett, S.T.A. 1992a. Dynamics of associations between plants in ten old fields during 31 years of succession. *Journal of Ecology* 80: 291–302.

Myster, R.W. & Pickett, S.T.A. 1992b. Effects of palatability and dispersal mode on spatial patterns of trees in oldfields. *Bulletin of the Torrey Botanical Club* 119: 145–151.

Myster, R.W. & Pickett, S.T.A. 1994. A comparison of rate of succession over 18 yr in 10 contrasting old fields. *Ecology* 75: 387–392.

Pickett, S.T.A. 1982. Population patterns through twenty years of oldfield succession. *Vegetatio* 49: 45–59.

Pickett, S.T.A. & Cadenasso, M.L. 2005. Vegetation succession. In: van der Maarel, E. (ed.) Vegetation ecology. pp. 172–198. Blackwell Publishing, Malden, MA.

Pickett, S.T.A., Cadenasso, M.L. & Bartha, S. 2001. Implications from the Buell-Small Succession Study for vegetation restoration. *Applied Vegetation Science* 4: 41–52.

Pickett, S.T.A., Cadenasso, M.L. & Meiners, S.J. 2009. Ever since Clements: from succession to vegetation dynamics and understanding to intervention. *Applied Vegetation Science* 12: 9–21.

Rankin, W.T. & Pickett, S.T.A. 1989. Time of establishment of red maple (Acer rubrum) in early oldfield succession. *Bulletin of the Torrey Botanical Club* 116: 182–186.

Reynolds, H.L. & Haubensak, K.A. 2009. Soil fertility, heterogeneity, and microbes: towards an integrated understanding of grassland structure and dynamics. *Applied Vegetation Science* 12: 33–44.

Walker, L.R. & del Moral, R. 2003. Primary succession and ecosystem rehabilitation. Cambridge University Press, New York.

Walker, L.R. & del Moral, R. 2009. Lessons from primary succession for restoration of severely damaged habitats. *Applied Vegetation Science* 12: 55–67.

Yurkonis, K.A. & Meiners, S.J. 2004. Invasion impacts species turnover in a successional system. *Ecology Letters* 7: 764–769.

Yurkonis, K.A. & Meiners, S.J. 2006. Drought impacts and recovery are driven by variation in local species turnover. *Plant Ecology* 184: 325–336.