*Journal of the Torrey Botanical Society* 137(1), 2010, pp. 113–119

# A comparison of tree replacement models in old fields at Hutcheson Memorial Forest

**Randall W. Myster**[1,2]
Department of Biology, Oklahoma State University, 900 N. Portland Ave., Oklahoma City, OK 73107

Myster, R. W. (Department of Biology, Oklahoma State University, 900 N. Portland Ave., Oklahoma City, OK 73107). A comparison of tree replacement models in old fields at Hutcheson Memorial Forest. J. Torrey Bot. Soc. 137: 113–119. 2010.—In order to understand how trees replace themselves during the conversion from agricultural field back into eastern deciduous forest, I first used data sampled in ten old fields over the first 20 years after abandonment to generate six different models of tree replacement. Each of the six models was then used to generate abundance predictions for six common tree taxa (species or genera) from year 21 to 30. Finally each model tested those predictions against the actual data sampled during those same years (21–30) focusing on the predicted rank abundances of the six test tree taxa using Spearman's rank correlation coefficients. I found that: 1) models generally predicted tree abundances and tree replacements well, with the exception of *Juniperus virginiana*, 2) although some matrix models became constant and some patch models became zero over time, most of the time matrix models had a higher abundance prediction than the patch models for the same species, and 3) among the matrix models, model 3 (which used cover values) had the highest values—especially for the wind-dispersed species—and among patch models, model 4 (which used the number of plots) was often as great or greater than models 5 or 6 (which used stem counts and cover values, respectively)—especially for the bird-dispersed species. Taken together the results suggested that models using cover were closer to the data sampled in the fields compared to the other models within their type (matrix or patch), and that patch models were better estimators of stem densities than matrix models, perhaps due to the inherent dampening properties of matrixes.

Key words: agro-ecology, Markov matrix models, New Jersey USA, patch models, succession.

Models are important research tools for understanding ecological processes. They are formal descriptions of inference, for example the models about successional mechanism aid in the analysis of succession data and in the prediction of vegetation change. Two objectives of modeling are to produce models that are realistic (even though models must always be a partial representation of any system) and make valid predictions (often tested against similar data not used to generate the model). Being able to make these accurate predictions is critical to making good management and restoration decisions. Finally, the best models are applicable over the range of conditions encountered in a specific kind of research and are composed of parameters that can both be measured directly and follow ecological principles (Shugart and West 1980, Bugmann 2001).

Individual species are logical units for modeling ecological phenomena, requiring few unreasonable assumptions. Among individual population-based models, Markov models that show the stochastic process of the birth and death of trees have proved useful in describing eastern deciduous forest communities and contributing to our understanding of species replacements (Facelli and Pickett 1990, Balzter 2000). These Markov models are phenomenological and formulated as transition probabilities (Waggoner and Stephens 1971), such as the proportion of saplings underneath the crown of individual tree species (Van Hulst 1979). Another useful kind of models are patch models, central to understanding patch dynamics across landscapes, and in describing and predicting vegetation. These models use small independent patches of land of different age and successional stage (Wu and Levin 1994) like those recovering after agriculture.

The world's terrestrial vegetation is continuously undergoing an individual plant-plant replacement process, leading to community plant patterns, making plant replacements fundamental in understanding ecosystem structure and function (Busing 1996, Myster 2001, Myster 2007). In particular, replacements in areas after agriculture are a critical

---

[1] I would first like to thank Hutcheson Memorial Forest, Rutgers University and S. T. A. Pickett for allowing me to assist in the sampling of these plots and for the use of the data for analysis. I also thank J. Yates for help with the computations, and S.T.A. Pickett and J.R.A. Sierra for commenting on a previous draft of the manuscript.

[2] E-mail: rwmyster@gmail.com

Received for publication March 9, 2009, and in revised form December 3, 2009.

part of agro-ecology and are important to ecosystems all over the world (Borhidi 1988, Matson et al. 1997) for both scientific concerns (e.g., forest regeneration, maintenance of biodiversity) and social issues (e.g., restoration, sustainability, global climate change).

In order to model and better understand tree-tree replacements after agriculture, old field data collected in New Jersey, USA (e.g., the Buell-Small succession study in New Jersey USA: Buell et al. 1971, Myster 1993) was used because it shows the processes of tree establishment, growth, and mortality. I applied Markov and patch models to this data set also because 1) data were measured directly in the field, 2) the data set contains many fields collected over decades starting at the time of abandonment, 3) the plots are not continuous allowing an assumption of low interaction among patches, and 4) exact spatial position is not needed in these models and was not measured in this data set.

The objectives were to generate and test six different tree replacement models (see Busing 1996, Taylor and Zisheng 1992). With matrix models each cell of the matrix represents the probability that a species would be replaced by another species over a given time step. With patch models the abundance of a species at some time is a function of its abundance at the last time of sampling, how many new tree stems of this species were added since then, and how many tree stems of this species have died. Within each broad kind of model, three different attempts to define the influence of one species on another were employed using 1) number of plots where both species were found, 2) number of stems of each species found in these common plots, and 3) amount of cover of each species found in the common plots. It was expected that models using percent cover would be best at predicting the actual abundances of old field trees, with some mathematical limitations (Shugart and West 1980, Facelli and Pickett 1990). Finally, the output of each model was statistically compared for validation to the actual, sampled rank abundance data from the permanent plots.

**Material and Methods.** The study site was Hutcheson Memorial Forest Center (HMFC) located in Somerset County, New Jersey, USA (40°30′ N, 74°34′ W). The old-growth forest at HMFC has a *Quercus*-*Carya* canopy and a *Cornus florida* L. understory (Bard 1952, Myster 1993). The silty-loam soils of the area are derived from underlying red shales of the Brunswick formation. Annual precipitation averages 112 cm and is distributed fairly evenly throughout the year with a mean annual temperature of 11.7 °C and defined seasonally.

I used data collected in 10 recovering agricultural fields adjacent to the forest (see maps in Buell et al. 1971). These fields were abandoned in different years between 1958 and 1966, varied in size between 0.35 and 0.75 ha, and were sampled annually until 1980 when they were sampled every other year. Besides the year of abandonment, fields also differed in past crop (*Dactylis glomerata* L., soybeans, sorghum), season of abandonment (Spring, Fall), and whether they were plowed at abandonment or not (Myster and Pickett 1994). Forty-eight non-continuous 2.0 × 0.5 m plots were arranged in a grid within each field at the time of abandonment. Both percent cover of each plant species and the number of stems of each tree species were sampled in each plot at each sampling time. Plant cover is a multi-layer measure that can exceed 100%. Because individual stems were not tagged, no other information, such as spatial location, height, basal diameter or age, was sampled on these tree stems and, consequently, models needing those data were not used. Plant nomenclature followed Gleason and Cronquist (1963).

The first 20 years of the data set (17 in the case of two of the fields and 19 for two others) was used to generate six different tree replacement models. Models 1, 2, and 3 used a 6 × 6 Markov matrix of replacement probabilities (Horn 1976, VanHulst 1979) with rows and columns defined by the species of the six most common tree taxa—individual species or several species of the same genera with similar biology—which comprised over 95% of the tree stems sampled in the plots over the first 30 years (Myster and Pickett 1992). The six tree taxa were 1) *Acer negundo* L. and *A. rubrum* L., 2) *Fraxinus americana* L., 3) *Juniperus virginiana* L., 4) *Cornus florida*, 5) *Prunus serotina* Ehrh. and *P. avium* L., and 6) *Quercus alba* L., *Q. rubra*, *Q. coccinea* Münchh., *Q. robur* L., *Q. palustris* Münchh., and *Q. velutina* Lam.; all sorted within their group by decreasing abundance. These taxa encompass all of the seed dispersal vectors and successional types present at HMFC, that is wind dispersed/early successional (*Acer*, *Fraxinus*), bird dispersed/mid-successional (*Juniperus*, *Cornus*, *Prunus*), and mammal dispersed/late successional (*Quercus*). All taxa were present in the first year of sampling except *Quercus* spp. which were not present until year 13 (Myster and Pickett 1992).

The cells in the matrix ($m_{ij}$) were defined in three different ways. For model 1, each cell with both species *i* and species *j* contained the number of plots from all 10 fields and over the first 20 years of succession, that had both species *i* and species *j* in them. For model 2, each cell contained the number of stems of species *j* in those plots that also had species *i* in them. For model 3, each cell contained the total cover of species *j* in those plots that also had species *i* in them. Each model was a different attempt to capture the probability that species *i* will be replaced by species *j*, by defining co-occurrence and potential influence of species *j* over species *i* in a different way. Implicit in this approach is the assumption that light capture and competition is critical in the success and failure of tree seedlings in old fields (also assumed in gap models; Bugmann 2001). Each matrix was normalized so that all totals down each column were equal to one. It was necessary to pool stem data over space (many plots, 10 fields) and over time (the first 20 years of succession) in order to get enough stems of each species into the models to make them realistic and to make predictions more meaningful. This approach of pooling of data was done in the original formulations of Horn (1976) and Van Hulst (1979) where several individual trees of the same species were sampled for under-story seedlings in order to construct transition probabilities. The models needed two decades of data for their formulation and then were run over one decade of successional time.

Models 4, 5, and 6 were patch models (Shugart and West 1980, Wu and Levin 1994, Wilson 1995), each having six parts, one for each tree taxa. Each of the parts had the following form: number of stems of tree species at time ($t + 1$) = (number of stems of tree species at time *t*) + (number of new stems at time [$t + 1$]) − (number of stems that died between time [$t + 1$] and time [*t*]). The number of new stems at time ($t + 1$) was found by a linear regression (SAS 1985) of the number of new stems for this species in all plots and fields (dependant variable) and the sampling years (independent variable). Similarly, the number of stems that died was found by a linear regression (SAS 1985) of the number of dead stems for this species in all plots and fields (dependant variable) as well as sampling years (independent variable). Whereas these models treated each old field as a patch, the sum total of output over all ten old fields was presented. As was true for the matrix models, model 4 used the number of plots, model 5 used the number of stems (as shown in the example above), and model 6 used the cover of stems gained or lost. All models were non-mechanistic, but the different definitions of influence suggested a key role for competition, especially for light, in these old fields (Myster 1993). In addition, these models may have wider implications because the patch size of the old field may be similar to some other disturbances and because they are individual-tree based (Bugmann 2001). However other common models could not be used on this data, for example the gap model JABOWA was not appropriate because old fields are too different from gaps (Myster 1993, Myster 2007), and the data needed for more individually-based, object-oriented, spatially-explicit, and physiology-based models could not be collected in these plots.

Each model was then used to generate the number of stems for each tree taxa for year 21, year 22, and so on to year 30 over all plots and fields, with the underlining assumption of some process uniformity between the decades. The matrix models used a vector of six species stem numbers at year 20 to generate by matrix multiplication a vector of six species stem numbers at year 21, which was used to generate the vector at year 22, etc. The patch models used individual stem counts of each species at year 20 (the same starting vector as the matrix models) to generate the abundances for the subsequent years, using the results from the linear regressions. Finally, validation of the predictive ability of each model (Wilson 1995) was done by comparing its tree rankings at year 30 to the tree rankings from the permanent plot data at year 30 through the use of Spearman's rank-correlation coefficients (Myster and Pickett 1992, Zar 1999, Balzter 2000). Because ranks come from ten old fields (df = 8) any $r_s$ value above 0.73 is considered significant (Ludwig and Reynolds 1988).

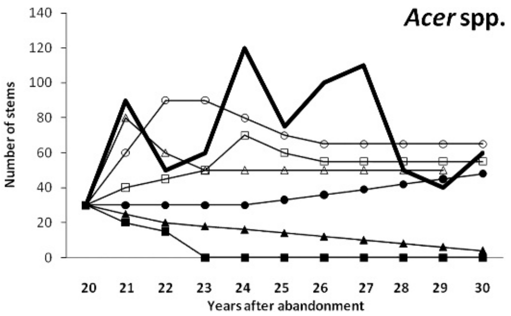

FIG. 1. Matrix model output for *Acer* spp. covering years 20–30 where model 1 is indicated by an open triangle, model 2 is indicated by an open square, and model 3 is indicated by an open circle. Patch model output for *Acer* spp. covering years 20–30 where model 4 is indicated by a closed triangle, model 5 is indicated by a closed square, and model 6 is indicated by a closed circle. Models 1 and 4 are based on plots, models 2 and 5 are based on stems, and models 3 and 6 are based on cover. The actual abundance data sampled in the permanent plots is indicated as the thick black line.

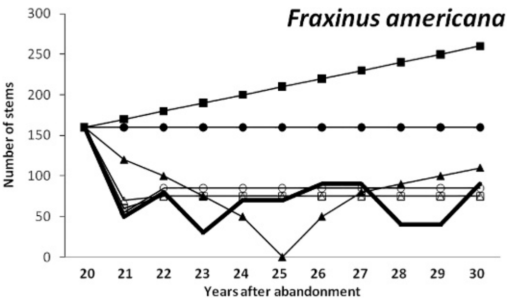

FIG. 2. Model output data for *Fraxinus americana* labeled as in Fig. 1. The actual abundance data sampled in the permanent plots is indicated as the thick black line.

**Results.** For the two wind-dispersed and small-sized seed species *Acer* spp. and *Fraxinus americana*, the actual stem densities showed a decline between the years 20 and 30 to only a few stems per field. All models mirrored this decline with a slightly negative slope line (Figs. 1 and 2) and contain within their boundaries the actual data, especially later in the sequence. The three matrix models had higher stem numbers than the three patch models, with model 3 at the higher projected abundances. For *Acer* spp., model 5 became zero, which also occurred for *Fraxinus* models 4 and 6.

For the three bird-dispersed species and medium-sized seed species *Juniperus virginiana*, *Cornus florida*, and *Prunus* spp., the actual stem counts also showed a decline but with stabilizing fluctuations. These levels were at least as high as for the wind-dispersed species and higher in the case of *Juniperus*. *Juniperus* models were generally lower than the actual data except years 26–29 when *Juniperus* data was within model variation (Fig. 3). Interestingly, patch models 4 and 6 had the highest and patch model 5 had the lowest predictions for *Juniperus*. All models, except model 4 between the years 24–26, predicted higher stem densities for *Cornus* than the actual data, with model 5 increasing up to 400 stems (Fig. 4). Model 4 may still have been increasing after 30 years, but all others had stabilized at numbers greater than actual. The abundance levels of the matrix models were lower than those of the patch models for *Cornus*. Finally, for *Prunus* spp. the patch models were lower than the matrix models, with models 5 and 6 becoming zero (Fig. 5). All *Prunus* spp. models were still slightly decreasing after 30 years.

For the largest-sized seed and the only mammal-dispersed species *Quercus* spp., actual stem numbers remained the lowest among all species (Fig. 6). Matrix models quickly became linear and patch model 5 became zero. However, model 4 increased dramatically up to over 300 stems and then started to decline.

Spearman's rank analysis showed models 1, 2, 4, 5, and 6 to be significantly similar to the actual ranks of the six test species groups ($0.821 < r_s < 0.934$), and model 3 to also be similar ($r_s = 0.905$). Data from the permanent plots show that wind-dispersed species (*Acer* spp., *Fraxinus americana*) were replaced by bird-dispersed species (*Juniperus virginiana*,

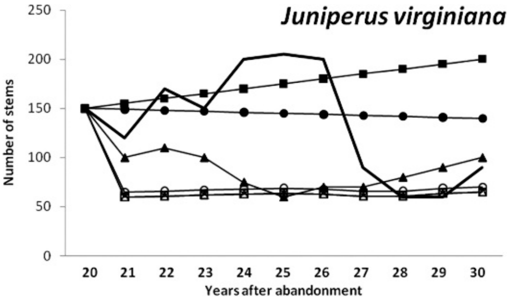

FIG. 3. Model output data for *Juniperus virginiana* labeled as in Fig. 1. The actual abundance data sampled in the permanent plots is indicated as the thick black line.

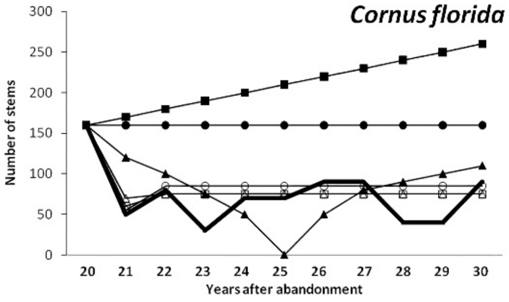

FIG. 4. Model output data for *Cornus florida* labeled as in Fig. 1. The actual abundance data sampled in the permanent plots is indicated as the thick black line.

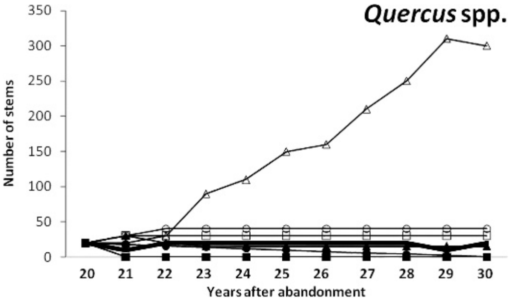

FIG. 6. Model output data for *Quercus* spp. labeled as in Fig. 1. The actual abundance data sampled in the permanent plots is indicated as the thick black line.

*Cornus florida*, *Prunus* spp.), with animal-dispersed species (*Quercus* spp.) slowly increasing, reflected in all the models while the three patch models showed the trends more clearly than the Markov models, which flattened out with time.

**Discussion.** Whereas most tree rank abundances were within model predictions, *Juniperus* was the outlier taxa and kept the models from being more significant. As predicted, matrix models had a tendency to become constant with time (see discussions in Van Hulst 1979, Facelli and Pickett 1990), and patch models could become zero due to regressions having negative slopes. In addition, for many taxa the matrix models had a higher prediction than the patch models. Patch models 5 and 6, in particular, went to zero for several taxa. Among the matrix models, model 3, which used cover values, had the highest values, especially for the wind-dispersed species. Among patch models, model 4, which used the number of plots in common, was often as great or greater than models 5 and 6, especially for the bird-dispersed species. In general, models using cover as a way to estimate the potential influence of one species on another may have performed better than the other models probably because light capture is critical in recovering forest systems.

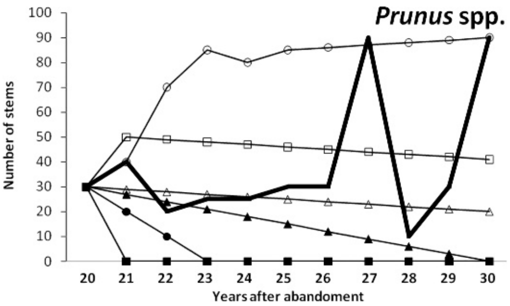

FIG. 5. Model output data for *Prunus* spp. labeled as in Fig. 1. The actual abundance data sampled in the permanent plots is indicated as the thick black line.

Old field mechanistic studies (see reviews in Myster 1993, Myster 2007) may help explain the higher stem counts for bird-dispersed species, especially *Juniperus virginiana*. Those studies showed the following *Juniperus virginiana* regenerative advantages compared to other species: 1) the dispersal of seeds by birds is greater than the dispersal by wind and far greater than the dispersal by mammals done by other species (McDonnell and Stiles 1983), 2) *Juniperus* seed loss by pathogenic disease is low (Gill and Marks 1991), 3) whereas seed predation is high for *Acer* spp., *Quercus* spp., and *Cornus* and medium for *Fraxinus*, it is low for *Juniperus* (Burton and Bazzaz 1991), 4) *Juniperus* and *Quercus* spp. seedlings may survive drought years better than other species, 5) *Acer spp.* and other wind-dispersed species may be more sensitive to frost-heaving and shade, and 6) herbivores prefer *Quercus spp.* and *Acer spp.* seedlings the most, *Fraxinus* and *Cornus* less, and *Juniperus* the least. In summary, the large abundance of *Juniperus* is easy to understand given its high dispersibility and greater chance of survival, due in part to its high competitive ability (Myster 1993, Meiners and Gorchov 1998).

Because many agricultural areas in both temperate and tropical America were once forested, the invasion, establishment, and growth of the functionally and structurally dominant trees (Bazzaz and Pickett 1980, Uhl

1988, Myster 1993, Nepstad et al. 1996) is a key to understanding the old field plant-plant replacement process (Myster and Pickett 1992, Myster 2001). In general, tree establishment is slow after agriculture due in part to multiple crop and grass effects (Myster 1993, Nepstad et al. 1996). Key "barrier" mechanisms include seed rain, seed predation, and competition, but seedling predation, frost heaving, and damage from falling stems and branches is also important (Vengris 1953, Myster and Pickett 1992, Bazzaz 1996). Competition, especially for light, may be critical and there was some evidence for it in the models because the models using cover did the best in predicting ranks. However more field experiments on seedling growth and competition in old fields (Meiners and Gorchov 1998) need to be done in order to completely understand plot data and modeling results.

A major application of this study is that it can be used for predicting the number of trees of these dominant species in entire old fields, if the starting abundances are known. Furthermore, knowledge gained from models such as the ones used in this study can allow old field restoration efforts to be done in a more complete manner with better management for various human needs (for example, quickening the rate of succession for faster forest timber use, holding the old field in a state where crop production is maximal, or altering the natural old field recovery pathway in some other way). Finally this study and other old field studies suggest future old field research conducted in a patch-wise manner needs to focus on 1) the ecophysiology of the dominant species as a possible driver of plant-plant replacements, 2) how individual plant species grow in the presence of different resources, and 3) the exact nature of crop "signature" effects after abandonment (Myster and Pickett 1992, Myster 1993).

## Literature Cited

BARD, G. E. 1952. Secondary succession on the piedmont of New Jersey. Ecol. Monogr. 22: 195–215.

BALZTER, H. 2000. Markov chain models for vegetation dynamics. Ecol. Model. 126: 139–154.

BAZZAZ, F. A. AND S. T. A. PICKETT. 1980. Physiological ecology of tropical succession: a comparative review. Annu. Rev. Ecol. Syst. 11: 287–310.

BAZZAZ, F. A. 1996. Plants in Changing Environments. Cambridge University Press, New York, NY. 320 p.

BORHIDI, A. 1988. Vegetation dynamics of the savannization process on Cuba. Vegetatio 77: 177–183.

BUELL, M. F., H. F. BUELL, J. A. SMALL, AND T. G. SICCAMA. 1971. Invasion of trees and secondary succession on the New Jersey Piedmont. Bull. Torrey Bot. Club 98: 67–74.

BUGMANN, H. 2001. A review of forest gap models. Clim. Change 51: 259–305.

BUSHBACHER, R. J. 1986. Tropical deforestation and pasture development. BioScience 36: 2–28.

BUSING, R. T. 1996. Estimation of tree replacement patterns in an Appalachian *Picea-Abies* forest. J. Veg. Sci. 7: 685–694.

BURTON, P. J. AND F. A. BAZZAZ. 1991. Tree seedling emergence on interactive temperature and moisture gradients and in patches of old-field vegetation. Am. J. Bot. 78: 131–149.

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

FACELLI, J. M. AND S. T. A. PICKETT. 1990. Markovian chains and the role of history in succession. Trends Ecol. Evol. 5: 27–30.

FEARNSIDE, P. M. 1993. Deforestation in Brazilian Amazonia: The effect of population and land tenure. Ambio 22: 537–545.

GILL, D. S. AND P. L. MARKS. 1991. Tree and shrub seedling colonization of old fields in Central New York. Ecol. Monogr. 61: 183–205.

GLEASON, H. A. AND A. CRONQUIST. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Van Nostrand, Princeton, NJ. 810 p.

HORN, H. S. 1976. Markovian properties of forest succession, p. 187–204. *In* J. M. Diamond and M. L. Cody [eds.], Ecology of Communities. Harvard University Press, Cambridge, MA.

LUDWIG, J. A. AND J. F. REYNOLDS. 1988. Statistical Ecology: A Primer on Methods and Computing. John Wiley, New York, NY. 337 p.

MATSON, P. A., W. J. PARTON, A. G. POWER, AND M. J. SWIFT. 1997. Agricultural intensification and ecosystem properties. Science 277: 504–509.

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: 109–116.

MEINERS, S. J. AND D. J. GORCHOV. 1998. Effects of distance to *Juniperus virginiana* on the establishment of *Fraxinus* and *Acer* seedlings in old fields. Amer. Midl. Nat. 139: 353–364.

MYSTER, R. W. 1993. Tree invasion and establishment in old fields at Hutcheson Memorial Forest. Bot. Rev. 59: 251–272.

MYSTER, R. W. 2001. Mechanisms of plant response to gradients and after disturbances. Bot. Rev. 67: 441–452.

MYSTER, R. W. 2007. Post-agricultural succession in the Neotropics. Springer-Verlag, New York, NY.

MYSTER, R. W. AND S. T. A. PICKETT. 1992. Dynamics of plant associations in ten old fields during 31 years of succession. J. Ecol. 80: 291–302.

MYSTER, R. W. AND S. T. A. PICKETT. 1994. A comparison of rate of succession over 18 yr in 10 contrasting old fields. Ecology 75: 387–392.

Nepstad, D. C., C. Uhl, C. A. Perira, and J. M. C. De Silva. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. Oikos 76: 25–39.

Shugart, H. H. and D. C. West. 1980. Forest succession models. BioScience 30: 308–313.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annu. Rev. Ecol. Syst. 15: 353–391.

Taylor, A. H. and Q. Zisheng. 1992. Tree regeneration after bamboo die-back in Chinese *Abies-Betula* forests. J. Veg. Sci. 3: 253–260.

Tilman, D. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, NJ. 360 p.

Uhl, C., R. Buschbacher, and E. A. S. Serrao. 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. J. Ecol. 75: 663–681.

Van Hulst, R. 1979. On the dynamics of vegetation: Markov chains as models of succession. Vegetatio 40: 3–14.

Vengris, J. 1953. Weed populations as related to certain cultivated crops in the Connecticut River Valley, Mass. Weeds 2: 125–134.

Waggoner, P. E. and G. R. Stephens. 1971. Transition probabilities for a forest. Nature 225: 93–114.

Wilson, J. B. 1995. Variance in species richness, niche limitation and vindication of patch models. Oikos 73: 277–279.

Wu, J. and S. A. Levin. 1994. A spatial patch dynamic modeling approach to pattern and process in an annual grassland. Ecol. Monogr. 64: 447–464.

Zar, J. H. 1999. Biostatistical Analysis. Prentice-Hall, Inc., Upper Saddle River, NJ. 663 p.