

# Post-Agricultural Succession in the Neotropics

Randall W. Myster  
Editor

# Post-Agricultural Succession in the Neotropics

 Springer

Randall W. Myster  
Ecosystems Studies  
Institute for Tropical Ecosystems Studies  
University of Puerto Rico at Rio Piedras  
PO Box 21910  
San Juan, PR 00931-1910  
rmyster@lternet.edu

ISBN: 978-0-387-33641-1

e-ISBN: 978-0-387-33642-8

Library of Congress Control Number: 2007937949

© 2008 Springer Science+Business Media, LLC

All rights reserved. This work may not be translated or copied in whole or in part without the written permission of the publisher (Springer Science+Business Media, LLC, 233 Spring Street, New York, NY 10013, USA), except for brief excerpts in connection with reviews or scholarly analysis. Use in connection with any form of information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed is forbidden.

The use in this publication of trade names, trademarks, service marks and similar terms, even if they are not identified as such, is not to be taken as an expression of opinion as to whether or not they are subject to proprietary rights.

Printed on acid-free paper.

9 8 7 6 5 4 3 2 1

springer.com

*To Olia, for all her love and support*

*“Seek simplicity, but distrust it.”*

*Alfred North Whitehead*

# Preface

It was 1985, and I remember walking into the office of Peter Morin at Rutgers University. He told me of some boxes with computer punch cards that had been littering his office for years and of his desire to get rid of them. Because of my background in computer science, I said I would take a look. The cards were in bad shape: moldy, broken in places, and full of cockroaches that were living on what was left of the rubber bands that once had held them together. This was the Buell-Small successional data set. I cleaned up the cards, ran them through an old card-reader, and finally transferred the data onto magnetic tape which I could access using my office computer.

While I was at Rutgers, I also managed to add five years to the data set by going out to Hutcheson Memorial Forest with Steward Pickett and others where we sampled the old fields that comprised the Buell-Small study. Accompanying us was a kindly and cheerful old woman, the last surviving member of the team of scientists who had the foresight to set up those permanent plots in the late 1950s and early 1960s. Her name was Helen Buell. She had an infectious sense of humor—her bumper-sticker read “I brake for *Verbascum*”—which came in handy as we crawled through rose bushes and prickly raspberries. I have heard she is gone now, but I would like to remember her here.

Inspired by the work with the Buell-Small data set, I set up post-agricultural plots in the Neotropics that are reported on in several papers and in the first chapter of this book. I believe, as many others do, that such plots are critical to a complete understanding of vegetative changes after agriculture. I hope that those data and other data analyzed and interpreted by the authors of the present book will be a valuable contribution to this scientific undertaking, as has been true for the data from the plots set up so many years ago in the temperate fields of New Jersey.

R. W. M.

# Contents

## **Part I Patterns of Living and Non-living Components of Old Fields After Abandonment**

<b>1 Introduction</b> . . . . .	3
Randall W. Myster	
<b>2 Trends in Above and Belowground Carbon with Forest Regrowth After Agricultural Abandonment in the Neotropics</b> . . . . .	22
Erika Marín-Spiotta, Daniela F. Cusack, Rebecca Ostertag and Whendee L. Silver	
<b>3 Post Sugar Cane Succession in Moist Alluvial Sites in Puerto Rico</b> . . . . .	73
Oscar Abelleira Martínez and Ariel E. Lugo	
<b>4 Soil Fungi and Macrofauna in the Neotropics</b> . . . . .	93
Yiqing Li and Grizelle González	
<b>5 Earthworms and Post-Agricultural Succession</b> . . . . .	115
Grizelle González, Ching Yu Huang and Shu-Chun Chuang	

## **Part II Mechanisms and Tolerances that Cause Plant-Plant Replacements Producing Old Field Vegetation Patterns**

<b>6 Factors Affecting the Species Richness and Composition of Neotropical Secondary Succession: A Case Study of Abandoned Agricultural Land in Panama</b> . . . . .	141
Elaine R. Hooper	
<b>7 Seed Dispersal by Cattle: Natural History and Applications to Neotropical Forest Restoration and Agroforestry</b> . . . . .	165
Clara Luz Miceli-Méndez, Bruce G. Ferguson and Neptalí Ramírez-Marcial	

<b>8 The Roles of Disperser Behavior and Physical Habitat Structure in Regeneration of Post-Agricultural Fields</b> . . . . .	192
K. Greg Murray, Kathy Winnett-Murray, Jason Roberts, Katherine Horjus, William A. Haber, Willow Zuchowski, Mark Kuhlmann and Tammy M. Long-Robinson	
<b>9 Neotropic Post-Dispersal Seed Predation</b> . . . . .	216
Randall W. Myster	
<b>10 Facilitation Versus Competition in Neotropical Old-Fields: A Case Study After <i>Pinus taeda</i> Cultivation in Brazil</b> . . . . .	221
Gislene Ganade, Lessandra Zanini and Ingo Hübel	
<b>11 Recruitment of Dry Forest Tree Species in Central Brazil Pastures</b> . . . . .	231
Aldicir Scariot, Daniel L. M. Vieira, Alexandre B. Sampaio, Ernestino Guarino and Anderson Sevilha	
 <b>Part III Restoration, Management, and the Future of Post-Agricultural Areas</b>	
<b>12 Microbial Biomass in Native Amazonian Ecosystems and Its Adaptation to Deforestation and Pasture Introduction and Management</b> . . . . .	247
Brigitte J. Feigl, Carlos Eduardo P. Cerri, Carlos C. Cerri and Marisa C. Piccolo	
<b>13 Management for Sustainability and Restoration of Degraded Pastures in the Neotropics</b> . . . . .	265
Florencia Montagnini	
<b>14 Conclusions, Synthesis, and Future Directions</b> . . . . .	296
Randall W. Myster	
<b>Index</b> . . . . .	305



## List of Contributors

### **Carlos C. Cerri**

Centro de Energia Nuclear na  
Agricultura (CENA)  
Universidade de Sao Paulo  
CP.96, 13400-970  
Piracicaba, (SP), Brazil

### **Carlos Eduardo P. Cerri**

Centro de Energia Nuclear na  
Agricultura (CENA)  
Universidade de Sao Paulo  
CP.96, 13400-970  
Piracicaba, (SP), Brazil

### **Shu-Chun Chuang**

Institute of Zoology  
National Taiwan University  
No. 1 Roosevelt Road  
Section 4, Taipei 106  
Taiwan

### **Daniela Cusack**

Department of Environmental Science,  
Policy & Management  
University of California, Berkeley  
137 Mulford Hall #3114  
Berkeley, CA 94720-3114

### **Brigitte J. Feigl**

Centro de Energia Nuclear na  
Agricultura (CENA)  
Universidade de Sao Paulo  
CP.96, 13400-970  
Piracicaba, (SP), Brazil

### **Bruce G. Ferguson**

El Colegio de la Frontera Sur Carretera  
Panamericana y Periférico Sur s-n  
Barrio Ma. Auxiliadora San Cristóbal  
de Las Casas  
Chiapas  
México CP 29260

### **Gislene Ganade**

Laboratório de Ecologia  
da Restauração Biologia  
Universidade do Vale do Rio dos Sinos  
CP 275, São Leopoldo  
RS, Brasil 93022-000

### **Grizelle González**

International Institute  
of Tropical Forestry  
USDA Forest Service  
1201 Ceiba St.  
San Juan, PR 00926-1115

### **Ernestino Guarino**

Embrapa Recursos Genéticos e  
Biotecnologia  
Parque Estação Biológica - PqEB - Av.  
W5 Norte (final)  
Caixa Postal 02372  
70770-900 Brasília DF – Brazil

### **William A. Haber**

Apartado 50-5655  
Monteverde de Puntarenas  
Costa Rica

**Elaine R. Hooper**

Department of Forestry  
and Environmental Studies  
Yale University  
210 Prospect St  
New Haven, CT 06511

**Katherine Horjus**

Department of Ecology  
and Evolutionary Biology  
University of California  
Santa Cruz, CA 95062

**Ching Yu Huang**

Institute of Ecology  
University of Georgia  
Athens, GA, USA

**Ingo Hübel**

Laboratório de Ecologia da  
Restauração, Biologia  
Universidade do Vale do Rio dos  
Sinos, CP 275  
São Leopoldo  
RS, Brasil 93022-000

**Mark Kuhlmann**

Department of Biology  
Hartwick College  
West Street, Oneonta  
New York 13820

**Yiqing Li**

College of Agriculture,  
Forestry and Natural Resources  
Management  
University of Hawaii  
200 W. Kawili St.  
Hilo, HI 96720

**Tammy M. Long-Robinson**

12024 E. Pleasant Lake  
Manchester, MI 48158

**Ariel E. Lugo**

International Institute  
of Tropical Forestry  
USDA Forest Service  
Ceiba Street 1201  
Jardín Botánico Sur  
Río Piedras PR 00926-1115

**Erika Marín-Spiotta**

Department of Environmental Science,  
Policy & Management  
Univeristy of California, Berkeley

Current address:

U.C. Santa Cruz, Rm. 2125,  
USDA/ARS  
800 Buchanan St.  
Albany, CA 94710

**Oscar Abelleira Martínez**

International Institute  
of Tropical Forestry  
USDA Forest Service  
Ceiba Street 1201  
Jardín Botánico Sur  
Río Piedras, PR 00926-1115

**Clara Luz Miceli-Méndez**

El Colegio de la Frontera Sur Carretera  
Panamericana y Periférico Sur s-n  
Barrio Ma. Auxiliadora  
San Cristóbal de Las Casas  
Chiapas, México  
CP 29260

**Florencia Montagnini**

School of Forestry  
and Environmental Studies  
Yale University  
370 Prospect St  
New Haven, CT 06511

**K. Greg Murray**

Department of Biology  
Hope College  
Holland, MI 49423

**Randall W. Myster**

Institute for Tropical Ecosystem Studies  
University of Puerto Rico at Rio Piedras  
P.O. Box 21910  
San Juan,  
PR 00931-1910

**Rebecca Ostertag**

Department of Biology  
University of Hawaii at Hilo  
200 W. Kawili St.  
Hilo, HI 96720

**Marisa C. Piccolo**

Centro de Energia Nuclear na  
Agricultura (CENA)  
Universidade de Sao Paulo  
CP.96, 13400-970  
Piracicaba, (SP), Brazil

**Neptalí Ramírez-Marcial**

El Colegio de la Frontera Sur Carretera  
Panamericana y Periférico Sur s-n  
Barrio Ma. Auxiliadora  
San Cristóbal de Las Casas  
Chiapas, México  
CP 29260

**Jason Roberts**

128 Nichols St.  
Lewiston, ME 04240

**Alexandre B. Sampaio**

IBAMA  
SCEN Trecho 2 - Ed. Sede - Caixa  
Postal 09870  
70818-9 – Brasília, DF – Brazil

**Aldicir Scariot**

Embrapa Recursos Genéticos e  
Biotecnologia  
Parque Estação Biológica - PqEB - Av.  
W5 Norte (final)  
Caixa Postal 02372  
70770-900 Brasília DF – Brazil

**Anderson C. Sevilha**

Embrapa Recursos Genéticos e  
Biotecnologia  
Parque Estação Biológica - PqEB - Av.  
W5 Norte (final)  
Caixa Postal 02372  
70770-900 Brasília DF – Brazil

**Whendee L. Silver**

Department of Environmental Science,  
Policy & Management  
University of California Berkeley  
137 Mulford Hall #3114  
Berkeley,  
CA 94720-3114

**Daniel L. M. Vieira**

Embrapa Tabuleiros Costeiros  
Av. Beira Mar, 3250 - jardins  
Caixa Postal 44  
49025-040- Aracaju, SE - Brazil

**Kathy Winnett-Murray**

Department of Biology  
Hope College  
Holland, MI 49423

**Lessandra Zanini**

Laboratório de Ecologia da Restauração  
Biologia, Universidade do Vale do Rio  
dos Sinos  
CP 275, São Leopoldo  
RS, Brasil 93022-000

**Willow Zuchowski**

Apartado 50-5655  
Monteverde de Puntarenas  
Costa Rica

**Part I**  
**Patterns of Living and Non-living**  
**Components of Old Fields After**  
**Abandonment**

# Chapter 1

## Introduction

Randall W. Myster

### 1.1 Rationale

Ecosystems were originally defined as units of the earth's surface which includes both organisms and the physical factors forming the environment (Tansley 1935). As the science of ecosystem ecology developed, ecosystems came to be categorized by function and structure (Odum 1953), with an emphasis on integration and indirect interaction (Muller 1997). While all ecosystem functions deal with energy capture/transfer and nutrient cycling, plant-based productivity and decomposition have come to be considered among the most critical (Watt 1947).

To develop a deeper understanding of ecosystem functions, we need to know the pattern of an ecosystem's abiotic and biotic responses which define function, on the one hand, and the processes and mechanisms that regulate the responses, on the other. In particular for the biota, it has long been recognized that plants and other taxa respond not only to gradients (Whittaker 1975, Kessell 1979, Walter 1979) but also to disturbances (i.e., disruptions of ecosystem structure that occur largely on gradients: Gleason 1926, Pickett and White 1985). Consequently, the vegetation mosaic of any landscape results both from the environmental variation expressed on gradients and from historical disturbances (Risser 1987, Turner and Dale 1991).

Gradients are gradual, directional, and large-scale (from a plants' perspective) changes in environmental factors (Whittaker 1975, Hallet al. 1992). Although gradients are mainly a spatial phenomenon, they may also show seasonal variation and even be modified over long time periods, for example, by changes in climate. Individual plants of a given species exist within certain ranges of environmental conditions (Good 1953) that, when combined with others of the same species, translate into distribution patterns (usually bell-shaped, Gaussian Curves) across gradients for that species (Whittaker 1975). Even though these curves correspond with direct gradients, such as elevation, slope, and aspect, they actually reflect species-specific responses to indirect environmental factors, such as the plant resources of temperature, light, water, and soil nutrients, which correlate with the direct gradients. Such plant growth responses exist in a hierarchy of survivorship, growth, allocation, and architecture.

Unlike gradients, disturbances are local, discrete, and patchy (Pickett and White 1985). However, similar to gradients, they create combinations of resources and

other influences that plants respond to. Indeed, plant distribution patterns over successional time, after a disturbance, are just as species-specific and bell-shaped as they are over gradient space (Pickett 1982, Myster and Pickett 1988).

Any mechanism involving interactions with individuals of another species taxa (e.g., dispersal, predation, herbivory) and any tolerance to a plant resource/abiotic environmental cue (e.g., light, water) that affect any part of a plant's life-cycle can form a response curve. Importantly because plants interact with each other by affecting their local resource environment, interactions such as competition and facilitation are expressed as tolerances. Taken together, response curves for each species define that species' "niche" (Whittaker 1965, Grubb 1977, Parrish and Bazzaz 1982, Bazzaz 1996) that can be quantified using yes/no questions at each life-stage and for each tolerance or mechanism that affects it. Typical questions during a tolerance investigation could be: Will this seed germinate at a given temperature? Will this seedling have a positive carbon balance at a given light level? During a mechanism investigation, typical questions include: Will this seed be dispersed at a given distance from the forest? Will this seedling survive at a given herbivore density? Each time the answer is "yes", a point that represents a particular individual plant is marked along the natural variation scale of the abiotic/biotic environmental cue being investigated, such as the level of temperature, light, distance, or predator density. When the responses of many individuals from the same life-stage and the same species are also marked on the same natural variation scale and then counted, a frequency diagram for the entire species is created.

Because these curves are frequency diagrams and because individual plants can be chosen at random, the response curves/surfaces express probabilities (after normalization: Zar 1999) of how individual plants of that species will respond to the natural variation in the working of a given mechanism or in the availability of a given resource.<sup>1</sup> These response curves give the individual response variation within a plant species for a given life-stage and environmental cue, and are generally wider for species that come early in successional time compared to species that appear later (Bazzaz 1979, 1996). Usually, a few of the plant mechanisms or resources dominate, making the probabilities associated with them key to how the individual plants of that species use the strategies of capture, congruence, and capacitance (Bazzaz 1996). Furthermore, the fact that the response curves have the same shape as plant distribution patterns both over space (Whittaker 1975) and over time (Pickett 1982, Myster and Pickett 1988) suggests that the distribution of a plant species is an outcome of that species' niche probabilities.

Conducted for decades over many of the most common gradients on earth, studies of succession after agriculture (also called old field succession) have helped ecologists gain insights into the processes that structure plant communities and into the role of history and initial conditions in community development (Myster and Pickett 1990b, 1994). Examination of old fields has led to the rise of important ecological theories, such as the initial floristic composition hypothesis (Egler 1954)

---

<sup>1</sup> As an example of a response surface which expresses probabilities, see Figure 3 in Burton and Bazzaz (1991) for emergence of five common old field trees in the American temperate zone.

and the resource ratio hypothesis (Tilman 1988). Using permanent plots established at abandonment as the backbone of old field research (e.g., the Buell-Small old field plot study in New Jersey USA: Buell et al. 1971, Myster and Pickett 1990a), scientists have been successful in finding the pattern of response over time after abandonment from crops (e.g., plant cover [Myster and Pickett 1992b] and diversity [Myster 2003b]) and in discovering many of the mechanisms that determine the pattern (Myster 1993, Bazzaz 1996). Furthermore, studies of post-agricultural succession have provided a framework for comparison and evaluation of various theories of succession and community development (Finegan 1984).

A considerable amount of old field and pasture research has taken place in the temperate regions of the United States (e.g., Oosting 1942, Bazzaz 1968, Buell et al. 1971, Pickett 1982, Tilman 1988, Myster 1993) and Europe (Castro et al. 1986, Miles 1979). The recovery of agricultural areas, however, is vital to ecosystems all over the world (Borhidi 1988). In the tropics, for example, the cutting down of wooded areas (Grainger 1988, Fearnside 1993) for agriculture and pasture (Skole and Tucker 1993) is the major cause of deforestation (Buschbacher 1986, Uhl et al. 1988, Fearnside 1993, Thomlinson et al. 1996). It should come as no surprise then that recovery of Neotropical areas after agriculture (Donfack et al. 1995, Fernandes and Sanford 1995, Quintana-Ascencio et al. 1996) is relevant to such important issues as forest regeneration (Grainger 1988, Brown and Lugo 1990, Myers 1991, Singh 1993, Skole and Tucker 1993), forest ecosystem restoration (Brown and Lugo 1990, Lugo 1992), sustainability of agriculture (Brown and Lugo 1990, Serrao and Toledo 1990), maintenance of biodiversity (Brown and Lugo 1990, Aide and Cavelier 1994), and impacts of global climate change on forest dynamics (Padoch and Vayda 1983, Hobbie 1992, Maberley 1992, Keller et al. 1993). Neotropical areas recovering from agriculture may also serve as a buffer between “primary” forest and more intensely human-influenced areas (Brown and Lugo 1990). Last but not least, it is expected that with future increase of global warming forest disturbance in general and old field succession in particular will affect larger and larger parts of the earth (Bazzaz 1996).

The nature of the recovery of old fields depends on their disturbance “regime,” which is characterized by severity, size, spatial location, and frequency (Myster 2001). The measurement of severity is best accomplished by sampling the loss of plant biomass and determining whether such loss includes loss of plant meristems (Raunkaier 1934, Pickett and White 1985, Tilman 1988, Myster 2001). Severity of old fields is moderate, compared to the more severe landslides (Myster 2001), because old fields maintain an intact soil profile, roots, and humus layer despite the removal of above-ground vegetation. In size, old fields do not usually exceed a few tens of hectares (they are larger, however, than many Neotropical treefall gaps: Brokaw 1982), and crops that are planted in them often require specific locations (e.g., Coffee grows well in the mountains while Banana and Sugarcane do best in the valleys). Frequency of old field disturbance includes the number of times a field has been cultivated, the duration of each cropping period, the time between fallow periods, and the order of crop rotation. Usually fields are fallow longer than they are in crop and can be either reused with different crops and fallow periods until abandoned or used for 5-10 years until productivity declines. As the length of

time an area is in crop increases, the length of successional, or recovery, time may also lengthen. For example, a short cropping period can lead to large contributions from the seed bank and trees may regenerate quickly from stump or root sprouts, whereas an increased cropping period brings about the decay of rootstocks and tree stumps, thus providing for grass invasion and prolonged tree invasion. Among other conditions that influence old field recovery are historical effects of the past crop (a crop's "signature": Myster and Pickett 1988, 1990b, 1994), the year of abandonment, the season of abandonment, the percent of border with forest (Bazzaz 1968), and a field's plowing record (whether the field was plowed under or left fallow when abandoned: Myster and Pickett 1990a).

Studies of post-agricultural succession in the temperate zone have demonstrated the particular importance of past crops in determining old field patterns (e.g., alteration of successional pathways and species composition and abundance for up to 8 years after abandonment: Myster and Pickett 1988, 1990b, 1994). Hence, a major focus of this book will be on the examination of fields after common Neotropical crops, such as Maize (*Zea mays*), Sugarcane (*Saccharum officinarum*), Banana (*Musa* spp.), Coffee (*Coffea* spp.), Cassava (*Manihot esculenta*), Beans (*Phaseolus* spp.), and Rice (*Oryza* spp.), and after pasture grasses that usually establish themselves after cropping but can also be purposely planted (e.g., *Setaria sphacelata*). Pastures will be treated as a kind of old field succession for several reasons. First, they are usually converted from depleted agricultural fields when cows are allowed to enter. Second, they may continue to have remnants of past crops growing in them for some years. And third, they can be planted with native and exotic grasses or be colonized by local grass species due to cattle activity (e.g., trampling of vegetation, creation of hummocks, deposition of dung, and soil compaction).

Two forest-clearing techniques that are the most common in the Neotropics will also be discussed in this book. Both methods, while increasing light quantity and contact of rainfall with the soil, eventually decrease soil fertility. The first technique is mechanical clearing that aims at removing woody biomass (e.g., by using a bulldozer) and brings about changes in physical properties of the soil. The other technique is shifting, or "slash and burn" (Uhl 1987), agriculture that occurs when natural vegetation is first cut down to the ground and then burnt. Although burning produces a short pulse of nutrients like phosphorus, it generally volatilizes both organic matter and nitrogen while raising soil temperature and, in the long term, makes soil poor in both nutrients and the seed bank. Shifting agriculture also entails a rotation of fields rather than crops that is accompanied by long fallow periods (Grigg 1978). The decision as to when to rotate fields and for how long to leave them fallow depends on such factors as weed and insect loads in the fields, soil fertility, production, labor availability, and local dietary needs (Staver 1990). The implementation of either one of these forest-clearing methods also causes carbon loss, a mixing of the soil horizons, and a higher degree of soil aeration (Bazzaz 1996).

Both mechanical clearing and shifting agriculture lower the level of advanced regeneration from sapling banks and from root/stem resprouting (Uhl et al. 1988) so that seed and seedling dynamics dominate regeneration after agriculture. Consequently, an understanding of old field succession demands knowledge of invasion and establishment at the seed and seedling phases of the plant life-cycle (Grubb 1977, Myster 1993).



Old field recovery goes through several structural and conceptual stages: (1) domination by past crop and its various effects, (2) patch dynamics of grass, past crop remnants, asexual shrubs, and other plants, (3) tree invasion, and (4) development of a closed-canopy “secondary” forest. Although individual plants may or may not colonize bare ground during these stages, they always become involved in the on-going process of plant-plant replacement (Busing 1996). Plants enter this process because they grow and interact asymmetrically (Bazzaz 1996)—one individual is always gaining advantage over another. As a result, the plants that are growing best replace the plants that are growing worst, are in senescence or dead. However, plant-plant replacement does not necessarily involve two plants only, for more than one plant can be replaced by just one or only one plant can be replaced by more than one. Because individual plants are “planted” in the soil, they have a defined physical space which can be occupied and reoccupied as plant-plant replacements proceed. Every land plant in the world sooner or later assumes these roles-of the “replacer” and the “replaced.”

Because plants move very slowly, we naturally do not see them and their communities changing. Yet, they are always both engaged in and are the product of the dynamic process of plant-plant replacement. Plant-plant replacements determine which plants are present at every point in space and time, for example, during a typical “static” plant growth and allocation field experiment or a “snapshot” plot sampling. Even in those cases, however, plant niches and their interaction with local environmental cues will determine how those plants grow. Fundamentally, neither species nor patches are replaced in communities. It is individual plants that are replaced by other individual plants. I suggest that plant communities do not go through continuous cycles of disturbance (regeneration) => stability (growth) => disturbance (regeneration)—like a corn field— but instead are undergoing plant-plant replacements at all times.

After a closed canopy has developed, old field plants may eventually enter a thinning state when dead plants in the canopy are replaced not with new individuals but with modified growth of existing plants. There is a physiological limit to this kind of growth, however, and at some point every plant will die and be replaced. Furthermore, although there can be a growth phase for perennial plants between replacing and being replaced, it is rare, transitory, and, consequently, over-emphasized in plant ecological studies. This focus on individual plant-plant replacements eliminates the need for many of the old dichotomies of plant ecology, such as primary/secondary forests, natural/human disturbances, successional/nonsuccessional communities, and pioneer/climax species. This conceptual model *unifies* various old theories of plant community organization because plant-plant replacements define not only the successional dynamics of old fields but the dynamics of any plant community.

Replacements are controlled by species tolerances and mechanisms that “activate” the niches of the species involved in the replacement. Tolerances include germination and growth while mechanisms encompass dispersal, seed pool, seed predation, seed pathogens, seed germination, seedling predation, seedling pathogens, seedling herbivory, and/or seedling competition (e.g., Myster and McCarthy 1989, Myster and Pickett 1993, Myster 1994, 2003a, 2003c, 2004a, 2006, 2007). The process of plant-plant replacement is at the heart of the dynamic nature of terrestrial

plant communities both over successional time and over space (e.g., at the edges of plant distributions where gradients have a major effect on plants: Whittaker 1975, Myster 2001).

For those who still need to be convinced of the dynamic nature and ubiquity of plant-plant replacements, I suggest setting aside a plot of ground, marking a few hundred plants, and coming back in a few years (longer for perennial plants) to see how many individuals have been replaced. The data I have from permanent plots sampled for decades in a variety of both Neotemperate and Neotropical old fields clearly show that replacements are working everywhere and always. Replacements are also a very common phenomenon in so called “primary” Neotropical forests (e.g., in the 50 ha plot located at Barro Colorado Island, Panama <http://ctfs.si.edu/datasets/bci>). It seems that plants wait not to be counted (*sensu* Harper 1977) but to be replaced!

The working model of plant-plant replacements entails a strong possibility that a plant will be replaced by another plant (whether of the same or of a different species) when the probabilities expressed in the species’ niche of that plant are lower than the probabilities expressed in the species’ niche of the other plant, those probabilities being activated by the combination of abiotic and biotic conditions at a given point in space and time and for that particular life-stage in the plants’ development. I suggest that it is the smallest probability—from among the many niche “slices” for each species that are activated by local environmental conditions—that will be the most limiting and, therefore, most critical in determining whether or not one plant will replace another.

Replacements create changes in plant abundances, which may also create changes in plant composition that lead to the emergence of other patterns at larger spatial and temporal scales (e.g., successional rate and direction, patch dynamics, plant distribution, exotic plant invasion, plant associations). Care must be taken, however, with the observation of these plant patterns. For example, even though individual plants continue to be replaced, preservation of species abundances and/or species composition at a larger scale of organization may still occur, giving the impression of a “coexistence” of species (when the identity or number of plant species remain the same despite changes in plant abundances) or of a plant community at “equilibrium” (when neither plant species nor plant abundances change). Existence of high-level patterns that do not change very much over time should not obscure the fact that such patterns are the product of a dynamic and ever changing process of plant-plant replacement. Any plant pattern is only a snapshot of the vegetation at a given instance in time and at a specific scale of observation, whereas plant-plant replacements occur continuously.

Because plant niches express probabilities, plant-plant replacement itself must be a probabilistic process. In fact, succession is probabilistic (Pickett 1982), for it is made up of a multitude of plant-plant replacements that take place over time (for example, when all the individuals of a given species leave a disturbed area and/or an individual of a new species arrives, creating a change in species composition: Myster and Pickett 1994, Brokaw and Busing 2000). Again, the dynamics of any plant community is probabilistic because a plant community—and any of its plant-based structures and functions—is defined by its’ resident plants that have been brought forth by a probabilistic plant-plant replacement process (Pickett 1982, Myster and

Pickett 1988). Thus the ultimate reality of every plant community are the plant-plant replacements, for they produce vegetation changes at any and all scales.

Along with succession, plant associations, and species coexistence/equilibrium, distribution of plant species exemplifies how plant-plant replacements determine patterns of a plant community at higher levels of organization. Since plant distribution patterns are shaped by plant-plant replacements, there is a strong possibility that distribution of a species will *increase* if, under given conditions, the species' niche probabilities are higher than those of another species' at the edges of the two species' distribution where the species meet, or *decrease* if the first species' probabilities are lower. For example, red cedar (*Juniperus virginiana* L.) is expanding its range in the United States by replacing plants of various other species at the edges of its distribution. The success of red cedar's invasion finds its explanation in the species' regeneration niche (those parts of a plants' niche that represent seeds and seedlings: Grubb 1977) that includes higher probabilities in seed dispersal, extended seed viability in the soil, lower seed predation, lower herbivory, and higher drought resistance than many other species (reviewed in Myster 1993).

## 1.2 Species Associations in Permanent Plots

Studies in the temperate zone of the Americas show that the spatial and temporal distribution of old field plants is not random and that it is associated with various factors (such as the location of "nurse" trees and plant resource levels: Myster and Pickett 1992a, Myster 1993). In the course of an investigation of these temporal and spatial patterns, numerous questions present themselves: When do species appear and when do they leave? How long are they present? Are there edge effects from the forest? Do species clump together and, if they do, does this autocorrelation change with time? Chronosequences supply some evidence to answer these questions. However, inasmuch as they place different fields sampled at different times sequentially on a time line, this approach offers only, at best, a partial solution. The true answers come from regularly sampled permanent vegetation plots that are established at the abandonment of agricultural fields because such plots show the actual sequences of plant abundance and species change over time (Pickett 1982) an important aspect of the dynamic nature of plant communities (Myster 2001).

As case studies, let us consider plots in natural pasture in Puerto Rico and plots in former Banana plantations, former Sugarcane plantations, and seeded pastures in Ecuador. The first study site is a natural pasture that had been grazed for decades before it was abandoned. It borders the Luquillo Experimental Forest (LEF) of northeastern Puerto Rico, USA (18°20'N, 65°45'W: Aide et al. 1995, Liu and Zou 2002), close to the town of Sabana. The LEF, a long-term ecological research (LTER) site of the National Science Foundation ([www.luq.lternet.edu](http://www.luq.lternet.edu)), is a tropical montane wet forest with tabonuco (*Dacryodes excelsa*), ausubo (*Manilkara bidentata*) and motillo (*Sloanea berteriana*) below 600m, palo colorado (*Cyrilla racemiflora*) and palm (*Prestoea montana*) between 600m and 850m, and cloud

forest above 850m (Waide and Lugo 1992). The study pasture is located at the lower elevations and receives between 2m and 5m of rainfall per year, with an average temperature of 18°C. Its soils are fertile and volcanoclastic in origin (Thomlinson et al. 1996).

Twenty-five 5m × 2m contiguous plots were laid out on the border with the forest (Myster 2003b), the long side parallel to the forest in order to maximize any edge effects and to facilitate comparison to the Buell-Small plot study in New Jersey, USA (Myster and Pickett 1990a). Since island diversity in plant species is greatly reduced compared to mainland diversity, the plots were big enough to capture diversity in these agrosystems (Myster 2004a). The plots did not have any remnant trees or sprouting tree roots at the beginning of the study, and their tree seed bank was very small (Myster 2006). Starting in May of 1997 and continuing annually for 10 years, the plots were sampled for percent cover of each plant species. Percent cover—an indication of a species' ability to capture light and, therefore, to dominate these areas in the process of becoming forested communities (Myster 2003b)—was estimated visually in relation to each plot's area.

The analysis of the data obtained from these plots showed that grass dominated throughout the first 5 years after abandonment, constituting 75% of the plant cover after 5 years, while forbs declined to 40% and ferns and woody species increased to 45 and 15% respectively. Common trees included *Syzygium jambos*, *Calophyllum calaba*, and *Tabebuia heterophylla*. Common shrubs were *Clidemia hirta* and *Miconia* spp., both of which invaded from the forest. The community parameters that peaked within the first 5 years after abandonment were productivity (at 400 g/m<sup>2</sup>/yr), total basal area (at 1,000 cm<sup>2</sup>), and richness (at 19 species: Myster 2003b).

The second study site comprises recovering Banana plantations, Sugarcane plantations, and seeded pastures at the Maquipucuna Reserve, Ecuador (0°05'N, 78°37'W; www.maqui.org; Sarmiento 1997, Rhoades et al. 1998, Rhoades and Coleman 1999, Zahawi and Augspurger 1999, Myster 2004a, 2004b). Maquipucuna lies between 1,200m and 1,800m and is classified as tropical lower montane wet forest (Edmisten 1970). It has deeply dissected drainages with steep slopes and receives between 2m and 5m of rainfall a year. The temperature ranges between 14°C and 25°C, with an average temperature of 18°C. The reserve's fertile andisol soil is developed from volcanic ash deposits (Myster and Sarmiento 1998).

In June of 1996, 6 agricultural fields were selected: two Sugarcane (*Saccharum officinarum*) plantations, two Banana (*Musa* sp.) plantations, and two pastures seeded in *Setaria sphacelata*.<sup>2</sup> All 6 fields were 2 ha rectangles located within a few hundred meters of each other at the lower elevations of the reserve, on the border with the primary forest. In each field, twenty-five 5m × 2m contiguous plots were laid out, with the long side on the forest border. This forest is also tropical montane wet forest.

---

<sup>2</sup> Although native to Africa, the *Setaria* grass is being planted more and more extensively in the Neotropics because it can withstand heavy grazing by spreading asexually and can form large crowns. Well accepted by cattle, the *Setaria* grass is tolerant of relatively cold temperatures and short-term waterlogged conditions, both common at the Maquipucuna Reserve.

Starting in 1997, these subplots were sampled annually for 10 years for percent cover of each plant species. Maquipucuna plant taxonomists, trained at the University of Georgia, USA, where voucher specimens are kept on file (Myster and Sarmiento 1998, Zahawi and Augspurger 1999), assisted in the identification of species by using specimens located on site. The analysis of the data from the first 5 years after abandonment showed that the resident graminoid dominated in Sugarcane (at 50% after 5 years), in Banana (at 70%), and in pasture (at 90%), that forbs and ferns were at low levels everywhere, and that woody species increased in Sugarcane (at 45% after 5 years) and in Banana (at 25%) but remained sparse in pasture (at 10%). Common trees included *Acalypha pladichephalus*, *Costus* sp., *Vernonia patens*, and *Piper aduncum* while common shrubs were *Pilea* sp. and *Miconia* spp. After 5 years, both total basal area and species richness were greatest after Sugarcane (at 700 cm<sup>2</sup> and 59 species respectively), lower after Banana (at 600 cm<sup>2</sup> and 49 species), and lowest after pastures (at 100 cm<sup>2</sup> and 25 species: Myster 2007).<sup>3</sup>

The plot data were used to implicate plant interactions and successional mechanisms by generating spearman coefficients of rank associations (SAS 1985, Milbau et al. 2005). The analyses showed that the actual number of associations among species was much lower than the potential number of 3,250 per field (all pairs of 26 species over the 10-year period). For example, the pasture in Puerto Rico had a total of 362 associations, 55 of which were negative (Table 1.1), while one of the two Banana fields in Ecuador had a total of 168 associations, 12 of them being negative (Table 1.2).

Because controlled field experiments have confirmed that species that interact significantly also form significant associations with each other (Tirado and Pugnaire 2005), the statistics from the case studies (Tables 1.1–1.7) point to a low level of species interactions in these fields (as was also seen in temperate old field plots in New Jersey, USA: Myster and Pickett 1992b). These results support the view of communities as loosely-organized assemblages of species that are created mainly by tolerance parts of individual species' niches (Gleason 1926, Whittaker 1975) rather than as tightly-linked entities that are structured by species interactions.

Most of the significant associations in the study plot data were positive (unlike those, mainly negative, associations that were computed from plots in temperate old fields: Myster and Pickett 1992b). This suggests that facilitation in these early-successional plots where plants are under stress (see Chapter 10) may be more important than competition among those relatively few species that are actively interacting. In the Puerto Rican pasture (Table 1.1), species that formed many positive associations included the trees *Syzygium jambos*, *Guarea guidonia*, *Ocotea leucoxylon*, and *Prestoea montana*. Among major inhibiting species were the grass *Panicum* spp., the fern *Gleichenia bifida*, and the tree *Tabebuia heterophylla*. In

---

<sup>3</sup> The data from the plots in Puerto Rico (LTERDATB #97) and in Ecuador (LTERDATB#101) are housed in the archives of the LEF LTER site. Visit the Luquillo web site ([www.luq.lternet.edu](http://www.luq.lternet.edu)) for further details.



**Table 1.2** Significant spearman rank correlation coefficients among all plant species in the *Ecuador Left Banana Plantation* over the first 10 years of succession. Significant positive associations are indicated by a “+” and significant negative associations are indicated by a “-”. Plant species and families are indicated as follows: *Acalypha pladichephalus* (A), *Begonia* spp. (B), *Geonoma undata* (C), *Cyathea* spp. (D), *Musa* spp. (E), *Pilea* spp. (F), *Anthurium* spp. (G), *Trichipterix pilosissima* (H), *Nectandra* spp. (I), *Ochroma* spp. (J), *Baccharis* spp. (K), *Anthurium* spp. (L), *Setaria* spp. (M), *Boconia frutescens* (N), *Piper aduncum* (O), *Erythrina megistophyla* (P), *Vernonia patens* (Q), *Hedyosum* spp. (R), *Commelina diffusa* (S), *Althernantera* spp. (T), *Siparuna piloso-lepidota* (U), *Solanum* spp. (V), *Vernonia* spp. (W), *Digitaria sanguinalis* (X), *Inga* spp. (Y) and *Passiflora* spp. (Z).

	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	
A	+				+	+	++		+	+		-	++	-					++	+					++	
B		++	++	++	++++	+	+		++	+	++	-								+	+	+				
C			+++	+	+	+++	+	+++		+				-												
D					+	+	+	+++						-	+-	+										
E					++	+											+								+	
F							++	+		++	+								+						+	
G							+++	+++		+		-														
H								+++	+	++	+								+		+	++		+		
I									++			-								+						
J										+++	++			-					+	+	+	+	+	+	+	
K												++	++	++										+	+	
L												+					+		+	+	+			+		
M															+										+	
N																									+	
O																+++	+-									
P																++										
Q																++	++									
R																		+++	+							
S																			++	+						
T																				+	+					
U																						+++++				
V																										
W																							++			
X																							++	+++		
Y																								+	+	
Z																										

one of the two Banana fields, key species with many positive associations included *Begonia* spp., *Trichipterix pilosissima*, and *Ochroma* spp. (Table 1.2). However, the past crop in that field (*Musa* spp.) did not play a significant role. In the other Banana field, *Begonia* spp., *Cuphea* spp., and *Brugmansia* spp. were very active (Table 1.3). In one of the two Sugarcane fields, key species included members of the families Asteraceae, Verbenaceae, and Pupillionacia. The past crop (*Saccharum officinarum*), however, was not implicated (Table 1.4). In the other Sugarcane field, *Cuphea* spp. and *Piper aduncum* were important, but the past crop was not (Table 1.5). In the Ecuadorian pastures, negative associations were more common than positive associations, especially when the planted pasture grass *Setaria sphacelata* was one of the species (Tables 1.6–1.7).

Although the results in species associations strongly suggest species interactions (see Tirado and Pugnaire 2005 and references therein) among some tropical plant species (as for some temperate plant species: Myster and Pickett 1992b), any further comment would be premature, given the lack of tropical studies involving these species (see Chapter 14). When augmented with the findings of future tropical experiments, however, these results will allow greater synthesis of research effort and more viable interpretations of post-agricultural succession in the Neotropics.

**Table 1.3** Significant spearman rank correlation coefficients among all plant species in the *Ecuador Right Banana Plantation* over the first 10 years of succession. Significant positive associations are indicated by a “+” and significant negative associations are indicated by a “-”. Plant species and families are indicated as follows: *Acalypha pladichephalus* (A), *Costus* spp. (B), *Musa* spp. (C), *Solanum muricatum* (D), Piperaceae (E), *Setaria* spp. (F), *Tagetes terniflora* (G), *Begonia* spp. (H), *Cuphea cartagenensis* (I), Polypodiaceae (J), *Vernonia patens* (K), *Brugmansia* spp. (L), *Digitaria sanguinalis* (M), Urticaceae (N), *Chusquea* spp. (O), *Nectandra* spp. (P), Piperaceae (Q), *Commelina diffusa* (R), *Erythrina megistophyla* (S), *Heliotropium* spp. (T), *Inga* spp. (U), *Musa acuminata* (V), *Chenopodium album* (W), *Crataegus monogyna* (X), *Boconia frutescens* (Y) and *Cecropia monostachyma* (Z).

	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
A		+	-	-	+	+++	+	+							+	+									
B			+	-	++				-	+									+				-	+	
C						+			++		++	+	+	+						+		+			+
D									+	+			+	+	+									++	+
E						+++			-	+	+				+						+				
F						-					-						+	+			++				
G							++++	++	+	+							+								
H								++	+	+				+	++	+									
I									+	+	+	+				+				+	++	+	+		
J										+-		+		+										++	+
K											+++							+							
L												++	+		+	+	+	+	+	+	+				+
M													+++	+++					+		+				
N														+++										+	+
O																	+++								
P																		+++	++						
Q																			++++	++	+				
R																				+				+	+
S																					+	+			
T																						+++	+		
U																							++	+	++
V																									
W																								+	
X																									++
Y																									

### 1.3 About this Book

Examined in this book are vital concerns of post-agricultural recovery in the Neotropics, such as common clearing, planting, cultivation, harvesting and abandonment practices, the post-agricultural environment and disturbance regime, and successional mechanisms. In addition, this book has advantages over other studies of tropical disturbances in that it focuses directly on post-agricultural areas and includes real data of successional pattern and process while investigating the function and structure of old fields and presenting a conceptual framework that both current and future Neotropical studies can use and add to.

All work that is reported in the book chapters has been done in the Neotropics, the American landmass and associated islands that lie between the Tropic of Cancer (23.5°N) and the Tropic of Capricorn (23.5°S). Between these latitudes, the sun remains in the sky the longest over the course of a year compared to the rest of the earth, which leads to a greatly reduced seasonality and prolonged growing period. Responding to this geographic variation, the chapter authors share their expertise



**Table 1.4** Significant spearman rank correlation coefficients among all plant species in the *Ecuador Right Sugarcane Plantation* over the first 10 years of succession. Significant positive associations are indicated by a “+” and significant negative associations are indicated by a “-”. Plant species and families are indicated as follows: *Acalypha pladiccephalus* (A), Asteraceae (B), *Digitaria sanguinalis* (C), Polypodiaceae (D), *Nectandra* spp. (E), *Stachys micheliana* (F), Piperaceae (G), *Lantana camara* (H), Verbenaceae (I), *Erythrina megistophyla* (J), *Piper aduncum* (K), *Rubus* spp. (L), *Commelina diffusa* (M), *Elephantopus mollis* (N), *Cecropia* spp. (O), *Costus* spp. (P), *Miconia* spp. (Q), Passifloraceae (R), Fabaceae (S), *Chusquea* spp. (T), Marantaceae (U), *Pilea* spp. (V), *Hieracium* spp. (W), Sabicea spp. (X), *Columnnea* spp. (Y) and Orchidaceae (Z).

	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
A	+-	+	+	++			++			+-	+									+	+				
B			+	+	+	++++	-	++														+	++	+	
C														+							++	++	-	++	
D				+			-	+-	-	+			++	++	+				+		+				
E					+	++			-																+
F						+		++					+				+	+	+					+	
G								+		+						+							+		
H								+	+++								+	+	++	++					
I										+		++	+							+			+		
J										+	++	++								+	+				
K											++						+						+		+
L												-	++											+	
M														+	+				+++	+					
N														+									+	+	+
O																			+				+		
P																			+	+					
Q																	+++								+
R																		++	+						+
S																			++	++	++	+	+	+	++
T																				+++	+			+	
U																					+	+			
V																									
W																							+		
X																									
Y																									+

and relate studies over a wide range of the major gradients of temperature and rainfall found throughout the Neotropics.

The book is divided into three sections, each of which develops and expands upon key points of post-agricultural succession in the Neotropics:

- I. Patterns of living and non-living components of old fields after abandonment.
- II. Mechanisms and tolerances that cause plant-plant replacements, producing old field vegetation patterns.
- III. Restoration, management, and the future of post-agricultural areas.

There are no clear-cut boundaries, however, among the three parts. The book offers a lot of “cross-fertilization,” for most of its chapters discuss issues that formally belong to more than one section. This multilateral approach presents itself as the best way for a comprehensive investigation of the complex phenomenon of post-agricultural succession in the Neotropics.

We begin the book by exploring permanent plot data in areas that used to be Neotropical Banana plantations, Sugarcane plantations, and pastures. We continue by examining the above- and below-ground Carbon (C) dynamics after crop agriculture and pasture and by discussing the mechanisms of C sequestration in these areas and the methods of studying soil C dynamics. Next, we focus on species composition,



**Table 1.7** Significant spearman rank correlation coefficients among all plant species in the *Ecuador Right Pasture* over the first 10 years of succession. Significant positive associations are indicated by a “+” and significant negative associations are indicated by a “-”. Plant species and families are indicated as follows: *Setaria sphacelata* (A), *Erythrina megistophyla* (B) and *Polypodiaceae* (C).

	B	C
A	-----	---
B		
C		

soil C, and nutrients after pastures and after Sugarcane and tree plantations. The role of alien species is introduced at this point to be developed in chapters that follow. We finish the first section by concentrating on the living part of the soil: the fungi, macrofauna, and earthworms. With all three kinds of organisms, the patterns of their diversity and their abundance during succession are explored. Also examined are the effects that these organisms may have on soils and on ecosystem functioning and the possible distribution of these organisms among functional groups.

In the second section of the book, we discuss what is known about mechanisms and tolerances that lead to plant-plant replacements during succession. First, we look into the complete suite of plant mechanisms and tolerances in Neotropical wet forest. Then we move on to seed dispersal by cattle and by birds. Raised in the discussion are questions of how these types of dispersal affect viability and germination and how the animal vectors themselves affect and, in turn, are affected by the vegetation structure in old fields. Next, studies that explore variation in the working of seed predation are reviewed, and issues of facilitation and competition are investigated in field experiments. Finally, plant mechanisms and tolerances in Neotropical dry forest are examined.

In the final part of the book, we address the issues of restoration, management, and future conditions of agricultural fields. Discussed are the role of microbes in restoration and sustainability of cropping systems as well as the ways in which agricultural practices affect microbial diversity. Also explored are different kinds of pasture degradation, objectives in pasture restoration, and specific techniques, such as intercropping and not clearing trees, from Costa Rican studies. We conclude the book by assessing the *status quo* of research in the area of Neotropical succession after agriculture along with research perspectives and their relation to ecological paradigms. Finally, specific avenues for future old field studies are presented.

We hope that these studies of old fields after agricultural disturbance will also enhance an understanding of natural transition from grassland/meadow to forest and a comprehension of fluctuations in the development of plant communities. This knowledge will enable researchers and land managers not only to predict and manipulate the nature of land recovery but also to more skillfully utilize lands with various kinds of vegetation cover, from lands on which woody vegetation is desired (e.g., forests, surface mines, road-sides) to lands on which woody vegetation should be removed (e.g., rangelands, roadsides, utility corridors).

**Acknowledgment** I wish to thank Mr. Michael Malahy for his help in analysis of the plot data. I also wish to thank Mr. Bert Witteveen for logistic help at Maquipucuna Reserve and Dr. Nick Brokaw for logistic help at Luquillo Experimental Forest. Finally, I thank Ms. Eda Melendez and her staff for their help with the LTER data sets. I received support from grant DEB-0218039 from the National Science Foundation to the Institute of Tropical Ecosystem Studies, University of Puerto Rico, and the USDA Forest Service, International Institute of Tropical Forestry as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest. Additional support was provided by the Forest Service (U.S. Department of Agriculture) and the University of Puerto Rico.

## References

- Aide, T. M., and Cavelier, J. 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology* 2:219–229.
- Aide, T. M., Zimmerman, J. K., Herrera, L., Rosario, M., and Serrano, M. S. 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. *Forest Ecology and Management* 77:77–86.
- Bazzaz, F. A. 1968. Succession on abandoned fields in the Shawnee Hills, southern Illinois. *Ecology* 49(5):924–936.
- Bazzaz, F. A. 1979. The physiological ecology of plant succession. *Annual review of Ecology and Systematics* 10:351–371.
- Bazzaz, F. A. 1996. *Plants in Changing Environments: Linking Physiological, Population, and Community Ecology*. Cambridge: Cambridge University Press.
- Borhidi, A. 1988. Vegetation dynamics of the savannization process on Cuba. *Vegetatio* 77:177–183.
- Brokaw, N. V. L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14:158–160.
- Brokaw, N. V. L., and Busing, R. T. 2000. Niche versus chance and tree diversity in forest gaps. *Trends in Ecology and Evolution* 15:183–188.
- Brown, S., and Lugo, A. E. 1990. Tropical secondary forests. *Journal of Tropical Ecology* 6(1): 1–32.
- Buell, M. F., Buell, H. F., Small, J. A., and Siccama, T. G. 1971. Invasion of trees in secondary succession on the New Jersey piedmont. *Bulletin of the Torrey Botanical Club* 98(2):67–74.
- Burton, P. J., and Bazzaz, F. A. 1991. Tree seedling emergence on interactive temperature and moisture gradients and in patches of old-field vegetation. *American Journal of Botany* 78: 131–149.
- Buschbacher, 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. *Journal of Vegetation Science* 7:685–694.
- Castro, I. A., Sterling, S., and Galiano, E. F. 1986. Multi-species pattern analysis of Mediterranean pastures in three stages of ecological succession. *Vegetatio* 68(1):37–42.
- Donfack, P., Floret, C., and Pontanier, R. 1995. Secondary succession in abandoned fields of dry tropical northern Cameroon. *Journal of Vegetation Science* 6(4):499–508.
- Edmisten, J. 1970. Some autoecological studies of *Ormosia krugii*. In *A Tropical Rain Forest*, ed. H. T. Odum and R. F. Pigeon, Chapter D-8. Springfield, Virginia: National Technical Information Service.
- Egler, F. E. 1954. Vegetation science concepts. I. Initial floristic composition, a factor in oldfield vegetation development. *Vegetatio* 4:412–417.
- Fearnside, P. M. S. 1993. Deforestation in Brazilian Amazonia: the effect of population and land tenure. *Ambio* 22(8):537–545.
- Fernandes, D. N., and Sanford Jr., R. F. 1995. Effects of recent land-use practices on soil nutrients and succession under tropical wet forest in Costa Rica. *Conservation Biology* 9(4):915–922.
- Finegan, B. 1984. Forest succession. *Nature* 312:109–114.

- Good, R. E. 1953. *The Geography of the Flowering Plants*. London: Longmans.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53:1–20.
- Grainger, A. 1988. Estimating areas of degraded tropical lands requiring replenishment of forest cover. *International Tree Crops Journal* 5(1-2):31–61.
- Grigg, D. B. 1978. *The Agricultural Systems of the World*. Cambridge: Cambridge University Press.
- Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological review of the Cambridge Philosophical Society* 52:107–145.
- Hall, C. A. S., Stanford, J. A., and Hauer, F. R. 1992. The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. *Oikos* 65:377–390.
- Harper, J. L. 1977. *Population Biology of Plants*. London: Academic Press.
- Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* 7:336–339.
- Keller, M., Veldkamp, E. Weitz, A. M., and Reiners, W. A. 1993. Effect of pasture age on soil trace-gas emissions from a deforested area of Costa Rica. *Nature* 365:244–246.
- Kessell, S. R. 1979. *Gradient Modeling: Resource and Fire Management*. New York: Springer-Verlag.
- Liu, Z., and Zou, X. M. 2002. Exotic earthworms accelerate plant litter decomposition in a Puerto Rican pasture and a wet forest. *Ecological Applications* 12(5):1406–1417.
- Lugo, A. E. 1992. Comparison of tropical tree plantations with secondary forests of similar age. *Ecological Monographs* 62(1):1–41.
- Mabberley, D. J. 1992. *Tropical Rain Forest Ecology*. New York: Chapman and Hall.
- Milbau, A., Nijs, I., De Raedemaecker, F., Reheul, D., and De Cauwer, B. 2005. Invasion in grassland gaps: the role of neighbourhood richness, light availability and species complementarity during two successive years. *Functional Ecology* 19(1):27–37.
- Miles, J. 1979. *Vegetation Dynamics*. New York: John Wiley
- Muller, F. 1997. State-of-the-art in ecosystem theory. *Ecological Modeling* 100:135–161.
- Myers, N. 1991. Tropical deforestation: the last situation. *BioScience* 41:282.
- Myster, R. W. 1993. Tree invasion and establishment in old fields at Hutcheson Memorial Forest. *The Botanical Review* 59(4):251–272.
- Myster, R. W. 1994. Contrasting litter effects on old field tree germination and emergence. *Vegetatio* 114(2):169–174.
- Myster, R. W. 2001. Mechanisms of plant response to gradients and after disturbances. *The Botanical Review* 67(4):441–452.
- Myster, R. W. 2003a. Seed regeneration mechanisms over fine spatial scales on recovering Coffee plantation and pasture in Puerto Rico. *Plant Ecology* 166(2):199–205.
- Myster, R. W. 2003b. Vegetation dynamics of a permanent pasture plot in Puerto Rico. *Biotropica* 35(3):422–428 .
- Myster, R. W. 2003c. Effects of species, density, patch-type, and season on post-dispersal seed predation in a Puerto Rican pasture. *Biotropica* 35(4):542–546 .
- Myster, R. W. 2004a. Regeneration filters in post-agricultural fields of Puerto Rico and Ecuador. *Plant Ecology* 172(2):199–209.
- Myster, R. W. 2004b. Post-agricultural invasion, establishment and growth of Neotropical trees. *The Botanical Review* 70(4):381–402.
- Myster, R. W. 2006. Shrub vs. grass patch effects on the seed rain and the seed bank of a five-year pasture in Puerto Rico. *Ecotropica* 12:12–19.
- Myster, R. W. 2007. Early successional pattern and process after Banana, Sugarcane and Pasture in Ecuador. *The New Zealand Journal of Botany* 45:35–44.
- Myster, R. W., and Pickett, S. T. A. 1988. Individualistic patterns of annuals and biennials in early successional old fields. *Vegetatio* 78(1-2):53–60.
- Myster, R. W., and McCarthy, B. C. 1989. Effects of herbivory and competition on survival of *Carya tomentosa* (Juglandaceae) seedlings. *Oikos* 56(2):145–148.

- Myster, R. W., and Pickett, S. T. A. 1990a. The Buell successional study at Hutcheson Memorial Forest Center. *Permanent Plotter* 3:2–3.
- Myster, R. W., and Pickett, S. T. A. 1990b. Initial conditions, history and successional pathways in ten contrasting old fields. *American Midland Naturalist* 124(2):213–238.
- Myster, R. W., and Pickett, S. T. A. 1992a. Effects of palatability and dispersal mode on spatial patterns of trees in old fields. *Bulletin of the Torrey Botanical Club* 119(2):145–151.
- Myster, R. W., and Pickett, S. T. A. 1992b. Dynamics of associations between plants in ten old fields during 31 years of succession. *Journal of Ecology* 80(2):291–302.
- Myster, R. W., and Pickett, S. T. A. 1993. Effects of litter, distance, density and vegetation patch type on postdispersal tree seed predation in old fields. *Oikos* 66(3):381–388.
- Myster, R. W., and Pickett, S. T. A. 1994. A comparison of rate of succession over 18 yr in ten contrasting old fields. *Ecology* 75(2):387–392.
- Myster, R. W., and Sarmiento, F. O. 1998. Seed inputs to microsite patch recovery on two Tropandean landslides in Ecuador. *Restoration Ecology* 6(1):35–43.
- Odom, E. P. 1953. *Fundamentals of Ecology*. Philadelphia: Saunders.
- Oosting, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *American Midland Naturalist* 28:1–126.
- Padoch, C., and Vayda, A. P. 1983. Patterns of resource use and human settlement in tropical forest. In *Tropical Rain Forest Ecosystems*. Volume A, ed. F. B. Golley, pp. 301–313. New York: Elsevier.
- Parrish, J. A. D. and Bazzaz, F. A. 1982. Niche responses of early and late successional tree seedlings on three resource gradients. *Bulletin of the Torrey Botanical Club* 109:451–456.
- Pickett, S. T. A. 1982. Population patterns through twenty years of old field succession. *Vegetatio* 49(1):45–59.
- Pickett, S. T. A., and White, P. S. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Orlando, FL: Academic Press.
- Quintana-Ascencio, P. F., Gonzalez-Espinosa, M., Ramirez-Marcial, N., Dominguez-Vazquez, G., and Martinez-Ico, M. S. 1996. Soil seed banks and regeneration of Tropical rain forest from Milpa fields at the Selva Lacandona, Chiapas, Mexico. *Biotropica* 28(2):192–209.
- Raunkaier, C. 1934. *The Life forms of Plants and Statistical Plant Geography*. Oxford, UK: Clarendon.
- Rhoades, C. C., and Coleman, D. C. 1999. Nitrogen mineralization and nitrification following land conversion in montane Ecuador. *Soil Biology and Biochemistry* 31(10):1347–1354.
- Rhoades, C. C., Eckert, G. E., and Coleman, D. C. 1998. Effect of pasture trees on soil nitrogen and organic matter: implications for tropical montane forest restoration. *Restoration Ecology* 6(3):262–270.
- Risser, P. G. 1987. Landscape ecology: state of the art. In *Landscape Heterogeneity and Disturbance*. *Ecological studies* 64, ed. M. G. Turner, pp. 123–145. New York: Springer-Verlag.
- Sarmiento, F. O. 1997. Arrested succession in pastures hinders regeneration of Tropandean forests and shreds mountain landscapes. *Environmental Conservation* 24(1):14–23.
- Serrao, E. S. A., and Toledo, J. M. 1990. The search for sustainability in Amazonian pastures. In *Alternatives to Deforestation: Steps Toward Sustainable Use of the Amazon Rain Forest*, ed. A. B. Anderson, pp. 195–214. New York: Columbia University Press.
- SAS User's Guide: Statistics. 1985. Version 5th edition. Cary, NC: SAS Institute.
- Singh, K. D. 1993. The 1990 tropical forest resources assessment. *Unasylva* 174:10–19.
- Skole, D., and Tucker, C. 1993. Tropical deforestation and habitat fragmentation in the Amazon: Satellite data from 1978 to 1988. *Science* 260:1905–1910.
- Staver, C. 1990. Why farmers rotate fields in maize-cassava-plantain bush fallow agriculture in the wet Peruvian Amazon. *Human Ecology* 17(4):401–426.
- Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16:284–307.
- Thomlinson, J. R., Serrano, M. I., del M. Lopez, T., Aide, T. M., and Zimmerman, J. K. 1996. Land-use dynamics in a post-agricultural Puerto Rican landscape (1936–1988). *Biotropica* 28:525–536.