MODELING TREE GROWTH AND SEEDLING RECRUITMENT IN A SELECTIVELY LOGGED TEMPERATE FOREST

By

Meng-Hsueh Yu

A dissertation submitted to the Graduate Faculty in Biology in partial fullfilment of

the requirements for the degree of Doctor of Philosophy,

The City University of New York.

2012

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

Date

Chair of Examining Committee
Dr. Charles M. Peters
The New York Botanical Garden

Date

Executive Officer
Dr. Laurel. Eckhardt

Dr. Charles D. Canham
Cary Institute of Ecosystem Studies

Dr. Joseph W. Rachlin
Lehman College, CUNY

Dr. Dwight Kincaid
Lehman College, CUNY

Dr. Maria Uriarte
Columbia University

Supervising Committee

THE CITY UNIVERSITY OF NEW YORK

ABSTRACT

MODELING TREE GROWTH AND SEEDLING RECRUITMENT IN A SELECTIVELY LOGGED TEMPERATE FOREST

By

Meng-Hsueh Yu

Adviser: Dr. Charles M. Peters

Single-tree selection logging is similar to “background” tree mortality of individuals in unmanaged hardwood forests, and is believed to be suitable for shade-tolerant species in smaller areas of woodland. However, few studies have specifically evaluated this method for improving quality and controlling stocking of the residual stand necessary for sustained yields. In my dissertation study, I used likelihood methods and model selection to (1) quantify the effect of competition on tree growth, and (2) quantify the dispersion and abundance of tree seedlings following single-tree selection. My study system is a secondary oak-mixed forest in New York’s Catskill Mountains, USA.

In the tree growth results, models that treated neighbors as equivalent in their competitive effects were the most parsimonious for the four species studied due to insufficient neighbor numbers of any given species. One exception was eastern white pine, whose best model estimated separate competition coefficients for all five species of neighbors. I found most species had strong size-dependency in potential growth in the absence of competition. Furthermore, I found strong asymmetries in competitive interaction. Red maple and eastern white pine had strong crowding effects on three oak species, while oak species had little effect on the former.

I used inverse modeling to parameterize fecundity and seedling dispersion functions for red maple, which showed seedling dispersion is local. New recruits were predicted to have a high likelihood to fall beneath the canopy of the parent tree. Seedlings were dispersed away from the parent tree and located within the 20m mapping distance. Recruitment limitation can have substantial and long-lasting effects on community composition and dynamics. My results suggest seedling recruitment is a complex process involving multiple components for consideration.

Overall, my findings highlight the predicted change of residual composition within stands after removal of different species and tree sizes. It is recommended that both eastern white pine and red maple be removed gradually to stimulate growth of residual oak stock. Based on research at Camp Deerpark Forest, it is recommended that other private landowners in the Catskills apply the single-tree selection method for optimal woodland management.

ACKNOWLEDGEMENT

This dissertation would not have been possible without the help and encouragement of many individuals with whom I interacted on a daily basis.

Dr. Charles M. Peters has been a strong and supportive adviser to me throughout my graduate school career. I am grateful to him for introducing me to the manger of Camp Deerpark, Mr. Ken Bontrager, and suggesting Camp Deerpark forest as my study site. Dr. Peters has always given me great freedom to pursue my research work independently. He showed great patience and inspired me to continue onward when I almost quit the degree in the past year. He helped me outline a timetable for completion and helped manage my time so that I could continue teaching while writing my dissertation at same time. In reviewing my work, he offered painstaking insights and comments in both ecology and forest management while still respecting my voice. For all this, I hold much appreciation for him.

I would also like to acknowledgement the advice and guidance of Dr. Charles D. Canham. I believe that I would not have been able to complete my PhD without him. He helped me tremendously from the very beginning to think about the scientific questions and experimental designs that I raised in this dissertation through the use of R programming training. The major experiment materials for this study, including tree increment borer, camera, software and other equipment, was provided by Dr. Canham. I feel fortunate to have been his apprentice during my doctoral studies. Dr. Canham's

concern for graduate training and the future of the discipline, his strong opinions and his willingness to share them, have been great assets to me. Overall, Drs. Peters and Canham have engaged my ideas, invested considerable time (which is scarce), and energy (which is abundant) on my graduate research. I appreciate their support.

I also thank the members of my graduate committee for their guidance and suggestions, especially Drs. Maria Uriarte and Jeseph Rachlin. I had learned statistical modeling in ecology and evolutionary biology, including likelihood methods, model selection and R programming training, from Dr. Uriate's class at Columbia University. I thank her and Dr. Canham for waiving my tuition fee and allowing me to sit and learn in Dr. Uriate's ecology workshop in 2008. Dr. Uriarte offered a lot of input and helpful suggestions in my dissertation. I appreciate Dr. Rachlin for his practical advice, encouragement, and financial assistance by affording me the opportunity to work as an adjunct lecturer at Lehman College over many years. I appreciate his encouragement. I remember that Drs. Rachlin and Peters hosted a special meeting to encourage me to finish my degree. I appreciate them. I also thank Dr. Kincaid for supplying scholarships that waived my tuition for several years. I thank him for his comments in my both qualifing exam and defense examination. I also thank the graduate center, CUNY, for supporting me with fellowships.

I thank the Camp Deerpark board, camp manager Ken Bontrager, staff, and the Bontrager family for their generous hospitality, for the use of the facilities, and for providing accommodation, food and temporary volunteers in summers. I thank Ken's wife, Deborah, their six children, and Deborah's parents for their warm welcome when I stayed at the camp in summers. I thank the Camp Deerpark volunteers, especially Ken's oldest son, Malachi Bontrager. Malachi worked very hard for me in my early field work in the forest while he was still a teenager. Working at the camp independently or with staff and volunteers together has been one of the great and enjoyable work experiences of my graduate career.

Several individuals deserve special mention for their contributions to this dissertation. I thank my best friends Chingyi Tsai and Chung-Tsai Lee, who assisted in field data collection and intellectual support. I believe that my field experiments in the forest would not have been able to go as smoothly or timely without their assistance for two summers. Also, they have encouraged me to pursue my dreams since I met them. They have been a wonderful source of advice and encouragement for me. I treasured all precious moments we shared.

Athena Tiwari and Jack Henning have played a significant role in helping to complete this dissertation. They both were my main proofreaders and helped polish my writing, and offered helpful discussions. Although they both work as graduate students and adjunct lecturers, they still took time from their busy schedule to help me out. Their help is tremendous, particularly in the past few months. I met Athena when I first enrolled in the graduate program and she has been a great friend ever since. I knew Jack when Dr. Rachlin invited him to give a presentation in phylogeny class in my first year at

CUNY. I shared an office with him and he was always willing to listen when I needed to talk. He is very sweet and always gave me some surprises for special events.

Several friends also proofread my drafts, poster and powerpoint slides over these many years. They are Ana G. Ribeiro, Diane Gharbaran, Haiyang Lu, Louis Putzel, Mike Baxter, Rena Quinlan, Ryan Huish, Vinson Doyle and William Perez. In particular, I thank Haiyang and Louis for always having a good word and a friendly greeting. I treasured all precious moments we shared. Furthermore, I want to thank Dr. Yiching Lin for her encouragement and suggestion to contact Dr. Canham as an adviser outside the campus to guide my study. Dan Flynn at Columbia University helped me resolve errors in R code writing during his work as a teaching assistant. Hannah Stevens at the New York Botanical Garden helped with GIS mapping.

I also gratefully acknowledge the department of biological sciences at Lehman College for offering me the opportunity to teach Anatomy and Physiology. I thank Dr. Maryam Bamshad, the course coordinator, for her teaching support. My former and current students have been an enormous asset. I have learned teaching, communication, and class managing skills from Dr. Bamshad and these students. These teaching experiences have boosted my confidence in giving a talk in public. I also thank Christine West, Dolores Vitanza, Mike, Tony Pappantoniou, and Patricia Carver in the department for administrative assistance, teaching material preparation and friendly greetings. Teaching at Lehman College has been one of the great learning experiences and enjoyable work experiences of my graduate career.

In addition to the good friends I mentioned above, I also want to thank the many good friends that I have made in the Bronx for their support throughout my time in graduate school at CUNY. They are Alejandra Vasco, Anlin Chen, Bob Lupo, Chin-I Chen, Elsa Meza, Hanbin Dan, Jason Kung, Jing Zhou, Kuo-Hsiang Huang, Judith Fitzgerald, Ruei-Shi Tuo, Paula Gore, Suying Yang, Vanya Petrova, Ulyana Muñoz-Acuña, Yayi Huang, Yunghsuan Huang, and Ziping Lieu. I particularly thank Elsa, for her very sweet and warm care; she acted like a sister or a mother to me. I owe a special debt to Ruei-Shi for lending me his Kindle as I reviewed literature and wrote this dissertation.

My deepest gratitude goes to my family for their unconditional love and support through my life; this dissertation is simply impossible without them. I am indebted to this day for all their care and love. As a typical father and mother in a Chinese family, they worked industriously to support our family and spared no effort to provide the best possible environment for us to grow up and go to school. They have never complained in spite of all the hardships in their lives. I have no suitable words that can thoroughly describe their everlasting love to me. I would like to thank you, my siblings, especially my eldest sister, Ming-Fen Yu. She has been a role model for me to follow unconsciously when I was a teenager and has always been one of my best counselors. I remember her constant support when I encountered difficulties. I also thank Shuhsuan Hu for her prayers for me in the past years. I also thank my two cats, MewMew and BoBo, for their company. Without their unconditional love, I would not have finished the degree.

Lastly, I offer my regards and blessings to all those beings that have supported me in any way during the completion of this dissertation.

Table of Contents

LIST OF TABLES

LIST OF FIGURES

CHAPTER ONE

INTRODUCTION

This chapter provides a brief review of important silvicultural terms related to my dissertation research, the history of silviculture, and recent ideas of how a shifting paradigm has impacted the silvicultural discipline. The chapter further reviews how new analytical tools, such as model selection and likelihood methods, can help silvicultural research to face the challenges of managing and maintaining structurally-complex stands.

1.1 Traditional Silvicultural Terms and the Role of Forest Management and Silviculture

Forests are long-lived, dynamic biological systems that are continuously changing with a slow and multistage process. Human-induced changes in forests by exploitation for wood production have influenced forest succession and further changed the face of many forest landscapes across the globe over centuries (Vale 1982, Perlin 1989, Kohm and Franklin 1997, Hall et al. 2002). This trend is unavoidable, and it is generally thought that sound forest management and carefully designed silvicultural treatments can improve the productivity and value of forest stands, maintain vigor and desired composition and stand structure, and achieve the landowner’s objectives in a managed forest (Leak and Sendak 2002).

Forest management objectives and silvicultural practices are often intertwined (Hann and Bare 1979, Hummel 2003). Forest management is a branch of forestry that concentrates on decisionmaking, planning, and applying scientific, economic, legal, and social principles to the administration and working of a designated forest area to achieve the landowner's specified objectives (Nyland 2007). It is often necessary to project these changes under current and future resource conditions in order to obtain relevant information for sound decision making.

Silviculture (*silva* = forest; culture, as in growing) is both a science and an art of focus on woody vegetation manipulation through control of stand establishment, growth, composition, quality, and structure of forests or woodlands in light of silvics and forest ecology, which is modified by economic and social considerations (Daniel et al. 1979, Smith 1986, Helms 1998, Nyland 2007, Puettmann et al. 2008). Silvics, which was synonymous with forest ecology until the 1960's (Toumey and Korstian 1937, Spur and Barnes 1964), is the foundation of silviculture and focuses on the ecological principles underlying of how trees grow, reproduce, and respond to environmental changes (Nyland 2007). Most definitions of silviculture include the concept of achieving the goals of landowners and of society, e.g. (Daniel et al. 1979, Smith 1986, Helms 1998, Nyland 2007). Silviculture applies a series of individual practices for creating, altering, and maintaining essential components and structures to make forests more productive and more useful to a landowner on a sustainable basis. These individual practices include genetic improvement, site preparation, promoting natural regeneration, planting, fertilization, release, thinning, and final harvest of individual trees or stands based on diameter or age (Daniel et al. 1979, Ledig and Smith 1981, Fujimori 2001, Nyland 2007).

1.2 Development of Silvicultural Systems

A silvicultural system is rooted in the principles of silviculture and reflects the forest managers' concept of how they control, facilitate, protect, and salvage different tree species within a stand by a planned program of treatments and processes based on integrated resource management goals (Smith 1986, Nyland 2007). The systems are classified either as even- or uneven-aged, primarily according to the regeneration methods used or by the number of tree age classes that result from treatment (Davis 1966, Matthews 1989).

A "stand" is defined as a spatially continuous community or group of trees growing together in a relatively uniform age and size class distribution, structure, composition and soil condition, which foresters can effectively manage as a unit (Oliver and Larson 1990, Kohm and Franklin 1997, Spies 1997, Helms 1998, Nyland 2007). Stands containing trees of a single cohort or one age class of regeneration that develop under full-light conditions are silviculturally classified as even-aged. Typical characteristics of even-aged stands are a narrow range of tree ages with one or two distinct and well-represented age classes with regeneration established relatively synchronously within a short period following a major disturbance. The even-aged silvicultural systems are subdivided into the clearcutting, shelterwood, or seed-tree systems.

Stands containing trees of a mixture of three or more distinct, well-represented age classes that develop with significant interaction with surrounding trees of different ages are classified as uneven-aged. In these uneven-aged silvicultural systems, mature or immature trees can be removed either as single, scattered individuals ("single-tree selection") or as small groups of individual trees ("group selection") (Davis 1966, Hann and Bare 1979, Matthews 1989). In some cases, foresters may simply use the term partial cutting, selection logging, or selection system to represent something other than clearcutting. Both types of selection logging open a similar amount of area for regeneration although the sizes of each forest opening are different (Nyland 2007). They both allow seedlings to germinate and grow in the space provided by the tree removal. In single-tree selection silvicultural system, foresters remove individual mature trees more or less uniformly across a stand and create small canopy openings (Nyland 2007). It is best suited for seedlings that propagate well in poor light under a forest canopy, such as those of sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.) in the U.S. northern hardwood forest regions. Group selection system creates relatively larger canopy openings in the canopy than single tree selection and, thus, benefits seedlings, such as black cherry (*Prunus serotina* Ehrh.) and white ash (*Fraxinus americana* L.), that propagate well in partial shade beneath the forest canopy (Yahner 2000). Both single-tree selection and group selection systems can maintain uneven-aged forest.

Even- and uneven-aged silvicultural systems have been applied to forests across the globe for centuries (Hann and Bare 1979, Nyland 2007). Changes in economic and operational considerations and in public attitudes, perceptions and goals have produced changes in silviculture. Conflicts often arise between political and social pressures, public involvement, economics, and inherent biological limitations. A compromise, therefore, is needed within the bounds of biological feasibility. These issues become a central theme in the changes sweeping forest management between even and uneven-aged silvicultural systems (Kimmins 1991, Buse et al. 1995, Curtis 1998).

Each silvicultural regeneration method serves a purpose. Clearcutting is an efficient system with lower costs for timber harvesting than other silvicultural systems, and it has proven successful for regenerating stands of desirable, shade-intolerant tree crop species (O'Hara 2001). However, clearcutting in even-aged silvicultural systems has been controversial since at least the 1960’s, and is often blamed for the lack of stand variability in the form of spatial patterns, species composition, density, and vertical structure, and for the high degree of environmental disturbance used by this regeneration method.

A milestone in capturing the global public attention was the publication of the Brundland report, “Our Common Future” (WCED 1987), whose central principle of sustainable development gained general acceptance. Indeed, whereas forest management in the 21st century still includes wood production to achieve sustained yield, the emphasis now is on managing forest diversity accompanied with multiple, complex objectives, including the improvement of the visual appearance of plantations, maintenance of specific levels of ecosystem processes, the protection of soils and water resources, maintenance or improvement of wildlife habitats, encouragement of regeneration/species diversity, and variability and integrity across the landscapes (Kohm and Franklin 1997, Nyland 1998, O'Hara 2001, 2002, Nyland 2007).

In response to criticisms of clearcutting, the interest in uneven-aged silviculture has been increasing as in many parts of the world (O'Hara 1998, 2001, 2002, 2009). Selection silvicultural systems were thought to be less damaging to the environment than even-aged systems since they offered a form of disturbance that corresponded more similarly to the patterns of nature. For example, for forest stability, foresters create the desired residual diameter distribution with each entry to a stand without dramatically changing forest structure and the composition of flora and fauna in the stand. However, although these uneven-aged systems are capable of achieving the multiple expectations of forest management, they are extremely difficult to implement, and in many cases represent an unattainable ideal (Mayr 1907, O'Hara 2002) . Foresters are now evaluating the effectiveness of uneven-aged silvicultural regeneration methods as an alternative to even-aged methods (O'Hara 1998, 2001, 2002, 2009). They continue to search for new ideas and approaches to develop procedures that provide flexibility for different management objectives and enhance the sustainability of forest treatment.

The single-tree selection system is probably the only silvicultural system that could be used to create small openings suitable to shade-tolerant species, instead of shade-intolerant species (Miller and Smith 1993a, b, Kohm and Franklin 1997, Miller et al. 1998, Leak and Sendak 2002, O'Hara 2002, Nyland 2007). Over time, diversity in such a forest would decline, as shade-intolerant species die out. Selective logging removes relatively few trees at a time and the growth of shade tolerant species replenishes the number of individuals moving out of each diameter class. Isaac (1956, 1967) showed that the single-tree, partial cutting system would not favor regeneration of shade-intolerant Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) in the Pacific Northwest and would lead a forest type shift to species components with more tolerant species (Isaac 1956, 1967). Similar results have been reported for other species and forest types (Curtis 1998, O'Hara 2002, 2009).

While single-tree selection has been compared to the natural gap disturbance regime in unmanged old-growth hardwood forests (Runkle 1982, Pickett and White 1985, Smith et al. 1997, Nyland 2007), it is more similar to “background” tree mortality of individuals (Canham pers. comm.). The regulated single-tree selection system must take into consideration both age-classes and species, giving rise to a selection system that does not remove a single tree without taking into consideration its reproduction and its relation to the future crop (Miller and Smith 1993a, Nyland 2007).

Single-tree selection methods have been designed to be applied to the regeneration of secondary forests, to rehabilitating degraded stand structures, and for abandoned agricultural lands that are overwhelmed by eastern white pine in northern USA (O'Hara 2002, 2009). It is also suitable for smaller areas or strips of woodland, and allows the landowner the flexibility to select species to be harvested based on the market value of the timber. The single-tree selection system needs careful planning, and frequent, light cuttings to ensure protection of regeneration and residual trees. With new understanding of the importance of disturbances in affecting stand structures, and the development of complex mixed-species and multi-aged stands, this knowledge will aid foresters to develop new ways of managing these stands (O'Hara 2002).

1.3 Challenges to Traditions in Silviculture

Foresters in both forest management and silviculture rely heavily on either silvics or forest ecology to aid decisions about how they can management forests in an efficient way and predictable way. Therefore, the interpretation of ecological concepts about the forest in forest ecology is more likely to from a management-oriented perspective (Kimmins 2004, Puettmann et al. 2008). For example, silvicultural treatments are often applied at the stand scale and over as a wide a range of sites as possible (Helms 1998). As such, early writing in forest ecology placed emphasis on the ideas of homogeneous stands instead of the importance of heterogeneity at different spatial and temporal scales. This leads only to stand levels of organization rather than all levels of organization (Puettmann et al. 2008).

In addition, some objectives and disciplines of silviculture influence establishment of the discipline of forest ecology. Puttmann et al. (2008) summarized five cores principles that have formed the basis of silvicultural thinking, study, and practice: (1) a dominant focus on trees (other components of forest ecosystems such as other plants, animals, and ecosystem processes were considered only in terms of their impact on individual tree survival and growth); (2) conceptualizing stands of spatially continuous groups of trees as uniform management units; (3) applying the same agricultural approach that was previously developed to maximize farm crop yields to the approach of silvicutural research; (4) the spatial scale-independent view of silvicutural practices; and (5) a strong desire for achieving orderly and predictable forest development . These principles have had a very influential impact in the development of both silvicultural and forest ecological researches and their implememtation.

Seymour et al. (2006) divided the history of silvicultural research in the United States into three time periods, which include the era of selective cutting (1925-1960s), the era of production forestry (1960-1990s) and the era of ecological forestry (1990-present) . In both the selective cutting era and the production forestry era, research moved towards a more agrarian model for silviculture, including practices that became increasingly dissimilar from natural processes (O'Hara 2009).

Kimmins (1991) described forestry as moving from an early, unregulated, exploitive stage, through a centralized administrative stage, to a stage in which forest management has become increasingly ecology-based, including ecological site classification, ecology-based tree crop species selection, conservation of the tree crop gene resource and an increasing concern for wildlife, fish, recreation, and landscape aesthetics. Today, rapidly changing forest management paradigms emphasize the creation and maintenance of structural diversity at the stand level to provide for biodiversity and assure long-term sustainability (O'Hara 1998, Seymour 2004). The methods and techniques applied by silviculturists to manage forests are frequently challenged by an incomplete knowledge of ecosystem processes as well as financial pressures that lead to unsustainable harvesting (O'Hara 2001, Puettmann et al. 2008).

Since “silviculture is to forestry as agronomy is to agriculture” (Smith et al. 1997), silvicultural research draws heavily from agricultural research techniques, particularly in experimental design and analytical methods (Puettmann et al. 2008). Starting in the late 1920s, the US Forest Service established large-scale silvicultural experimental forests, which were treated with a scientific research approach (Seymour et al. 2006). The British statistician, Sir R. A. Fisher, first developed the experimental design and analysis of variance (ANOVA) for agronomy (Yates 1964). By the 1940s, some of Fisher’s principles were applied to silvicultural research, which were influenced by traditional statistics (Seymour et al. 2006). These include minimizing the variation of any external factors that might influence experimental treatments, using null hypothesis testing to identify a “best treatment”, and emphasis on treatment-unit scale analysis of mean responses. However, these designed agricultural experiments cannot show ecological processes, and questions frequently arise about whether limited sample size, high variability in study conditions, or experimental constraints are responsible for the results when analyzing data from studies that are based on an agricultural research model; as a result, classical hypothesis testing rarely lead to an improvement in management practices (Puettmann et al. 2008). Puettman et al. (2008) analyzed the discipline of silviculture in relation to ecology and complexity science, and suggested that novel approaches that incorporate aspects of variability and uncertainty into management decisions are needed to respond to the new demands on silviculture in the twenty-first century.

1.4 New Analytical Tools Applied in Silviculture

In response to the rapidly changing demands and expectations on silviculture, and the global paradigm shifts in how forests are viewed, scientists and foresters have begun to embrace new methodologies in silviculture. These new tools address ecological questions related to processes, disturbance, variability, scale, and diversity through the use of innovative statistical techniques and quantitative models to predict the future behavior of some aspects in regard to their management (Kobe and Coates 1997, LePage et al. 2000, Canham et al. 2003, Clark 2003a, b, Coates et al. 2003, Canham et al. 2004, D'Amato and Puettmann 2004, Canham et al. 2006, Coates et al. 2009). With increases in computing power and improved computer capabilities, it has become far easier to estimate ecological models using model selection and comparison. These can be tested with likelihood methods and parsimony to compare the strength of evidence of competing models for making biological inferences (Johnson and Omland 2004, Canham and Uriarte 2006).

Model selection is grounded in likelihood theory and a set of reasonable competing hypotheses are simultaneously selected and evaluated (Johnson and Omland 2004). In model selection, the first step is to generate biological hypotheses and to transfer these verbal hypotheses to meaningful mathematical equations. Variables in the model should correspond to causal factors represented in the verbal hypothesis. The second step is to select appropriate functions define the relationship between independent variables and the response variable in terms of mathematical operators and parameters. The third step is to define the error structure of the model. One hypothesis might be depicted by two or more models, including different error structures, which may lead to an increase in the number of working hypotheses.

After a set of candidate models is created and specified, the analysis proceeds by fitting each candidate model to the observed data using a (log) likelihood calculation with maximum likelihood estimates (MLE) of the parameters of the model. The next step is to select the best model, supported by observed data from a set of candidate models. Once a best model is identified, the final step involves evaluation of the model by goodness of fit test, which tells how well the data are modeled by that distribution (Johnson and Omland 2004, Canham and Uriarte 2006).

The Akaike Information Criterion (AIC) is a criterion that enables inference to select a model from a set of models simultaneously, so that researchers can consider a best supported model or best set of similarly supported models. The researchers identify one candidate model with the minimum AIC value as a best model (Akaike 1973). AIC can also be used to rank competing models and to weigh the relative support for each one. The AIC is defined as:

$$\text{AIC} = -2(\text{maximized log likelihood} - \text{number of parameters in the model}).$$

This penalizes a model for having too many parameters. AIC serves the purpose of model comparison only, and it does not provide diagnostics about the fit of the model to the observed data. AICc is AIC with a correction for small sample size by increasing relative penalty for model complexity with small data sets (Burnham and Anderson 2002).

Maximum likelihood is the procedure of finding the value of one or more parameters that maximize the probability (likelihood) of the sample data. Likelihood is a central feature for model selection (Hobbs and Hilborn 2006). Parameter values associated with the maximum of the likelihood function are termed the maximum likelihood estimates (MLE) of that model (Burnham and Anderson 2002, Johnson and Omland 2004, Canham and Uriarte 2006).

The likelihood method approach and model selection is different from traditional hypothesis testing and has three primary advantages: (1) it deals with more than one hypothesis at the same time via appropriate distribution of the errors to calculate likelihood and model comparison; (2) models can be ranked from the best to the poorest support for each hypothesis; and (3) Akaike weights in model selection provide a basis for model averaging and can be used to make robust parameter estimates and predictions if more than two competing hypotheses have similar levels of support (Johnson and Omland 2004, Canham and Uriarte 2006, Puettmann et al. 2008).

Model selection is widely accepted and well developed in molecular systematics, molecular evolution, survival rates in mark-recapture studies, and landscape ecology (Johnson and Omland 2004). Recently, model selection and likelihood methods have provided robust parameter estimates for competitive interactions among canopy trees in tree growth and survival in several studies (Canham *et al.* 2004, Uriarte *et al.* 2004a, Uriarte *et al.* 2004b, Canham *et al.* 2006, Papaik and Canham 2006), thus justifying their use in the field of silvicultural management.

1.5 Organization of Thesis

There are several objectives of this study: (1) providing the possibility of quantitatively linking ecological theory to single-tree selection systems by using new analytical tools including model selection and maximum likelihood methods; (2) understanding the effects of tree competition on tree growth following single-tree selection logging; (3) understanding seedling dispersion patterns following selection logging; (4) an evaluation of selection logging in improving quality and controlling stocking of the residual stand necessary for sustained yield of desired species.

Chapter Two describes my study site - Camp Deerpark Forest - in terms of its locality, topography, geology and soil, regional climate, and vegetation. In addition, I address recent land-use history at Camp Deerpark Forest, and the development of its single-tree selection management system.

Chapter Three presents one core topic of my dissertation research, i.e., how crowding might slow the growth of surviving trees. I employed a likelihood method approach, and model selection techniques to understand tree radial growth at a neighborhood scale in forest structures following single-tree selection system. The general objective of this study is to assess competitive influences and responses on tree radial growth across co-occurring tree species following by single-tree selection at Camp Deerpark Forest.

Chapter Four focuses on the other core topic of my dissertation research, i.e. how a single-tree selection system influences the spatial distribution of seedlings in red maple *(A. rubrum* L.). I employed spatially-explicit techniques, inverse modeling methods, and model selection to analyze the effects of the single-tree selection silvicultural practice on the seed shadow dispersal curves in red maple. The objective in this study is to explore variation in seedling dispersion of red maple, the most common tree species in forests of the eastern U.S.

Chapter Five is the last chapter, and describes the implementation of a single-tree selection method in Camp Deerpark Forest. The chapter works as a platform to explain the implications of my research, and offer suggestions for the maintenance of forests in a suitable mode along with future directions for forestry research. The objective of this chapter is to present the forest management experience at Camp Deerpark Forest and to evaluate harvest impacts on both tree growth and seedling dispersion pattern based on my findings.

CHAPTER TWO

STUDY AREA

My dissertation research was conducted at Camp Deerpark Forest (CDF), nestled in the lower Shawangunk Mountains, southeastern New York (USA) at 41º29'N, 74º35'W. It is located in Westbrookville, southwestern corner of Orange County, 80 miles northwest of the New York metropolitan area, and is close to the borders of Pennsylvania and New Jersey (Figure 2.1).

2.1 Terrain, Geology, Climate and Soil Type

CDF is bounded by the lower ridge line of the Shawangunk Mountains and the Delaware, Neversink, and Mongaup Rivers. The elevation ranges from 240 m above sea level to 400 m above sea level at the highest upland within a short distance (240-400 m elevation).

The climate is the humid continental type, which prevails in the northeastern United States. The average annual mean temperature is about 10°C (49.46°F). In January, the average mean minimum temperature is approximately -9°C (15.5°F). The average annual mean precipitation is about 1214 mm (47.8 inches) with a fairly uniform distribution of precipitation during the year (Figure 2.2, 1995-2006, Port Jervis Station). Winters are

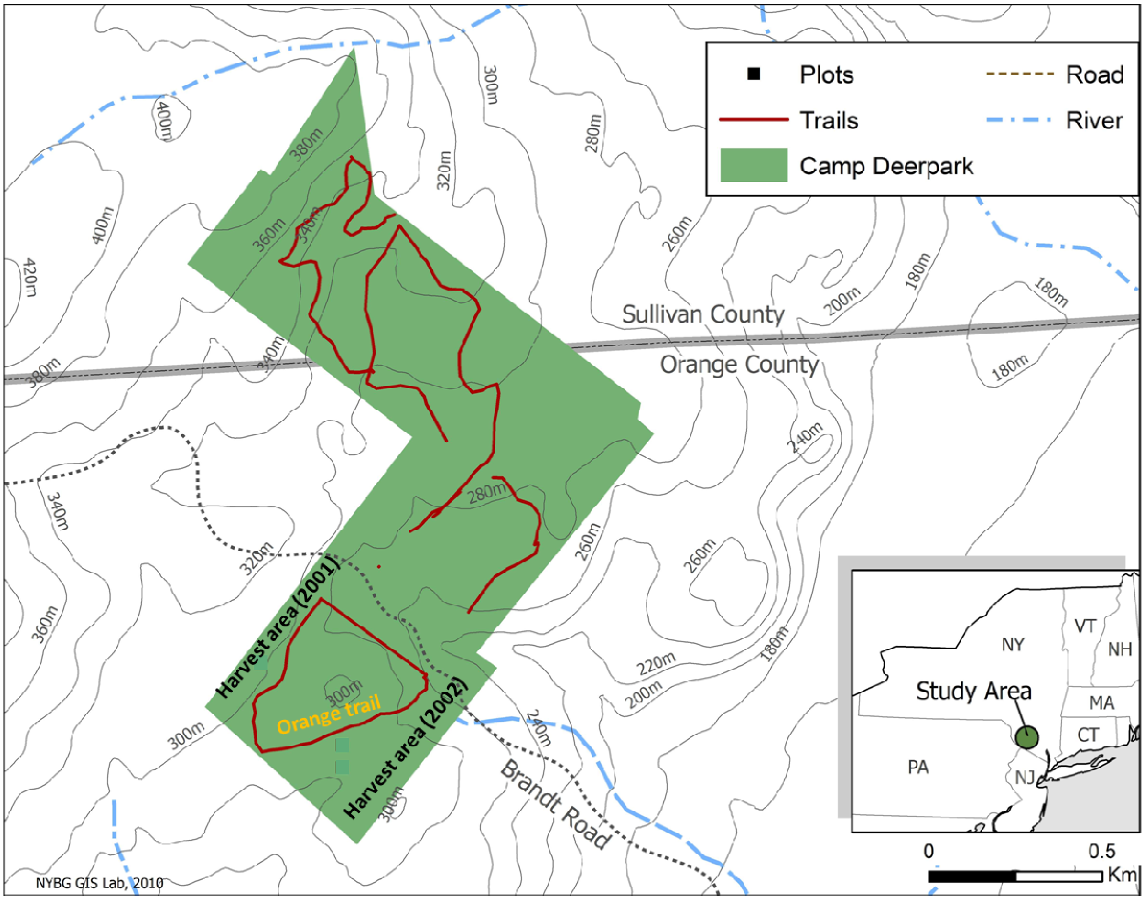

Figure 2.1. Location of the study area at Camp Deerpark Forest in New York State, USA.

cold and snow is common, persisting up to 4 months, and snowfall occurs from December to March. Climate data was extracted from URL at http://cdiac.ornl.gov/cgi-bin/broker?_PROGRAM=prog.climsite_monthly.sas&_SERVICE=default&id=306774.

Soils at CDF are a mix of Swartswood sandy loam (SxC) and Mardin gravelly silt loam (MbB), very stony on the surface and shallow over bedrock, moderately well to well drained. These mixed soils were formed from glacial till deposits on hill crests, hilltops and ridges in uplands, and have fragipan, an altered dense subsurface layer of hard soil

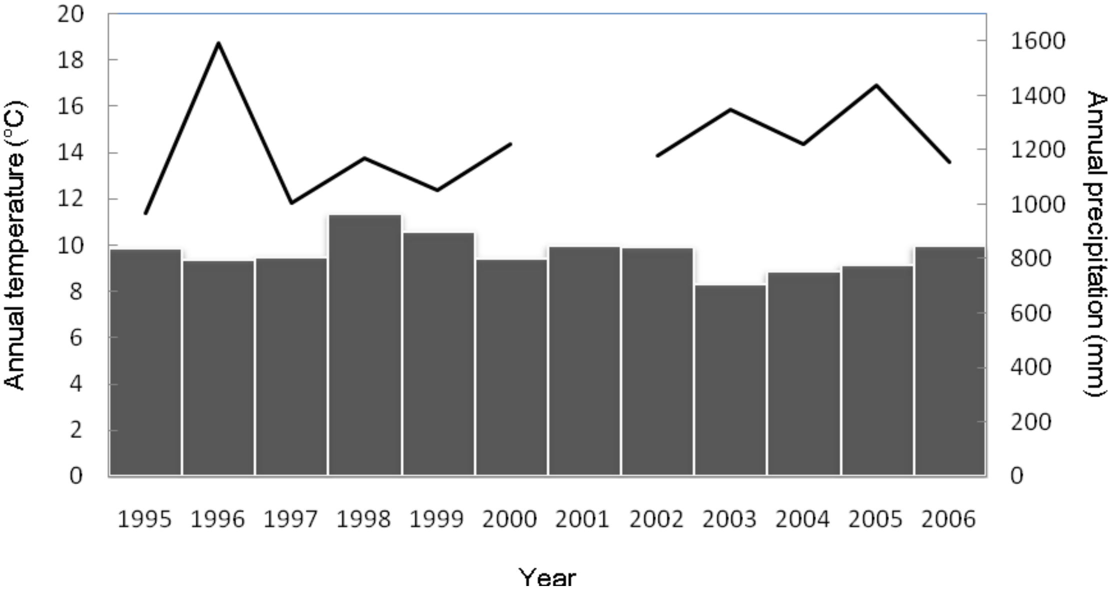

Figure 2.2. Annual temperature (histogram) and precipitation (line) from 1995 to 2006 at the Port Jervis Station, the closest weather station to Camp Deerpark Forest in New York State, USA.

that restrict water flow and root penetration. They have a lower slit content and higher sand content. Also, a few spots are somewhat poorly drained Wurtsboro soils or somewhat poorly drained Erie soils (Olsson 1981). Slopes range from 0% to steep slopes with a grade of 15% or more (Town of Deerpark Town Board 2003)

Natural organic matter content is low at CDF with 15 to 35% gravel or channery fragments mixed with large stones and boulders greater than 25 cm (10 inches) in diameter on the surface. The surface layer ranges from extremely acidic to strongly acidic in the Swartswood soil and extremely acidic to slightly acidic in the Mardin soil. Most of the Swartswood and Wurtsboro soils are not suitable for agriculture because of the large stones on the surface. However, the soils are suitable for timber production of commercial species such as northern red oak, sugar maple, white ash, and black cherry (Olsson 1981).

2.2 Forest Composition and Structure

Forests of this region are classified as a glaciated section of the Oak-Chestnut Forest Region, with the former abundance of chestnut replaced by the present oak-dominated forest type (Braun 1950). Based on the inventory data, CDF forests are dominated by eastern white pine (*Pinus strobus* L.), but with a diverse mixture of tree species with white oak (*Quercus alba* L.), chestnut oak (*Q. prinus* L.), red maple (*Acer rubrum* L.), red oak (*Q. rubra* L.), black oak (*Q. velutina* Lam.), and several species of hickory (*Carya* spp.) (Figure 2.3). Other species present but less common are sugar maple (*A. saccharum* Marsh.), sweet birch (*Betula lenta* L.), American chestnut (*Castanea dentata* (Marsh.) Borkh.), American beech (*Fagus grandifolia* Ehrh.), white ash (*Fraxinus americana* L.), blue ash (*Fraxinus quadrangulata* Michx.), butternut (*Juglans cinerea* L.), black walnut (*Juglans nigra* L.), black gum (*Nyssa sylvatica* Marsh.), pitch pine (*Pinus rigida* P. Mill.), black cherry (*Prunus serotina* Ehrh.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.). Oaks, and eastern white pine are known to reach greatest abundance on more xeric sites (Burns and Honkala 1990). Among the tree species, the species from most to least shade tolerant are American beech, eastern hemlock, red maple, white ash, red oak, and eastern white pine (Canham et al. 2006). Red maple, and white oak were classified as secondary species (Halkard E. Mackey and Sivec 1973). Shrubs common throughout the study area

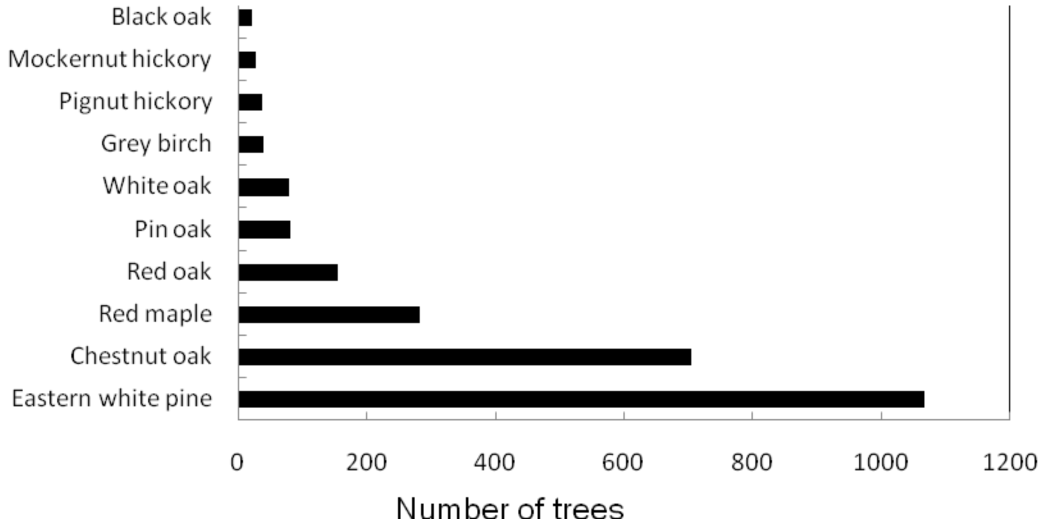

Figure 2.3 Abundance of top ten species in transect data at Camp Deerpark Forest, New York State, USA. The Inventory data was recorded for all species in 10% of the total area of 48 hectares.

are American witch hazel (*Hamamelis virginiana* L.), black huckleberry (*Gaylussacia baccata* (Wangenh.) K. Koch), lowbush blueberry (*Vaccinium pallidum* Ait.), and mountain laurel (*Kalmia latifolia L.*) (Camp Deerpark, unpublished).

The forestry survey group at CDP conducted a quantitative forest inventory before marking and harvesting trees in the forest. The inventory was conducted in 10% of the total area of 48 ha. All woody stems ≥ 10.0 cm in diameter at breast height (dbh) were identified, recorded, and measured for diameter. The transect data contained 2,612 stems from 30 woody species (Camp Deerpark, unpublished).

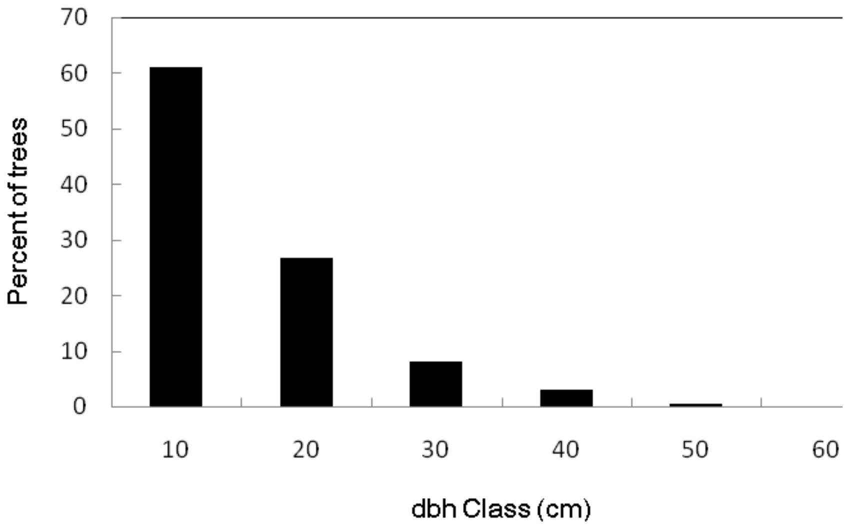

Figure 2.4. Distribution of trees by diameter (dbh) in transect sample at Camp Deerpark Forest, New York State, USA.

The diameter distribution of trees at CDF presents a reverse-J distribution with many small trees and a decrease in the number of large trees when the diameter increases (Figure 2.4). This reverse-J pattern is caused by the presence of many small eastern white pine trees. Stem dbh ranged from 10.0 to > 60.0 cm and stem density was 544 stems per hectare for stem dbh ≥ 10.0 cm. The largest-diameter trees were eastern white pine, eastern hemlock, and several of the oak species (Camp Deerpark, unpublished).

2.3 Land-Use History

The 100 ha CDF has a complex land-use history spanning more than three centuries. CDF was enveloped by forest before the 1860s. When the farm was plowed in the 1860s, settlers removed the rocks scattered over the landscape. As topsoil eroded, more rocks would be forced out of the subsoil and into the farmland. Farmers used these granite stones to build their own stone walls as boundary lines to animal fencing and to keep patches of forest discrete. They primarily planted corn, oats, rye, wheat and other agricultural crops (Foster et al. 1998).

By the 1930s, farming was abandoned and the land turned into pine forest. The CDF forest has not been disturbed by tree felling or farming since the 1960's, when the land was purchased and operated as a non-profit organization by New York City Mennonite Churches. The forest area to the south side of Brandt Road (see Figure 2.1) was logged in 1974, but only the highest-quality and most profitable trees were removed, and little consideration was given to the impact on forest health. After that, the forest grew naturally for two decades until the recent development of the forest management plan.

CDF provides many non-market benefits and outputs, such as ecological and social functions. CDF hosts a variety of church groups for retreats through the year, and is used for recreation such as hiking and camping. Their 10-day sleep-away summer camp education program for inner-city children and youth is another example of income provided from the sustainable use of a forest. CDF also harvests maple syrup as a non-timber forest product during the end-of-winter/early-spring thaw, and collects firewood by hand for campfires, fuel, and to reduce the risk of bushfires. No hunting is permitted in the camp, although there is some deer and turkey hunting on privately owned lands surrounding the camp forest.

A majority of the volunteer sources for these services are from Mennonite Churches. In general, these non-market outputs have direct benefits to the CDF landowners, and result in an interest with regard to the use of forested land in economic, social and ecological settings.

2.4 Recent Forest Management Program Using Single-Tree Selection

The idea of systematic forest management at CDF was raised in the summer of 1996 when Dr. Charles M. Peters of the New York Botanical Garden introduced the principal of sustained yield forestry to the CDF director, Ken Bontrager. The new forestry program received complete support from the CDF board. Since 1997, volunteers and staff have worked as the forestry working group, spending five years on a forest survey before proceeding to harvest timber. They conducted a 10% inventory of all forestland on the property, identified and marked all property lines, identified tree species composition and demography, and produced a map marking trails and roads. Finally, the team combined all this information into a data base to be used for management planning and the estimation of harvest levels.

Recently, the single-tree selection system has been applied at CDF. Single stems were cut in different regions of the forest in 2001, 2002 and 2004, guided by a management plan for sustained-yield forestry and based on the objectives of timber stand improvement (Palmer 2004). The basic principles of selective logging at the CDF include (1) the maximum annual allowable harvest volumes for chestnut oak, red oak, white oak, and eastern white pine must be harvested each year based on inventory and growth data;

(2) there must be at least one conspecific tree near the selected harvest tree to allow the residual conspecific either to grow faster or regenerate new recruits; (3) there must be only one tree removed within the tree fall radius of each harvest tree to produce minimal canopy openings and further inhibit seedling recruitment in eastern white pine; (4) in order to reduce canopy damage to other trees, the direction in which a harvested tree will fall is to be decided before cutting; (5) nest and den trees will be left to provide essential habitat requirements for cavity-using amphibians, reptiles, birds, and mammals; (6) trees with unusually large size, unique shape, unique locations or that are rare in some way or another have the potential to be described as “heritage” trees, and will be conserved; (7) unhealthy, defective, non-commercial species can be cut in order to maintain healthy and vigorous stands (Palmer 2004); and (8) the spatial location data of all harvest trees are entered in an ArcGIS database (Camp Deerpark Management Plan, unpublished).

Foresters at CDF have applied single tree selection to control strictly residual stand stocking and quality for long-term management. They want to use this prudent partial harvest practice to provide periodic income from timber sales, to inhibit large canopy opening from eastern white pine regeneration and growth by a continuous cover of merchantable trees, to provide growing space for residual trees, and to reproduce new shade-tolerant species trees for the future. This is necessary for monitoring the effectiveness of the uneven-aged method of single tree selection in meeting multiple objectives. If objectives are not being met, the forest management plan will be adjusted and adapted. My dissertation work can help them to evaluate the effectiveness of single tree selection in tree growth and seedling recruitment for sustained yield of desired species by using new analytical tools.

CHAPTER THREE

NEIGHBORHOOD ANALYSES OF EFFECTS OF CANOPY TREE COMPETITION ON TREE GROWTH IN A SELECTIVELY LOGGED FOREST

3.1 Introduction

Understanding the nature and role of competitive interactions among co-occurring species provides essential insight into processes structuring the forest community and maintaining species diversity. It is also critical to the development of sustainable management of forest ecosystems, particularly as applied to uneven-aged, partially-harvested silvicultural systems (Coates et al. 2003, Canham et al. 2004, Canham et al. 2006, Papaik and Canham 2006, Coates et al. 2009). In an effort to seek a balance between protecting natural systems and using them to meet societal demands, these low-impact, continuous-cover, uneven-aged and multi-species forest management systems have recently been applied as sustainable alternatives to large clear-cutting, even-aged and single species stands (*eg.* (Miller et al. 1995, Nyland 1998, Bliss 2000, Doyon et al. 2005, Puettmann et al. 2008)).

The popularity of partial harvesting management, however, presents a host of new scientific and silvicultural challenges (Puettmann et al. 2008). By mimicking natural disturbance regimes, trees of different sizes and species are logged and removed. As in a mature forest, removal of different species and tree sizes within a stand creates an almost infinite variety of permutations in residual standing trees. In a partially harvested forest, there is an almost infinite variety of spatial configurations and re-allocation of resources, such as light levels, between a given target tree and its neighbors, caused by the level of removal of different species and tree sizes within a stand (Beaudet et al. 2002).

The implication of the spatial distribution of seed trees selected for retention is profound because it has lasting effects on the future distribution and degree of regeneration, particularly given the limited dispersal distances of most tree species (Ribbens et al. 1994, Clark et al. 1999b, LePage et al. 2000, Greene et al. 2004). From an economic standpoint, it is important to evaluate the degree of release from competition among residual trees. Widespread application of partial harvesting practices, such as single-tree selection methods, can have dramatic effects on the growth and survival of residual trees (*e.g.* (Wimberly and Bare 1996, Berger and Hildenbrandt 2000, Coates et al. 2003, Canham et al. 2004, Papaik and Canham 2006, Coates et al. 2009)). The single-tree selection method is preferred because it is thought to be capable of yielding both periodic income from timber sales and strict control of residual stand quality for sustained yield of desired (shade tolerant) species on small holdings (Miller and Smith 1993b). Unfortunately, quantitative research has lagged concerning interspecific competitive effects on tree growth and mortality following single-tree selection methods (Jones and Thomas 2004, Pedersen and Howard 2004, Wiser et al. 2005).

From an ecological perspective, understanding the role of interspecific variability on a neighborhood process is crucial to the development of realistic forest models. Hubbell's neutral theory of forest ecology (Hubbell 2001) has generated much controversy, partly because of the assumption that all coexisting species have equivalent per capita fitness (e.g. (Chave 2004, Clark and McLachlan 2004)). This debate has highlighted the need for an analysis of empirical estimates of variances of interaction coefficients across competitive hierarchies (Freckleton and Watkinson 2001).

Regression analysis is frequently used for the study of competitive interactions between individual adult trees to assess the growth and survival of individuals as a function of the distribution and abundance of neighbors (Canham et al. 2004, Uriarte et al. 2004a, Uriarte et al. 2004b, Canham et al. 2006, Papaik and Canham 2006, Coates et al. 2009). Competitive interactions play a central role in mediating the establishment, survival, and growth of trees at local neighborhood scales. All these demographic processes are at local neighborhood scales and are well suited to the use of likelihood methods and model selection techniques.

The main objective of this study is to gain insight into the nature of tree competition by quantifying the relative magnitude of competitive interactions among coexisting species. Specifically, I asked the following questions: (1) Are different species of neighboring trees functionally equivalent competitors? (2) What role does neighborhood competition play in radial growth rates? (3) How does the magnitude of neighborhood competition vary with the size and spatial distribution of trees in the neighborhood? (4) Are smaller or larger trees less or more sensitive to the effect of crowding? (5) Are faster growing trees less or more sensitive to neighborhood competition? I used a spatially-explicit neighborhood analysis to develop likelihood-based regression models that explain the observed spatial variation in competition effects on tree radial growth rates as a function of size, abundance and distribution of individual trees at local neighborhood scales within Camp Deerpark Forest (CDF).

3.2 Materials and Methods

3.2.1 Location of sample plots and data collection

In this study, I set out three 40 x 120 m plots in the summer of 2007. One was located in the region where single-tree selection treatment was implemented in 2001, and the other two parallel plots, separated by a distance of 30 m, were in regions where trees were selectively harvested in 2002 (Figure 3.1). At each plot, I recorded the species, diameter at breast height (1.3 m), and mapped the location of each tree with a dbh $\geq$ 1.0 cm.

Increment cores were extracted using an increment borer at a height of 1.0 m from all healthy trees $\geq$ 10.0 cm dbh within 10 m of the center line of both sides of the main transect in each plot. Tree cores taken from black gum (*Nyssa sylvatica* Marsh.) were not used in the current study dataset because they did not have identifiable growth rings. A total of 443 growth trees were in the data set, with sample sizes varying between 33 and 233 for the five major study species (Table 3.1). Cores were mounted on a solid frame and finely sanded. I used a high-resolution color camera to take images of tree cores. I also used a high-resolution color camera connected to a stereoscope to take images of some tree cores in which growth rings were hard to indentify.

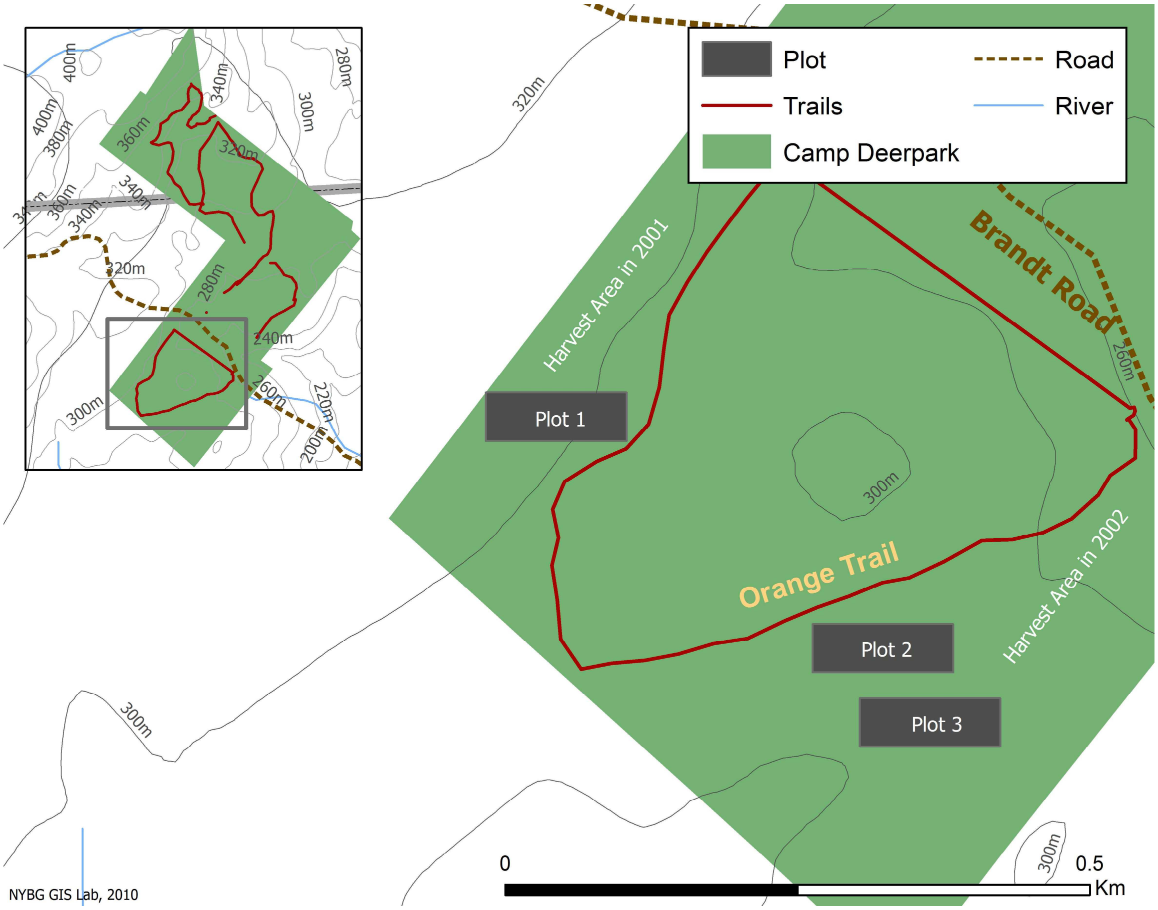

Figure 3.1. Location of three plots in the study area at Camp Deerpark Forest in New York State, USA.

Ring widths were measured with a digital ring analyzer. The most recent growth ring was discarded for trees obtained in 2007 because of incomplete radial growth. The average radial growth (mm year^{-1}) over the last 3 years (2004-2006) was used as the response variable. The growth rings between 2001-2003 were also discarded because growth variation may be large due to the changes in canopy structure resulting from the logging treatments (Canham et al. 2004).

Table 3.1. Number of individuals, core sample sizes, and mean±standard deviation (SD), minimum, and maximum dbh (cm) for the tree species included in neighborhood competition analysis on tree growth.

Species	Common name	*n*	Mean	Minimum	Maximum
Acer rubrum	Red Maple	75	14.5 ± 4.0	10.0	28.7
Pinus strobus	Eastern white Pine	233	20.5 ± 8.9	10.0	51.4
Quercus alba	White Oak	33	25.0 ± 6.6	11.9	38.1
Quercus prinus	Chestnut Oak	55	32.3 ± 9.8	13.7	56.5
*Quercus rubra**	Red Oak	47	33.0 ± 8.9	10.7	51.0

* May include black oak (*Quercus velutina*) because of the difficulty of separating these oak species in the field. Fertile collections are needed for positive taxonomic identification of oak species.

3.2.2 Neighborhood analysis of growth

I used a spatially explicit, maximum-likelihood, neighborhood model approach to examine tree competition in which the observed radial growth (RG) of a target tree was analyzed as a function of: (1) the potential growth of a hypothetical “free growing” tree with no crowding (PotRG); (2) initial target tree size (dbh, in centimeters); and (3) crowding of trees by neighbors (see details in Appendix II):

$$\mathrm{RG} = \mathrm{PotRG} \times \mathrm{Size\,effect} \times \mathrm{Crowding\,effect} \qquad \text{(Equation 1)}$$

RG and PotRG are measured in units of mm year^{-1}, and the remaining two sets of scalar modifiers ranging from 0 to 1 act to reduce potential growth. I compared two different functional forms to determine the shape of the size effect. As utilized in other recent studies (Canham et al. 2004, Uriarte et al. 2004a, Canham and Uriarte 2006, Papaik and Canham 2006, Coates et al. 2009), I also use a lognormal function, a traditional forest growth equation used for the shape of this effect because it is flexible and supported by both theoretical and empirical evidence (Zeide 1993):

$$\mathrm{Size\,effect} = e^{-\frac{1}{2}\left[\frac{\ln(\mathrm{dbh}/\delta)}{\sigma}\right]^2} \qquad \text{(Equation 2a)}$$

where δ is the dbh of the target tree at which PotRG occurs, and σ is the parameter to determine the breadth of the function. This functional form has been described to have the flexible characteristics for the effective range of adult trees because the shape of the relationship of growth and diameter may be monotonically increasing (i.e., when δ is very large), decreasing (i.e., when δ is very small), or may have a single "hump" and a skew to the left when δ is within the normal range of dbh (Canham et al. 2004, Uriarte et al. 2004a, Papaik and Canham 2006, Coates et al. 2009).

I also chose one general form of an exponential function, the power function, because it is one class of mathematical equations useful in the measurement and analysis of a series of data (Siegel and Swanson 2004), and because the power function consistently produced models with greater likelihood for my data after testing different types of formulations. The power function has the form:

$$\text{Size effect} = (\text{dbh})^{\alpha} \qquad \text{(Equation 2b)}$$

where the parameter α scales the radial growth to size and controls for the effects of initial plant size on radial growth.

Analysis of crowding effect is based on the tradition of distance-dependent analyses of competition, in which the net competitive pressure of all neighbors on the target trees is assumed to vary as a direct function of species, size of the neighbor, and as an inverse distance to neighboring trees (Wimberly and Bare 1996, Wagner and Radosevich 1998, Vettenranta and Miina 1999, Berger and Hildenbrandt 2000, Canham et al. 2004, Uriarte et al. 2004a, Uriarte et al. 2004b, Canham et al. 2006, Papaik and Canham 2006, Coates et al. 2009). The equation of the neighborhood competition index (*NCI*) on the target tree is given by:

$$NCI = \mathrm{dbh}_t \sum_{i=1}^{s} \sum_{j=1}^{n} \lambda_i \frac{\left(\dfrac{\mathrm{dbh}_{ij}}{100} \right)^2}{\mathrm{distance}_{ij}} \qquad \text{(Equation 3)}$$

The species-specific competition index (λ_i) ranging from 0 to 1 allows for differences among species in their competitive effects on the target trees. Then, for i=1…s species and j=1…n neighbors of species s within a fixed radius of 10 m of the target tree, a *NCI* specifying the net competive effect of the neighbors on the target tree is estimated using Equation 3. I choose a maximum radius of 10 m of the target tree for my analysis because this showed consistent results and produced models with greater likelihood after testing a range of radii.

In my analysis, I compared a series of hypotheses and competitive hierarchies with different assumptions of interspecific differences in the competition effects by different species of neighbors. This was motivated by my interest in understanding the consequences for timber production of the single-tree selection treatment, which changes the configuration conditions of residual trees within stands by removal of different tree species and tree sizes.

This comparison is also relevant to the current debate about which is more important in determining patterns of diversity and relative abundance in forests, i.e., (1) ecological neutrality because all coexisting species are functionally equivalent, or (2) niche differentiation because of interspecific differences in the competitive effects. I evaluated four alternate sets of competition models with different groupings of neighbors in Equation 3: (1) an "equivalent competitors" model in which all species had equivalent effects (i.e. fixing λ_i=1 for all neighbors), so that the significance and magnitude of competitive effects on tree growth could be compared; (2) an "intraspecific vs. interspecific" model that calculated different λ_i for conspecifics and heterospecific neighbors; (3) a "full" model that calculated separate λ_i for each species of competitors; and (4) a model of size effect in which the effect of target tree size on potential growth is estimated in the absence of neighborhood competition, i.e., omits the crowding effect term.

I assumed that radial growth declines by neighborhood crowding effects and scales as a negative exponential function of *NCI*. Crowding effect is defined as

$$\text{Crowding effect} = e^{-C \times NCI_i} \qquad \text{(Equation 4)}$$

where C is a species-specific parameter which determines the sharpness of the decline in growth due to an increment in NCI_i, and NCI_i is the neighborhood competition index for target tree i. In contrast to other recent studies, I used neither a linear reduction nor a sigmoidal reduction in growth with increasing crowding, because a linear reduction formulation requires truncating the function at some level of NCI to prevent predictions of negative growth. Recent studies have consistently found that the simple exponential reduction provides the best fit to the data in contrast to the formulation of a sigmoidal reduction (Canham et al. 2004, Uriarte et al. 2004a, Uriarte et al. 2004b, Canham et al. 2006, Papaik and Canham 2006).

I also tested two alternate variants of Equation 4 in which the effects of crowding on target tree growth varied as a function of target tree size or average growth rate prior to the harvest, respectively. First, I tested a model for the effect of target tree size on sensitivity to competition in order to understand whether a given level of crowding had a greater or lesser effect on smaller or larger target trees. To test this, I allowed the exponential decay term (C') in Equation 4 to vary as a function of target tree size (dbh):

$$C = C' \times (\mathrm{dbh})^{\gamma} \qquad \text{(Equation 5)}$$

where the coefficient γ adjusts the effect of *NCI*. If $\gamma = 0$, then there is no variation in sensitivity of target trees to crowding as a function of target size. If $\gamma < 0$, then sensitivity to crowding declines as the target tree dbh increases, i.e., smaller dbh target trees suffer a greater reduction in growth from a given level of crowding than do larger trees. If $\gamma > 0$, then larger trees are more sensitive to a given level of crowding than smaller trees.

In my analysis, I also tested a model for prior growth rate effect on sensitivity to competition. The formulation is given by:

$$C = C' \times (prior \times 10)^{\kappa} \qquad \text{(Equation 6)}$$

where *prior* is average radial growth rate prior to the harvest. If $\kappa < 0$, then sensitivity to crowding declines as the growth rate of the target tree increases, i.e., trees with reduced growth rate are more sensitive to a given level of crowding than trees with increased growth rate. If $\kappa > 0$, then fast growing trees are more sensitive to crowding. I tested this relationship because size- and/or age-dependence of growth rates is an expression of sigmoid growth curve pattern (Evans 1972), but may decline and result in a negative value due to external factors such as damage, disease, disturbance, treatment, competition, resource limitation, and climate conditions (Weiner and Thomas 2001).

3.2.3 Parameter estimation and comparison of alternate models

I used the likelihood method approach and model selection as alternatives to traditional null hypothesis testing for the analysis of neighborhood processes in forest systems (Johnson and Omland 2004, Canham and Uriarte 2006). I used simulated annealing (Goffe et al. 1994), a global optimization procedure, to estimate model parameters and support intervals that maximize the likelihood of observing the actual overall growth data from the given models. The analyses were done using the R language software (Version 2.6.2; see Appendix I for the R script used for the analyses). As in many of the earlier studies (Canham et al. 2004, Uriarte et al. 2004a, Uriarte et al. 2004b, Canham et al. 2006, Papaik and Canham 2006, Coates et al. 2009), the residuals (i.e., the difference between observed and predicted growth) were assumed to be normally distributed. Growth of each of the five species was analyzed. For each analysis, the regression model described by Equation 1 requires estimation of either $n + 5$ parameters in the power functional formulation or $n + 6$ parameters in the lognormal functional formulation for n species or groups of neighbors.

The fit of each alternate model was assessed using two different metrics: the R^2 of the regression (defined as 1 – SSE/SST; SSE, sum of square error; SST, sum of square total) of observed radial growth on predicted radial growth as a measure of goodness of fit, and the slope of the regression (with a zero intercept) as a measure of bias, with an unbiased model having a slope of 1. I use the Akaike Information Criterion corrected for small sample size (AIC_c) which incorporates both parsimony and likelihood in comparing alternate models (Burnham and Anderson 2002). When the difference in AIC_c between the two models is < 2 units, models are considered to have equivalent empirical support. In comparing models with a difference in $AIC_c > 2$ units, the model with the lowest AIC_c is considered to have larger empirical support. The model with the lowest $\mathrm{AIC_c}$ is considered to be the best candidate model. Asymptotic, two-unit support intervals, defined as the range of the parameter value that results in less than a two-unit difference in AIC_c, are used to assess the strength of evidence for individual maximum likelihood parameter estimates (Edwards 1992). This is analogous to a 95% support limit defined using a likelihood ratio test (Hilborn and Mangel 1997).

Together, Equation 2 through 6 comprise the complete model as described by Equation 1. For each target species analysis, I separately tested four alternate models that made different assumptions about the nature of competitive interactions described above in a power function and a lognormal function form. I also tested two additional terms nested in alternate models. I tested whether there was evidence that sensitivity to crowding varied as a function of the target tree size dbh by comparing models including γ in Equation 5 or as a function of the prior growth rate by comparing models including κ in Equation 6 versus models omitting either one of these terms.

3.3 Results

The three plots at CDF contain 1,879 individuals comprised of 11 species of trees with stems ≥ 1.0 cm dbh distributed among 9 genera and 8 families (Table 3.2). I

Table 3.2. Mean±standard deviation (SD), minimum, and maximum dbh, basal area, and density of trees ≥ 1.0 cm in three plots at Camp Deerpark Forest, New York State, USA.

Species (code)	Common name	No. trees	dbh Mean	dbh Min.	dbh Max.	Basal area (%)	Density (%)
Acer rubrum	Red maple	250	10.68 ± 5.27	2.8	29.8	5.4	13.3
Betula lenta	Sweet birch	25	10.92 ± 7.12	1.7	32.5	0.6	1.3
Castanea dentata	American chestnut	4	5.4 ± 1.75	2.9	7.0	0.0	0.2
Hamamelis virginiana	America witchhazel	152	3.88 ± 1.29	1.3	8.2	0.4	8.1
Nyssa sylvatica	Black gum	166	13.31 ± 5.64	3	27.3	5.3	8.8
Pinus strobus	Eastern white pine	975	13.21 ± 10.88	1	64.7	43.8	51.9
Quercus prinus	Chestnut oak	125	32.41 ± 9.92	7.5	61.8	22.0	6.7
*Quercus rubra**	Red oak	92	31.95 ± 9.74	10.7	51.0	15.7	4.9
Quercus alba	White oak	54	25.63 ± 6.89	11.9	41.5	5.8	2.9
Sassafras albidum	Sassafras	35	11.52 ± 2.77	7	17.3	0.8	1.9
Tsuga canadensis	Eastern hemlock	1	22.6	22.6	22.6	0.1	0.1

* * May include black oak (*Quercus velutina*) because of the difficulty of separating these oak species in the field. Fertile collections are needed for positive taxonomic identification of oak species.

analyzed growth of adult trees with their diameter ≥ 10.0 cm dbh of five of the most common species across the plots: eastern white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.), white oak (*Quercus alba* L.), red oak (*Q. rubra* L.), and chestnut oak (*Q. prinus* L.).

3.3.1 Model evaluation and comparison

For all five target species, I estimated the maximum likelihood parameter values for a series of alternate, nested growth models. All of the models produced unbiased estimates of growth, with a slope of observed radial growth on predicted growth very close to 1 (i.e. , 0.99-1.01). The percentage of variance (R^2) explained by the best full models ranged from 23% in red maple to 72% in eastern white pine (Table 3.3).

I compared all alternate, nested models described above using AIC_c. The best model is the model with the lowest AIC_c value. My analyses indicate that a power function form describing the shape of the size effect was always a better fit to the data for all species except white oak, for which a lognormal function was a far better fit to the data. For all five species, null models that ignored the effects of competition and predicted growth based on tree size alone were rejected in favor of models incorporating neighborhood competition.

The simplified models that considered all neighbors equivalent, i.e., grouped species of neighbors into a single estimated competition coefficient (λ) with the value of 1, were

Table 3.3. The Akaike Information Criterion (AIC) and R^2 (shown below in parenthesis) of alternate models. The Full model fit separate competition coefficients (λ) and a pre-harvest growth rate added for five target species of neighbors at Camp Deerpark Forest. The model with the lowest AIC is highlighted in **bold**.

		AIC - full models			AIC - reduced models		
species	*n*	without γ and κ	with γ	with κ	Equivalent competitors with κ	Conspecific vs. heterospecific	Size effects only
Red maple	75	112.0	116.2	92.7	**86.9**	108.4	101.5
		(0.09)	(0.07)	(0.32)	(0.23)	(0.00)	(0.00)
Easterm white pine	233	216.6	218.9	**125.0**	126.7	224.0	238.2
		(0.58)	(0.58)	(0.72)	(0.70)	(0.54)	(0.50)
White oak (*)	33	72.6	74.7	56.5	**37.9**		47.8
		(0.26)	(0.32)	(0.61)	(0.53)		(0.24)
Chestnut oak	55	64.9	62.3	19.1	**14.1**	57.1	50.1
		(0.27)	(0.34)	(0.7)	**(0.63)**	(0.22)	(0.22)
Red oak	47	74.5	77.2	55.4	**45.3**	64.1	57.9
		(0.37)	(0.38)	(0.61)	(0.54)	(0.35)	(0.33)

* using lognormal function form.

better for all four of the species (red maple, white oak, chestnut oak, and red oak) with the smallest sample size ($n \leq 75$). In each of these cases, the "equivalent" competitor model had the lowest AIC_c values and was superior to the model that contrasted conspecific versus heterospecific competitors. For eastern white pine with sample size of 233 individuals, the data supported the "full" model that considered interspecific differences in per-capita competitive effects for the species (i.e., estimates separate competition coefficient for all five species of neighbors) (Table 3.3).

3.3.2 Effects of tree size on potential radial growth

There were three different size-dependency patterns of variation in potential growth as a function of target tree size (Figure 3.2). Three of the tree species (eastern white pine, chestnut oak, and red oak) showed that potential tree growth was predicted to increase across the range of tree size. White oak reached a peak of maximum growth between 26 and 30 cm dbh and then showed declines in potential growth in larger size classes. The shape of the distribution for red maple was considerably flatter and had relatively uniform potential growth throughout the range of observed tree sizes (Figure 3.2). The predicted potential radial growth rates (i.e., crowding = 0) were remarkably different among species, ranging from a very low potential growth rate of 0.3 mm year^{-1} in red oak to 2.1 mm year^{-1} in white oak (Table 3.4).

3.3.3 Interspecific variation in sensitivity to crowding

The parameters C, γ, and κ estimate the competitive responses of target trees to

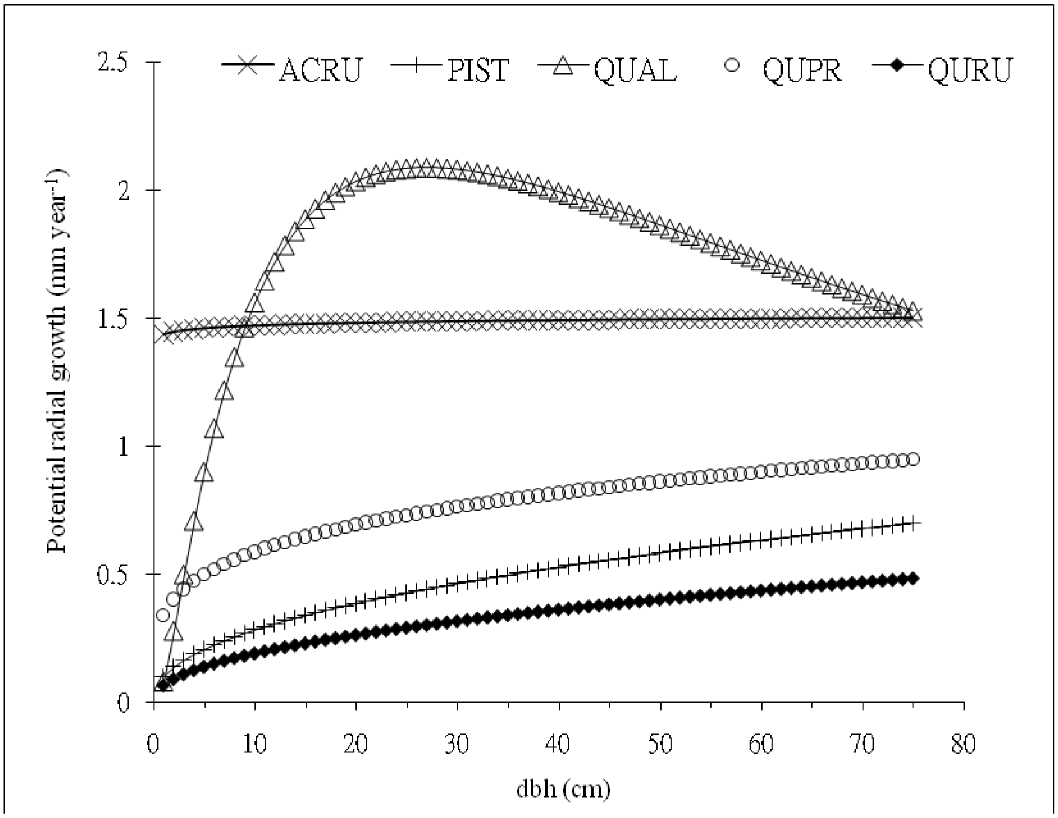

Figure 3.2. Predicted effects of variation in target size (dbh) on potential radial growth for each of the five species in the absence of crowding effects using either Equation 2a or 2b depending on the functional form supported. ACRU: *Acer rubrum* ; PIST: *Pinus strobus*; QUAL: *Quercus alba*; QUPR: *Q. prinus*; QURU: *Q. rubra*. (Note: Size effect = (dbh/30)^b).

Table 3.4. Maximum likelihood parameter estimates and two-unit support intervals (highlighted in **bold**) for the best full model (with pre growth rate κ) for each of five study species.

Species	Label	C	Max	α	Xo	Xb	κ
Red maple	MLE	33.634	1.488	0.010			-0.966
	Two-Unit S.I.	***27.92-40.11***	***1.30-1.69***	***0.01-0.06***			***-0.86-1.09***
Eastern white pine	MLE	103.908	0.464	0.450			-0.866
	Two-Unit S.I.	***96.64-111.08***	***0.44-0.48***	***0.44-0.46***			***-0.83-0.92***
White oak (*)	MLE	41.505	2.087342		26.910	0.564	-1.231
	Two-Unit S.I.	***33.20-52.34***	***1.90-2.25***		***23.68-30.20***	***0.41-0.90***	***-1.10-1.37***
Chestnut oak	MLE	64.627	0.704	0.256			-1.149
	Two-Unit S.I.	**57.52-73.40**	**0.66-0.74**	**0.24-0.27**			**-1.09-1.21**
Red oak	MLE	928.170	0.317	0.462			-1.829
	Two-Unit S.I.	**705.41-1000**	**0.30-0.34**	**0.44-0.49**			**-1.72-1.97**

* using lognormal function form.

crowding. The effects of target tree size on sensitivity to competition by neighbors are determined by the parameter γ. My analyses indicate that this parameter did not improve the maximum likelihood values or lower AIC_c values except chestnut oak as the full models included the target tree sizes term γ as a part of a negative exponential function for the crowding effects (Table 3.3). There was, however, evidence that sensitivity to crowding varied as a function of the target tree size for all of the five species (i.e., $\gamma \neq 0$). In all five species, the estimates of γ were negative, indicating smaller trees were more sensitive to crowding than larger trees (ranging from -0.02 in eastern white pine to -3.54 in white oak) (γ not shown). Among smaller trees of the five species, the least sensitive were the two most abundant species (red maple and eastern white pine).

The effects of prior radial growth rate in the response of a target tree to crowding by neighbors are controlled by the parameter κ. My analyses indicate that the best models are the models that included the prior radial growth rate κ, with $\kappa < 0$ (ranging from $-1.83 < \kappa < -0.87$, Table 3.4) in all five species. Thus, given a level of release (i.e. current level of crowding), species or target trees with that had slow growth prior to harvest do not respond as strongly as those with that had fast growth prior to harvest in response to the change in neighborhood crowding following harvest.

Thus, target trees with smaller prior radial growth rates were more sensitive to crowding than trees which had larger prior radial growth, i.e., slow-growing trees were much more sensitive to competition than fast-growing trees ($-1.8<\kappa<-0.9$; Table 3.4).

I plotted the predicted growth reduction in each species on the different variation in NCI, indicating predicted growth declines as a negative exponential of increasing NCI for the five species (Figure 3.3a-c). The calculations take into account the tree prior growth rate. Figure 3.3 represents three simple cases: (1) increased but very small growth rate of target tree, (2) increased but moderate prior-growth rate of a target tree, and (3) a case in which the prior-growth rate of a target tree was larger compared to the present rate.

In all three cases, white oak and eastern white pine are consistently the least and most sensitive to crowding, respectively. Red oak and chestnut oak are less sensitive to crowding when they have a larger prior-growth rate, but are more sensitive to crowding than red maple and chestnut oak when they have a smaller growth rate. For 10 mm prior growth rate stems under the maximum observed relative crowding (i.e., $NCI = 1$), observed growth was reduced to only 1.5-9.8% of potential (Figure 3.3a), and eastern white pine, red oak, and chestnut oak were the three species most sensitive to crowding. For 50 mm prior growth rate stems, predicted growth under maximum crowding ranged from 1.3% to 71.5% of potential (Figure 3.3c), and red maple, red oak, and eastern white pine were the three species with the greatest reduction in growth. This shifting of competitive hierarchies illustrates some of the complexities and challenges inherent in the management of mixed-species forests.

3.3.4 Variation in the per capita effects of crowding by different species of neighbors

In my analysis, I also estimated separate λ_i per capita effects of crowding by species i on species j from the best full models. Table 3.5 presents the matrix of

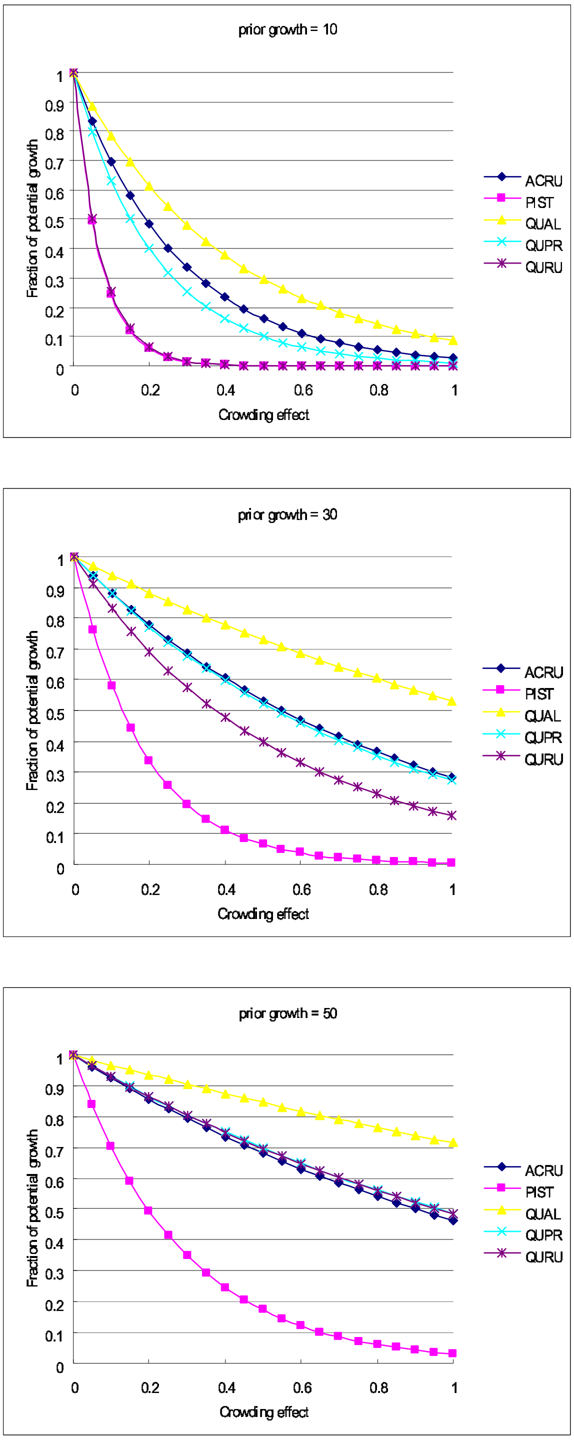

Figure 3.3. Predicted effects of variation in *NCI* (neighborhood crowding index) on each of the five target tree species in three different cases. (a) A target tree with prior growth rate of 1 mm. (b) A target tree with prior growth rate of 3 mm. (c) A target tree with smaller prior growth rate of 5 mm. ACRU: *Acer rubrum* ; PIST: *Pinus strobus*; QUAL: *Quercus alba*; QUPR: *Q. prinus*; QURU: *Q. rubra*.

Table 3.5. The matrix of per capita competition coefficient (λ) estimated from the best full model (see Table 3.3). The values in each row are the effects of the column species on the row species. The conspecific competition coefficients (diagonals) are shown underlined, and the strong competition coefficients (> 0.75) are shown in **bold**. The competition coefficients are scaled so that the strongest competitor of a given species has a value of 1.

	Red maple	Eastern white pine	White oak (*)	Chestnut oak	Red oak
Red maple	0.638	**0.990**	0.540	0.294	0.000
Eastern white pine	**1.000**	0.222	0.256	0.172	0.182
White oak (*)	0.507	**1.000**	0.003	0.000	0.671
Chestnut oak	**0.984**	**0.976**	0.000	0.166	0.164
Red oak	**1.000**	0.159	0.000	0.094	0.022
Mean	0.826	0.669	0.160	0.145	0.208

* using lognormal function form.

pairwise competition interaction, i.e., the matrix of coefficients λ. The λ value of 1 represents the per capita effects of the strongest competitor among the five possible species of neighbors. Most of the individual pairwise interactions were strongly asymmetric such that the effect of species A on B was much larger or smaller than the effect of B on A.

Over half, 52%, of the elements in the matrix of interspecific competition coefficients reflect very weak effects of crowding (λ < 0.25). Nearly one quarter, 24%, of the elements were considered as strong effects of crowding (λ > 0.75; 6 of 25 coefficients).

The strong competitive effects on any individual target trees are due to species of neighbors from red maple and eastern white pine. Red maple and eastern white pine are the first two species with strong competitive effects on most other target species and average competitive effect across all target tree species, i.e., the row averages in the matrix can be used as an approximate ranking of the relative strength of a species as a competitor. Among most elements, oak species of neighbors had little effect via crowding. The strength of intraspecific crowding was generally low for all species (0.03-0.22). The one exception to have relatively strong interactions was red maple, with a λ value of 0.64.

3.4 Discussion

Knowledge of the effects of competitive interactions among co-occurring species on tree growth is needed to understand growth variation (interspecific variability) on neighborhood process and population dynamics. Such knowledge is required to optimize forest management practices and, more precisely, for the development of spatially explicit individual-based forest simulation models such as SORTIE and SYMFOR (Pacala et al. 1996, Coates et al. 2003, Phillips et al. 2004).

In my study, all of the models produced unbiased estimates of growth, as indicated by slopes of predicted vs. observed were very close to 1. Goodness of fit tests (R^2) provides a reasonable estimate of the effects of neighborhood competition on tree growth. Compared to the results in the recent studies using the same maximum-likelihood methods and model selection approaches (*e.g.* (Canham et al. 2004, Uriarte et al. 2004a, Uriarte et al. 2004b, Canham et al. 2006, Papaik and Canham 2006)), my results were very good and high in explaining a percentage of variance by the best models, ranged from 61% in both white oak and red oak, to 72% in eastern white pine. The one exception to this percentage variance range is red maple, where only 32% of the variance in growth was explained by the models (see R^2 in Table 3.3).

Factors not accounted for in the models might contribute to prediction error including measurement error, plot sizes, and successional stages (Canham et al. 2006, Coates et al. 2009), herbivores, pests, pathogen attacks, tree damage by harvesting (Jones and Thomas 2004), and effects of past periods of suppression and release (Wright et al. 2000). From both a biological and a management perspective, the principle objective of growth estimation is to generate information on how forests may develop in the future. Given estimates of past growth, models fitted to data accommodating - uncertainty from any source of variability that affects observations - gives us much more confidence to further apply the resulting functions in forest simulation models (Clark 2003b, Coates et al. 2003, Canham et al. 2004, Canham et al. 2006, Puettmann et al. 2008, Coates et al. 2009).

3.4.1 Size effects

There has been no consistent model, function, or method to predict the relationship between tree size and growth (Russo et al. 2007). The types of allometric transformations or equations used depend in part on individual size and size variability of trees, taxonomy, and growth form (Stoll et al. 1994, Russo et al. 2007). I selected two functions, a lognormal function and a power function to estimate the effects of the size of the target tree on potential growth in my study. As in other recent studies (Canham et al. 2004, Uriarte et al. 2004a, Canham et al. 2006, Papaik and Canham 2006, Coates et al. 2009), I settled on a lognormal function for the shape of the size effect because it has flexible characteristics for accommodating a wide range of the shape of the relationship between potential growth and diameter (Canham et al. 2004), and several empirical studies have demonstrated that plant sizes are lognormally distributed (Stoll et al. 1994). I also estimated the growth of a tree by using a power function with invariant scaling exponent (α) because growth-diameter scaling is not actually equivalent for both small and large trees, and more specifically, younger, smaller trees show intrinsic exponential growth in the absence of competition (Stoll et al. 1994). I found that a power growth model (Equation 2b) fitted the tree growth-diameter relationship better than a lognormal function (Equation 2a) for all species but white oak.

In addition, the tree growth function in red maple, an early- and mid-successional species, was fairly flat (uniform), i.e., did not vary across the observed range of canopy tree sizes (Figure 3.2) and became less size-dependent (lower α, Table 3.4). Canham et al. (2006) used growth data from over 800 permanent plots along environment gradients in forests of Vermont and New Hampshire (northern New England) in the USA and found similar patterns of variation in potential growth in red maple although they used a lognormal function for the shape of the size effect. I also found that all the remaining four species except red maple had strong size-dependency in potential growth in the absence of competition or following a complete release.

For eastern white pine, chestnut oak, and red oak, growth rates were faster in smaller diameter trees (Figure 3.2), which lends support to the study of Canham et al.

2006, which found that growth rates in forests of northern New England were highest in the smallest size class (Canham et al. 2006). However, compared to their resulting shape of growth on size effects, the greatest disparity in my study was that growth increased with increasing target tree size in my study. There were few large diameter trees (greater than 40 cm dbh) included in my data set for these species and different functions applied, and these may account for the different shape of growth functions illustrated in Figure 3.2 (Coates et al. 2009).

I was surprised that white oak showed an optimal size at subcanopy stems (below 30 cm dbh), with a moderate decline in growth in larger size classes, even though this species is usually considered to have an ability to persist for long periods of time in suppression, to respond well after release, to be long-lived, and to ultimately become dominant in the forest (Rogers 1990, Abrams 1998). Moreover, predicted maximum growth (Table 3.4) for all five species was surprisingly low in my study. These results lead me to believe that most of the trees in my data set had encountered prolonged suppression. Two studies conducted in British Columbia in Canada (Canham et al. 2004, Coates et al. 2009) demonstrate that predicted relationships can be strongly influenced by the successional status of the stand.

Most trees at the Camp Deerpark Forest were established following abandonment of farming in 1930s, and a few of the higher-quality trees were removed in 1974. The majority of trees in my data set were subcanopy trees beneath a continuous canopy cover of larger trees. When released, the effects of past suppression did not disappear and the trees showed relatively low growth rates. These points highlight the importance of size variability, growth rate changes through diameter size classes, well-balanced data set of tree sizes, and the effects of suppression on the estimate of tree growth. These factors should be taken into account, particularly when determining the proper shape of the size effect term in Equation 1 for the simulation of the effects of partial harvest regimes.

3.4.2 Implication for theories of forest community organization

My results support both views of niche differentiation (Chesson 2000) and the neutral model of species interaction proposed by Hubbell (2001). Based on evidence from estimates of the strength of competitive effects of neighbors in my crowding functions, I found that the model that grouped all species of competitors as equivalent was a better fit to the data than models that discriminated between some species of competitors for four species. Only one species, eastern white pine, rejected the equivalent competitor model, i.e., showed support for the hypothesis that different species of competitors were not equivalent in their effects (Table 3.3). This is in contrast to results in earlier studies using similar distance-dependent neighborhood competition models (Canham et al. 2004, Uriarte et al. 2004a, Uriarte et al. 2004b, Canham et al. 2006, Papaik and Canham 2006, Coates et al. 2009). Some the results of these studies support, while others contradict the idea of ecological neutrality, and equivalent per capita fitnesses. One possible interpretation supporting both views is simply a methodological limitation: sample sizes for each species. Species that supported the most parsimonious model, and treated all species of neighbors as equivalent usually had relatively small sample sizes in the data set. Insufficient numbers of neighbors of a given species may provide less confidence to predict the power of the models in detecting interspecific differences in competitive effects.

3.4.3 Management implications of variable species response to competition and sensitivity to crowding

The results for quantitative estimates of the strength of interspecific competition between pairs of species reveal that most of the individual pairwise interactions were strongly asymmetrical in competitive interactions at the Camp Deerpark Forest (Table 3.5). Specifically, the asymmetric crowding effects on tree species appeared from a very specific and small subset of strong competitors within the guild (Table 3.5). The column averages in the matrix can be used as a ranking of the relative strength of species on crowding competition. I found that two of the most common early- and mid-successional species in the forest, red maple and eastern white pine, had strong crowding effects with high average per capita effects on other species, while the three oak species had little effect.

Previous studies have assumed that there is relatively strong competition between conspecific neighbors and this idea is implicit in most competition theory. I found no evidence to support this assumption in my data, with the exception of the results for red maple (Table 3.5). This relative weak effect via crowding in conspecific neighbors was a surprise. Coates et al. (2009) used growth data sampled across a wide range of stand ages, disturbance histories, tree species composition and competitive neighborhoods in British Columbia, and found that most species had weak intraspecific competition. Many studies report that plant individuals surrounded by conspecific species had lower growth or survival leading authors to conclude that there was strong intraspecific competition for resources, and further emphasizing the importance of negative density dependence. However, as of yet there are no empirical tests that examine variation among species and species abundances for the strength of negative density dependence (Comita et al. 2010). Coates et al. (2009) and my own study show that species with fewer individuals experience very weak intraspecific competition. Red maple is poorly regarded as a timber species due to susceptibility to defects and disease, poor form of individuals of sprout-clump, and is not harvested at CDF. As a result, the species occurs in a relatively high density, and presents strong competition by conspecifics.

Contrary to many previous studies of tree competition, I found support for the hypothesis that target trees are more sensitive to crowding when they are small than when they are larger (γ in Table 3.3). The least sensitive species were also the two most abundant taxa, red maple and eastern white pine. Furthermore, I found that faster growing trees are less sensitive to neighborhood competition.

My results highlight the strong asymmetries in species and the complexity of competitive effects and responses within the guild of intermediate shade tolerant and early- and mid- successional species in temperate forests. Moreover, small trees and slow-growing trees have a more pronounced growth response to crowding. Relatively low removal rates in the single-tree selection system may be less successful in favoring the growth of regenerating trees for intermediate to shade intoterant species unless careful attention is paid to the spatial distribution of the removed and retained canopy trees (Coates et al. 2003). From a management perspective, my results have implications for the design of silvicutural strategies that will optimize yield and keep the forest healthy through changes in the configuration conditions of residual trees within stands after removal of different species and tree sizes. In many cases, forest management must balance the growth response of residual trees with the preservative of aesthetic values for recreating, and, as a result, represents a compromise between different, frequently competitive objectives.

CHAPTER FOUR

SEEDLING RECRUITMENT BY RED MAPLE (*Acer Rubrum* L.) IN A SELECTIVELY LOGGED TEMPERATE FOREST: THE SPATIAL DISTRIBUTION OF PARENT TREES

4.1 Introduction

One of the most common deciduous trees in eastern North America, red maple (*Acer rubrum* L.) is widely distributed over a wide range of microhabitats. Recent evidence has shown that red maple has increased in dominance in the understory and mid-canopy of many oak (*Quercus*), pine (*Pinus*), and northern hardwood forests during the twentieth century (Lorimer 1984, Abrams 1998). As such, it may become a more prominent species in the overstory space during the next century eventually replacing other dominant trees in these mixed hardwood forests (Abrams 1998). The widespread expansion of red maple cannot be easily explained (Abrams 1998, Lambers and Clark 2005), either by its leaf physiology (Kubiske and Abrams 1994, Kubiske and Pregitzer 1996), its leaf morphological features (Abrams and Kubiske 1990, Kloeppel et al. 1993, Abrams and Mostoller 1995), its lower net photosynthetic rate (Abrams and Mostoller 1995, Kubiske and Pregitzer 1996) or its lower shoot growth and biomass in the low light environment (Canham et al. 1996). The seed does not form persistent seed banks in the soil since they have a shorter seed lifespan than most of co-occurring species. Seedlings are also noted for growing in large forest openings and gaps, with individuals producing a lower root biomass when establishing at lower light levels.

These issues are of relevance in the United States and Canada as interest in uneven-aged silviculture and the use of natural regeneration has grown over the last decade. As a result, the challenges of managing and maintaining structurally complex stands requires more mechanistic, spatially explicit models and robust parameter estimates to gain insights into the processes of regeneration abundance following logging.

Tree seedling recruitment is a critical stage that involves many processes in forest regeneration. Logging practices can alter these processes, exerting a controlling influence on seedling abundance and shaping the future forests (LePage et al. 2000). Natural seedling establishment should vary dramatically following selection logging since the removal of larger trees affects the potential source of seeds. In addition, removal of different tree species will change the composition of future seedlings represented. There is a great need to understand the effects of logging on both seed tree distribution and seedling establishment if the use of natural regeneration is to be successful method after logging (LePage et al. 2000).

The word “recruitment” refers to how new individuals are added into a population or community. For plants, the definition of recruitment covers a wide range of conditions from entry into the seed bank to individuals attaining a diameter at breast height to eventually entering the forest canopy (Ribbens et al. 1994). Recruitment involves a multistage process, with a suite of factors producing the observed pattern of seedling dynamics. Factors that block the recruitment of a species from its next stage of life history have the potential to change forest dynamics. For instance, yearly variation in seed production and the spatial distribution of seed source trees within a population first affect the distribution of seed deposition, and then later determine the local abundance and diversity of adult trees (Ribbens et al. 1994, Clark et al. 1999b, Greene et al. 2004). After the spatial distribution of seeds, numerous biotic and abiotic factors influence seed fates and reshape the distribution of the offspring, including light intensity, suitable microsites for seedling germination, and the abundance of seed or seedling predators (Schupp 1995, Clark et al. 1998, Nathan and Muller-Landau 2000).

A “seed shadow” is the density of seeds and seedlings, and the spatial pattern of seed dispersal and seedling dispersion in reference to the distance from parent trees (Clark et al. 1999b). After dispersal processes, seed shadow patterns affect how many seeds can successfully move to the seedling stage and the spatial locations of these recruits. The seed shadow further mediates gene flow between populations, shapes plant abundance, their distribution and community structure, plant invasions, metapopulation dynamics, and affects species coexistence and diversity (Nathan and Muller-Landau 2000, Levin et al. 2003). For these reasons, accurately quantifying seed dispersal and seedling dispersion is a critical step in understanding how plant populations and community structures are shaped (Russo et al. 2006).

Forest ecologists face challenges to characterize patterns of seed shadow because adult trees tend to be aggregated such that their individual seed shadows often overlap. Overlapping seed shadows make it extremely difficult to measure seed production and follow the fate of seeds after they have left their parent trees. In earlier studies, researchers chose isolated adult trees growing in the open or in edge stands so that the source of the seed would not be ambiguous, thus focusing measurements at locations around single, isolated individuals (Bjorkbom 1971, Carkin et al. 1978, Holthuijzen and Sharik 1985, Lamont 1985, Johnson 1988, Guevara and Laborde 1993). This approach, however, is not commonly applied because of two major limitations. The first limitation is that isolated adult trees are hard to find, especially in low-diversity northern hardwood forests. A second limitation is that the recruitment processes of isolated individuals may not be representative of the species within a larger population (Ribbens et al. 1994). In addition, the exposed crowns of parent trees in open stands have been reported to reproduce more seeds and have different dispersal conditions than crowns in a closed forest (Clark et al. 1999b).

Fortunately, alternative methods for analyzing seed dispersal and seedling dispersion have been proposed (Greene and Calogeropoulos 2002). Two general approaches (types of mathematical models) are represented by mechanistic and inverse mathematical models, which have been developed to simulate the pattern of offspring density decline with distance from the parent plants (Nathan and Muller-Landau 2000, Canham and Uriarte 2006, Pairon et al. 2006, Russo et al. 2006). Of the two, the inverse modeling approach, introduced by Ribbens et al. (1994), is the most economical and provides a powerful tool for estimating the fecundity of parent plants and the seed and seedling dispersal curves within forests (Ribbens et al. 1994, Clark and Fastie 1998, Clark et al. 1998, Clark et al. 1999b, LePage et al. 2000, Uriarte et al. 2005, Martin and Canham 2010).

The inverse modeling approach is so general and adaptable that it does not require the identification of the specific parent trees of each offspring from field data.

There are a range of assumptions regarding the seed dispersal or seedling dispersion kernel and error distribution of fecundity incorporated in this approach. The basic technique used in this approach is to select candidate probability distributions of distances, e.g. negative binomial and Poisson error structures, lognormal, Weibull and 2Dt kernel functions, that describe offspring dispersal distributions from mapped potential parent trees on a sample plot. Following this, maximum likelihood analysis estimates parameter values for dispersal functions to find the best fit to the offspring density and dispersion data (Ribbens et al. 1994, Clark et al. 1998, Clark et al. 1999a, LePage et al. 2000, Uriarte et al. 2005, Canham and Uriarte 2006)

Without a prior determination of the relationships of offspring-parents, the inverse modeling approach has produced compelling results in direct parental genetic analysis studies. Microsatellite markers have been successfully used to determine the exact source of dispersed fruits or seeds by genotyping the adult trees in the population and the maternal tissue of dispersed seeds or fruits such as endocarps. Pairon et al. (2006) studied black cherry (*Prunus serotina* Ehrh.), a bird-dispersed species, to assess the accuracy of an inverse modeling approach to locate the origin of the dispersed offspring using the microsatellite marker data by the direct parental genetic analysis. The results from this study showed an accurate prediction for identifying the source tree for fruits, and found that the results of dispersal curves obtained by both the inverse model and genetic approaches were similar. Compared with results of the genetic approach, lower seed density was found near the seed source plants and a greater dispersal distance prediction was obtained using an inverse modeling approach (Pairon et al. 2006).

A large number of seed dispersal studies have shown that seed density declines rapidly with distance from parent trees (e.g. (Nathan and Casagrandi 2004)). Ribbens et al. (1994) and Clark et al. (1999*b*) estimated seed dispersal under closed forest canopies using an inverse modeling approach and demonstrated that most tree species in northeastern America have spatial recruitment limitations with a relatively limited dispersal distance. They further suggested that the spatial distribution of seed trees will have strong effects on the distribution and abundance of regeneration because of spatial recruitment limitation (Ribbens et al. 1994, Clark et al. 1999b). Selection logging that alters spatial association and tree growth among residual trees may have further dramatic effects on mediating the coexistence among competing plant species.

In this research, I used the inverse modeling approach to answer the following questions related to logging: (1) Do patterns of seed shadow in a selectively logged forest resemble those in a natural closed forest? (2) Do stronger competitors have more abundant and more widely dispersed seedlings?

4.2 Materials and Methods

4.2.1 Location of seedling sample quadrats and data collection

Data were collected in 2008 from three 40 x 120 m plots where selection logging was implemented in 2001 and 2002 (Figure 4.1). Seedling quadrats were established and the seedling survey was done in the summer of 2008. After the plots were established, I set up 100 1.0 x1.0 m continuous seedling quadrats along the central line of the plot in each transect plot. Each 100 m long transect plot was capped on the east and west by an additional 10.0 m buffer zone in either direction. I also set twenty additional 1.0x1.0 m seedling quadrats located on each side with a 5-m interval to the central line of the plot to get sufficient seedling numbers. This resulted in a total of 140 1.0x1.0 m seedling quadrats for each transect plot (see Figure 4.1).

In my research, I defined seedling as any individual less than 15.0 cm in height. I also defined the age of seedlings based on examination of the cotyledon and bud scale

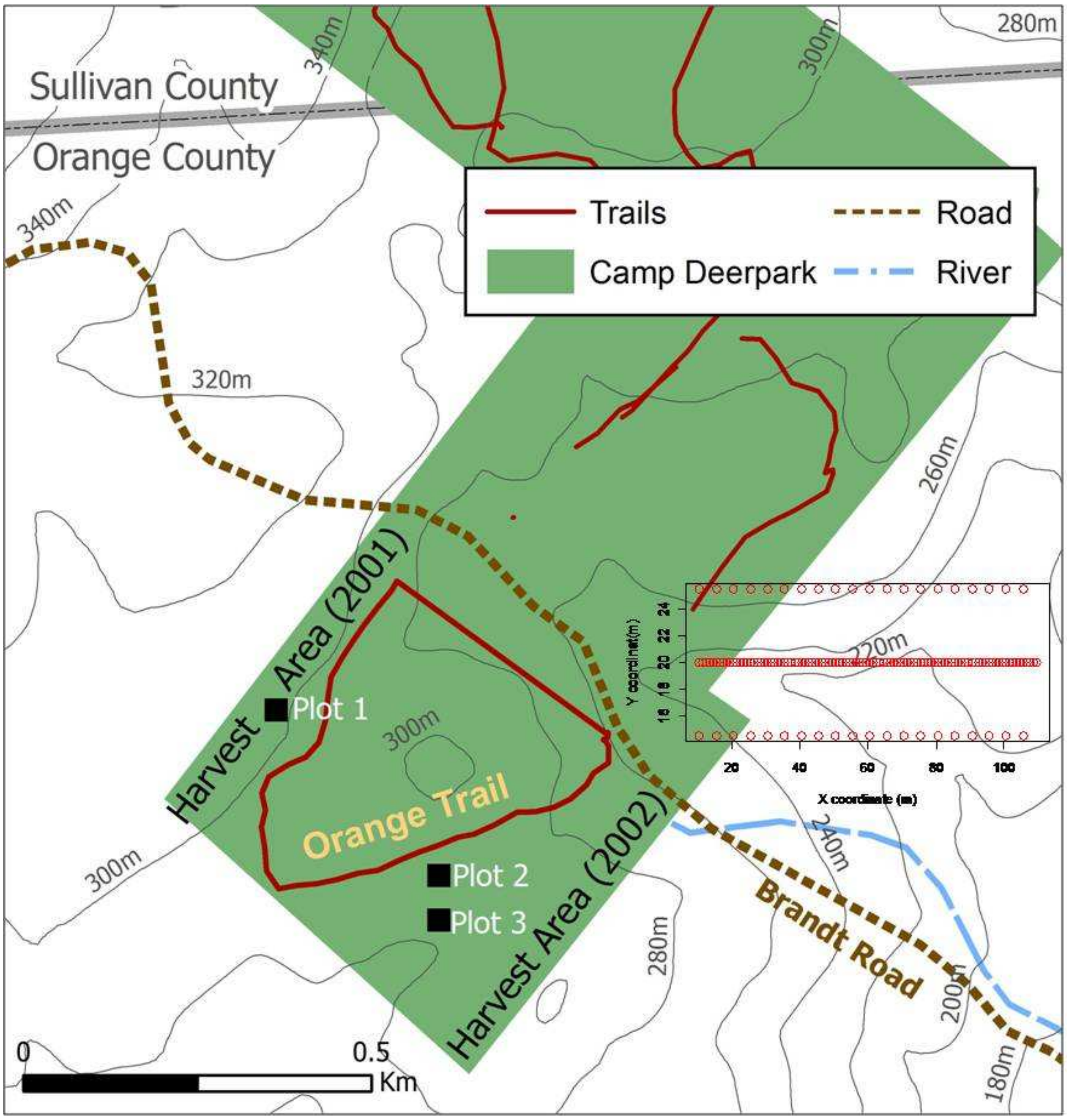

Figure 4.1. Location of three sample plots in the orange trail area at Camp Deerpark Forest in New York State, USA. In each plot, one hundred 1.0x1.0 m contiguous seedling quadrats were located along a central line with twenty 1.0x1.0 m quadrats positioned along both sides of the central line (inset diagram, lower right).

scar from terminal buds. The bud scale scar in red maple (*Acer rubrum* L.) is the best identifier after the cotyledons to determine whether a seedling has already gone through one winter, and is therefore at least a one-year old (Figure 4.2). Seedlings from new recruits were identified by still having their cotyledons or no bud scale scar,

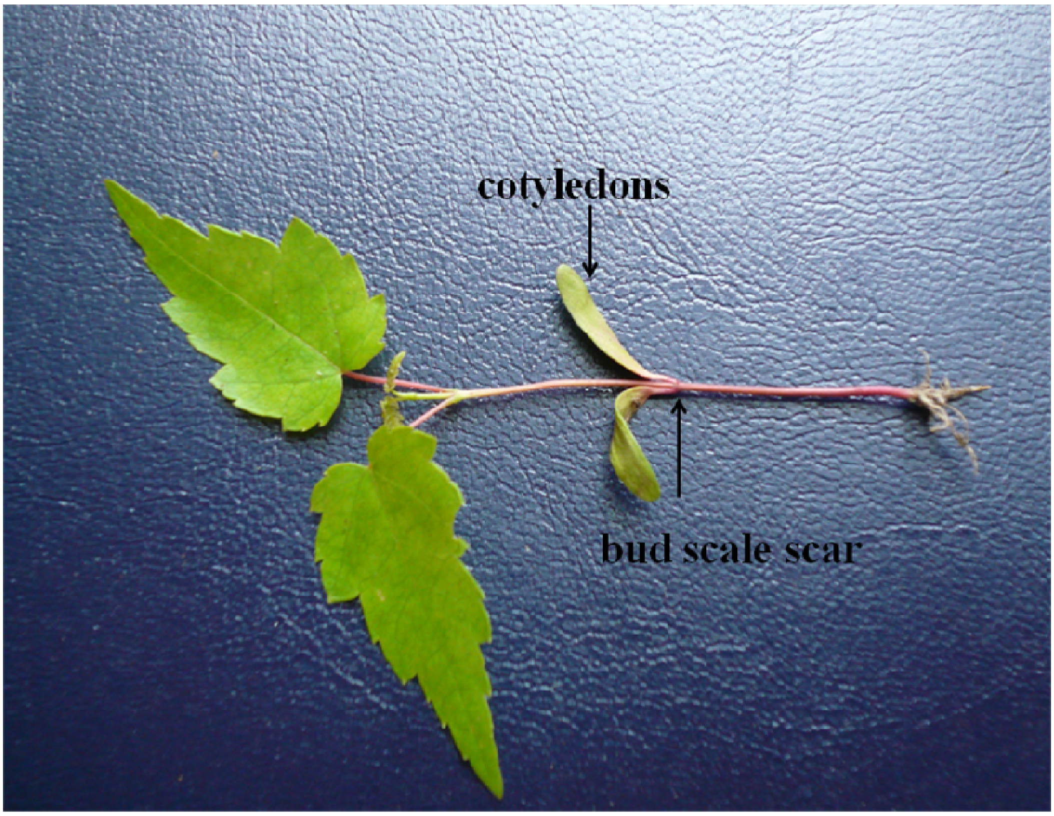

Figure 4.2.Red maple seedling (new recruit) with cotyledons and bud scale scar at Camp Deerpark Forest in New York State, USA.

whereas a 1-year seedling has a single ring bud scale scar; old seedlings have more than one ring of leaf scars. Seedlings are identified to species except with the red oak and black oak. Seedlings were censused in each 1.0x1.0 m seedling quadrat between July and August in 2008.

4.2.2 A maximum-likelihood analysis of recruitment pattern

Only the seedlings of red maple were included in this study because I did not have sufficient seedling sample sizes for other species. I followed the inverse modeling approach developed by Ribbens et al.(1994), Clark et al. (1998), LePage et al. (2000) and Uriarte et al. (2005) to analyze seedling dispersion around parent trees.

Two elements were used to predict the seedling dispersal shadow within the community: (1) an estimate of seedling production, i.e., the potential number of recruits produced by a local parent tree i ; and (2) the determination of a dispersal kernel function or probability density, describing the proportion of those seedlings that are located in a given quadrat at a certain distance from the parent trees. The seedling shadow is the product of these two elements (Equation 7; see details in Appendix II):

$$F(X_i) = \sum(\#\text{recuits per tree}) \times \left(\text{dispersal kernel of seedlings}, f(d)\right) \quad \text{(Equation 7)}$$

Following the inverse modeling approach, I used maximum-likelihood methods to predict seedling recruitment (numbers/m^2) in each sampled quadrat i based on the observed seedling data, tree size and distribution of local seed trees (Ribbens et al. 1994, LePage et al. 2000, Uriarte et al. 2005, Canham and Uriarte 2006).

The first element in the estimation of seedling production concerns the total potential number of seedlings produced by a tree. I assumed that this number is a function of stem diameter (dbh). The mean density of seedlings in a quadrat (the number of seedling per unit area) follows a negative binomial distribution, in which the dispersion of seedlings is more clumped compared to that in the Poisson distribution (Clark et al. 1999b). In addition, another parameter must be estimated for the negative binomial. This is a parameter of clumping, which allows the variance to fluctuate as a function of the mean (Uriarte et al. 2005).

$$\#recruits/tree = STR\left(\frac{dbh_k}{30}\right)^{\alpha} \qquad \text{(Equation 8)}$$

where dbh$_k$ is the dbh of the k=1,2, …. parent trees; STR (standardized total recruits) is the potential number of seedling recruits produced by a 30 cm dbh parent tree; α modifies STR as a power function of the actual dbh observed. Ribbens et al. (1994) observes that in this equation that, “STR and α tends to trade off with each other.” The site quality may influence per capita seedling recruitment, therefore, in my analyses, I set site-specific fecundity (STR) to allow STR to vary and estimated separate STR values for each plot. I also assume that the study trees are mature and can contribute to seed rain when their diameter reaches some threshold size. Therefore, I add one additional size threshold term $dbh_{threshold}$ to determine the size at which potential parents become reproductive and then drop data with trees less than dbh threashold for the analysis.

The second element (Equations 9.1 and 9.2) determines the proportion of those recruits that are located in a given quadrat in the vicinity of the parent tree. Many functional forms can be used to describe how seedling abundances vary with distance from the parent trees. Several previous studies used the Weibull function, developed by Ribbens et al. (1994) to test the individual dispersion curves (Ribbens et al. 1994, Clark et al. 1998, Clark et al. 1999b, LePage et al. 2000, Uriarte et al. 2005, Canham and Uriarte 2006, Martin and Canham 2010). The Weibull function, one form of an exponential function, assumes that the greatest seed/seedling density occurs at the base of the maternal parent trees and that recruit density declines monotonically with increasing distance from a parent tree. The Weibull function can also take on very different shape of dispersal curves (Greene et al. 2004).

Green et al (2004) compared lognormal, 2Dt, and two-parameter Weibull seed/seedling dispersal functional forms for trees (lognormal, 2Dt, and two-parameter Weibull) using published studies where the location of the source is known, and found that a lognormal dispersal kernel is preferred on mechanistic grounds. The lognormal dispersal kernel is also appropriate for tree species dispersed either by wind or by animals (Tackenberg 2003, Greene et al. 2004). Therefore, I chose the Weibull and lognormal kernels as the functional forms of the dispersal curve. I fit these two kernel function forms with the negative binomial error to test which function is a better fit to the red maple seedling data.

I tested the Weibull function used by Ribbens et. al (1994) and modified the equation of Weibull kernel by adding wind direction effect:

$$f(d) = \frac{1}{\eta} \exp^{-(\lambda - wind)(dist_i)^{\beta}} \qquad \text{(Equation 9a)}$$

where dist$_i$ is the distance from the *i*th seedling quadrat to the *k*th parent trees; η is normalization constant equivalent to the arcwise integration of the dispersal kernel; λ determines the rapidity of the decline in recruit numbers as the distance from the parent increases; β determines the shape of the distribution and has a varied β ranging from 1 to 3. I also added the wind direction term to the seedling dispersal kernel.

I also tested the lognormal function:

$$f(d) = \frac{1}{\eta} \exp^{-\frac{1}{2}\left[\frac{\ln\left(\frac{dist_i}{X_0 - wind}\right)}{X_b}\right]^2} \qquad \text{(Equation 9b)}$$

where X_0 is the distance at which maximum seedling dispersion occurs, and X_b determines the breadth or spread of the dispersal kernel. I added the wind direction term to this seedling dispersal kernel.

Red maple fruits are small and winged with two-seeded samaras.They spin as they fall from the tree and might provide a longer time and much greater distance for dispersal by wind. The equation of wind direction effect is given by:

$$wind = p_1 - [(p_2 \cos(angle - p_3))] \qquad \text{(Equation 10)}$$

where p_1 is replaced by X_0 for lognormal function form or λ for Weibull form given, p_2 estimates amplitude of anisotropic effect in meters, and p_3 determines the direction of maximum dispersal in radians from a source tree. *angle* is the angle from the seedling quadrat to a source tree.

Several previous seed dispersal studies have assumed that propagules are localized and originated from one of the potential parent trees within the mapped areas, but more recent studies also suggest adding a non-local, distance-independent "bath" of seed rain or seedling dispersion, in which the source of recruitments is from parent trees outside the mapped area, to the dispersal kernel model (Uriarte et al. 2005, Martin and Canham 2010). As in Martin and Canham's studies (2010), I added a bath term as an intercept to the model for seedling dispersion prediction from local source trees. The overall equation, combined Equation 8 with Equations 9.1 or 9.2. The potential number of seedling (R_{im}) in seedling quadrat *i* in plot site m is:

$$R_{im} = bath + STR_m \sum_{j=1}^{n} \left(\frac{dbh_{jm}}{30} \right)^{\alpha} f(d_{ijm}) \qquad \text{(Equation 11)}$$

for $dbh_{jm} > dbh_{threshold}$

where dbh_i is the diameter of $j=1\ldots$ n trees in site m with diameter greater than the estimated parameter $dbh_{threshold}$ within the distance of 20 m at Cmp Deerpark Forest. d_{ijm} is the distance from the seedling quadrat i to tree j in plot site m.

I used simulated annealing, a global optimization algorithm (Goffe et al. 1994) to estimate the parameter values under the maximum likelihood methods, and applied a two-unit asymptotic support interval (Edwards 1992) to assess the strength of evidence for individual maximum parameter estimates. I tested the influence of: (1) the spatial distribution and abundance of parent trees (as seed sources), and (2) the effects of wind direction, tree size, site quality and bath term on seedling recruitment for red maple following selection logging in the Camp Deerpark forest.

4.3 Results

4.3.1 Seedling dispersion

A total of 420 1.0 x1.0 m seedling quadrats were sampled in three plots at the Camp Deerpark forest. Nine species with 3,960 seedlings were recorded in 2008. Red maple was the principal seedling species with a total 3,440 seedlings in 2008. The maximum number of seedlings of red maple was 55 seedlings in 2008 in one 1.0x1.0 m seedling quadrat. Secondary species such as sassafras, black gum and American witchhazel were next in abundance after red maple. Eastern white pine, the most abundant tree species, had only 33 seedlings in 2008 (see Figure 4.3 a-c and Table 4.1). Red maple was the only species in which the seedling sample was sufficient large for inverse modeling in 2008 for the seedling dispersal curve. Therefore, I present calibrated functions only for this species in this chapter.

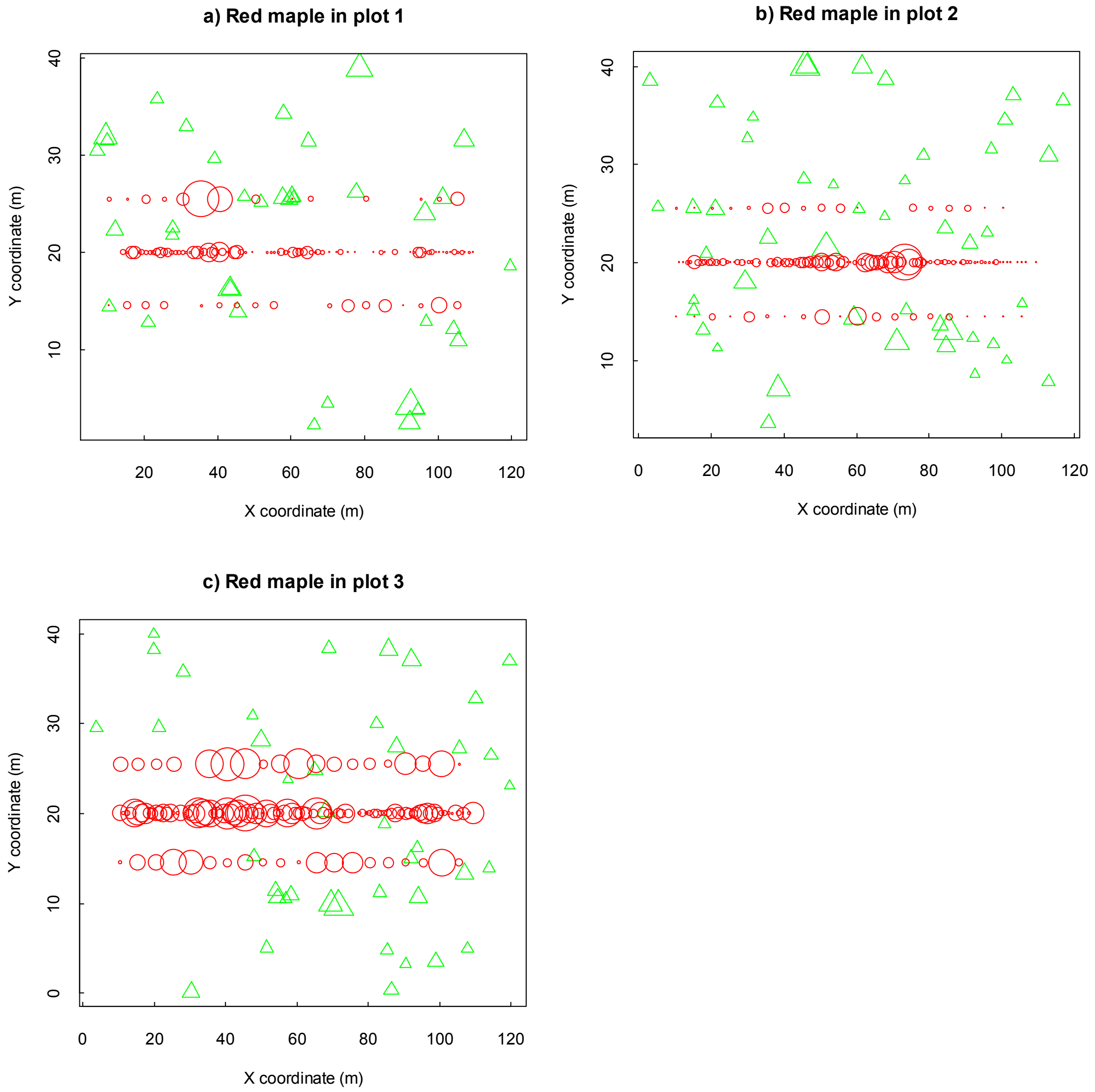

Figure 4.3 a-c. Map of trees and seedling density showing variation among the three plots. Trees are shown as green triangles to indicate relative size. Seedlings are shown as red dot circles to express relative seedling density in quadrats.

Table 4.1. Sample sizes of seedlings in 2008 at Camp Deerpark Forest in New York State, USA.

Scientific name	Species	Number of seedlings
Acer rubrum	red maple	3440
Betula lenta	sweet birch	54
Hamamelis virginiana	America witchhazel	243
Nyssa sylvatica	black gum	71
Pinus strobus	eastern white pine	33
Sassafras albidum	sassafras	100
Tsuga canadensis	eastern hemlock	0
Quercus prinus	chestnut oak	2
Quercus rubra/ Q. velutina	red oak/black oak (*)	16
	Unidentified	1
	Total	3960

* red oak group: may include black oak and red oak because of the difficulty of separating these oak species in the field.

Overall, average red maple seedling density was 8.2 ± 7.05 seedlings/m^2 in 2008. Seedling density in plot 1 was the lowest of the three plots (Table 4.2). There was a very low STR (<11 seedlings per 30 cm dbh parent tree) in 2008 (Table 4.3). The clumping parameter was small (<5) and indicated that the negative binomial is adequate to fit the seedling dispersion function for red maple (Table 4.3). It was also supported by the results of *AICc* for models fit with negative binomial error function compared to the Poisson.

Table 4.2. Sample sizes of seedlings in the three plots at camp Deerpark forest in 2008 in New York State, USA.

	(Year)		2008				
		Plot 1	Plot 2	Plot 3	Plot 1	Plot 2	Plot 3
Scientific name	Species	Seedlings	Seedlings	Seedlings	Parents	Parents	Parents
Acer rubrum	red maple	552	1458	1430	36	47	41
Betula lenta	sweet birch	12	17	25	6	7	0
Hamamelis virginiana	America witchhazel	10	134	99			
Nyssa sylvatica	black gum		9	62	5	33	76
Pinus strobus	eastern white pine	6	4	23	113	180	192
Sassafras albidum	sassafras	76	13	11	22	1	0
Tsuga canadensis	eastern hemlock				0	0	0
Quercus prinus	chestnut oak		2		29	38	57
Quercus rubra/ Quercus velutina	RO (*)	6	6	4	55	22	15
	Unidentified	1					
	Total	663	1643	1654	266	328	381

* red oak group: may include black oak and red oak because of the difficulty of separating these oak species in the field.

Table 4.3. Log likelihood, AIC, slope and R^2 for models used to analyze seedling abundance in red maple (50,000 iterations) in 2008. The most parsimonious model is the one with the lowest AICc. All models support Weibull dispersal kernel form. The full model includes terms of wind, site, tree size, and bath.

Seedling age	New Recruit 2008	1 year-olds 2008	2 year-olds 2008	All Seedlings 2008
Model	wind (*)	wind+site (*)	wind+site +size+bath	wind+site +size+bath
No of seedlings	669	1096	592	3440
No. of parameters	7	9	10	10
Maximum likelihood	-676.22	-833.37	-651.75	-1228.37
AICc	1366.71	1685.19	1324.04	2477.28
Slope	0.99	0.98	0.98	1.00
R^2	0.16	0.19	0.24	0.30
Clumping parameter	3.76	1.93	1.61	2.59
STR/n	0.66			
α (alpha)	0.72	0.00	0.31	0.18
X_0 or λ	103.81	106.08	151.37	58.84
X_b or β (beta)	2.51	1.92	3.00	3.00
amplitude (m)	103.01	98.60	151.23	199.94
direction (radians)	4.92	4.61	5.05	3.30
Bath (#/m^2)			1.03	0.00
Size threshold (cm)			24.33	18.62

Table 4.3. (cont.) Log likelihood, AIC, slope and R^2 for models used to analyze seedling abundance in red maple (50,000 iterations) in 2008. The most parsimonious model is the one with the lowest AICc. All models support Weibull dispersal kernel form. The full model includes terms of wind, site, tree size, and bath.

Seedling age	New Recruit 2008	1 year-olds 2008	2 year-olds 2008	All Seedlings 2008
Model	wind (*)	wind+site (*)	wind+site +size+bath	wind+site +size+bath
Site 1 STR/n	0.66	0.15	------	5.13
Site 2 STR/n	0.66	0.36	6.96	4.43
Site 3 STR/n	0.66	0.42	3.85	10.25

Note: all models set $\beta=3$ get the best result to support the observed data except the * models in new recruits and one year-old seedling data set in 2008.

Recruits in 2008 were predicted to have a high likelihood to occur beneath the canopy (directly fall below the centre of the bole of the parent tree). One-year old, 2-year old and mixed-age seedlings in 2008 were dispersed away from the centre of the stem and located within the 20m mapping distance (Figure 4.4).

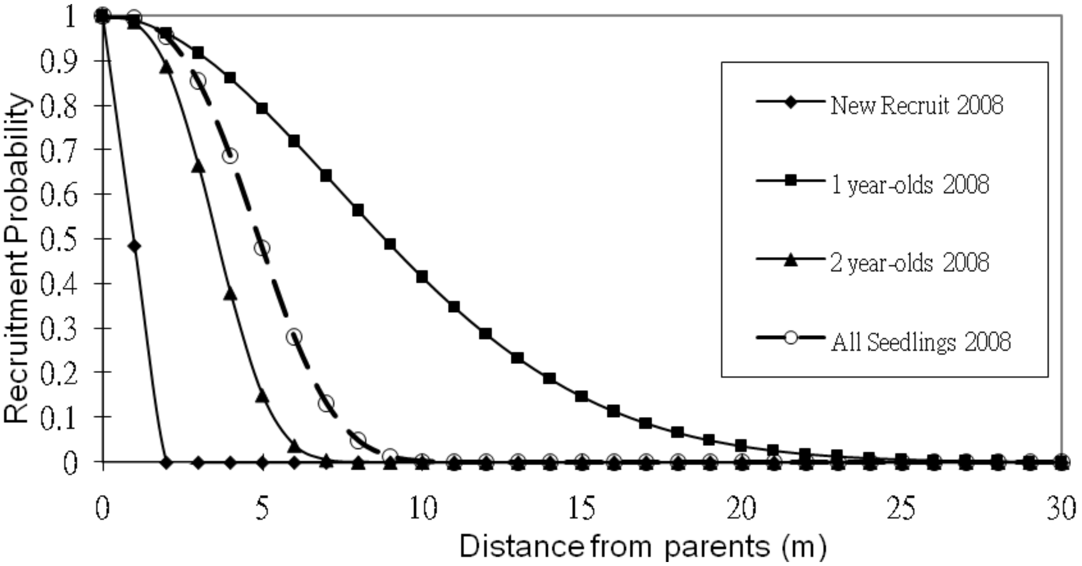

Figure 4.4. Predicted recruitment profile for red maple. Each line shows the predicted probability of seedlings in different age stage around the parent trees.

4.3.2 Likelihood comparisons

The Weibull kernel model was superior to the lognormal kernel in all mixed-age data sets in 2008, new recruits, and 1-year old and 2-year seedlings, with the lowest *AICc* for red maple (Table 4.3). The maximum likelihood model produced good fits for all five data sets of the red maple ($R^2 = 0.16$-0.30), as a result of the relatively large of sample sizes of both parents and seedlings.

Wind direction, tree size threshold, site, and bath recruitment all influenced patterns of seedling recruitment (Table 4.3). All seedling data sets supported a Weibull model that included wind direction effects. The full models including wind direction effects, tree size threshold, site and bath recruitment effects (contribution from non-local trees) gave better fits to seedling data set for the mixed-age in 2008 and 2-year old seedlings in 2008. New recruit entries in 2008 supported a simpler Weibull model that includes wind direction effects only (see Table 4.3). The estimated bath term, i.e. number of seedlings/m^2 from source outside the 20-m radius neighborhood) was slightly greater than zero or larger than one if the models including the bath recruitment term were supported (Table 4.3).

I assumed that the relationship between tree size (dbh) and seedling production was not fixed, and further allowed α, the coefficient relating tree diameter to seedling production, to vary in Equation 8. The maximum likelihood estimates of α for red maple ranged from 0.0002 to 0.72 (Table 4.3). My data supported a model in which parents must reach a threshold size before any seed production will occur (Table 4.3). The estimated minimum reproductive size ranged is 18.6 cm for all seedlings and 24.3 cm for 2 year-olds seedlings in 2008, respectively. Estimated values for α were fairly low for the remaining seedling data sets, indicating a weak relationship between parent size and seedling production once size at minimum reproduction is included as a factor (see Table 4.3).

4.4 Discussion

The use of the inverse modeling approach with maximum likelihood methods allows the exploration of alternative views for understanding patterns of seedling recruitment within a closed canopy, when one cannot directly observe dispersal, following single-tree selection logging in the Camp Deerpark forest. As employed here, this method appears as good or better than similar studies researching seedling establishment (Ribbens et al. 1994, LePage et al. 2000, Uriarte et al. 2005, Martin and Canham 2010). My results suggest seedling recruitment is a complex process involving multiple components, all of which have to be taken into consideration. Distance from local parent trees, sizes of potential parent trees, wind direction, non-local bath recruitment, site condition, interannual variation in seedling production, and negative density-dependent effects of parent trees on seedling recruitment were all influential in seedling recruitment and its spatial distribution in the five years following selection logging.

4.4.1 Seedling production

This study spanned one year of seedling sampling, which in retrospect may have not been long enough to gain a thorough insight into seedling production at Camp Deerpark due to the masting cycle evident in many forest trees. For example, Camp Deerpark was evidently not experiencing mast fruiting during my study since very few oak seedlings were found in the plots in 2008. In addition to interannual variation in acorn and seedling production, there are also many reports about recruitment failure for a number of North American oaks and in some regions throughout the Northern Hemisphere. The factors limiting seedling establishment include acorn infestation by weevils, high levels of acorn pre-dispersal and post-dispersal predation, intense herbivory by deer, small mammals and birds, and unsuitable microhabitat for oak recruitment (Mellanby 1968, Pérez-Ramos and Marañón 2008, Espelta et al. 2009, Bruun H. H. 2010). Eastern white pine, an indication of colonization in past disturbed forests, is the most abundant tree species currently at Camp Deerpark, although very few seedlings were present, which could be due to the low understory light levels present within the closed canopy (Shirley 1945).

Within the study period, variation in the tree size threshold of reproductive trees among years was evident in red maple (Table 4.3). I made the assumption that trees are non-reproductive if the estimated tree size was below the tree size threshold. The estimated minimum reproductive size for the red maple analyses ranged from the smallest size included in the analyses (18.6 cm) to 24.3 cm dbh. Tree size dbh tended to increase with the increasing age of seedling cohort (from new recruits to 2-year old seedlings). Martin and Canham (2010), who studied tree species in transition oak-northern hardwoods in northwestern Connecticut in USA, reported similar findings for four species, including red maple, which led them to suggest that seedlings produced by larger trees had higher survivorship.

A number of possible microsite factors may influence the observed pattern between tree size and reproductive output. Understory substrate favorability as pointed by LePage et al. (2000) is one possible mechanism that could produce this pattern. In my results, site condition is influenced seedling production for most seedling data sets except new recruit entries (Table 4.3). Any live trees, rocks, or fresh leaffall occupy space in seedling quadrats, thereby decreasing the area available for recruitment (LePage et al. 2000).

Previous studies using inverse modeling approaches applied either Poisson or negative binomial distributions to describe seed or seedling density distribution. The Poisson distribution was considered most suitable for wind-dispersed species that are capable of producing relatively large dispersal distances (Clark et al. 1999b). In my results, I found that the negative binomial provided a better fit to seedling data in red maple, a wind-dispersed species. I also found that red maple seedlings produced a small dispersal distance away from the parent trees in 2008. Uriarte et al. (2005) have argued that the negative binomial often produces models with higher likelihood, partly because they are very sensitive to the effects of a few outliers, which treats occasional extreme values as more likely than under a Poisson process, a finding which my results support. Based on the seedling data in 2008, 62.6% of seedling quadrats had less than 10 seedlings/m^2 and only 7 seedling quadrats had over 30 seedlings/m^2. These large numbers of seedlings in one or a few quadrats may favor a result with a more clumped seedling density, which could influence the better fit of the negative binomial for seedling production in red maple.

4.4.2 Seedling dispersion

Despite the amount of attention that has been focused on determining the appropriate shape for the dispersal kernels, there has been no consistent solution to this problem (see review in Green et al. 2004). Among previous studies, Weibull (Ribbens et al. 1994, Clark et al. 1998, Clark et al. 1999b, Canham and Uriarte 2006), lognormal (Tackenberg 2003) or both dispersal kernels (Stoyon and Wagner 2001, Greene et al. 2004, Uriarte et al. 2005, Martin and Canham 2010) were most commonly used in different species with a variety of life-history traits and dispersal syndromes. Further compounding the issue, the suitability of Weibull, lognormal and 2DT functional forms can vary between species (Greene et al. 2004). I tested both Weibull models and lognormal models and found that the Weibull kernels provided the best fit for seedling dispersion patterns through different age stages of seedling cohorts in red maple following single tree selection. However, Martin and Canham (2010) tested the same species in undisturbed transition oak-northern hardwood forests and showed that the lognormal kernels were superior to the Weibull kernels for both seed dispersal and seedling dispersion patterns. In addition to species specificity, Nathan and Muller-Laudau (2000) suggested that seed dispersal or seedling dispersion can also vary among populations and individuals at different distances from parents, in different microsites, and at different times.

As predicted by the Janzen-Connell escape hypothesis (Janzen 1970, Connell 1971), seedlings might benefit from increased parental distance because of a reduced impact of distance- and density-responsive seed and seedling predators and seedling survival increases, resulting in peak recruitment at some distance from the parent and little recruitment near adult conspecifics. This pattern should be more apparent in species with regularly distributed adult populations than for those with random or clumped distributions. My results in figure 4.4 showed that new recruits in red maple had a high likelihood to fall in the proximity of a conspecific adult. The results do not support the Janzen-Connell escape hypothesis. One possible explanation is the spatial distribution of adults in red maple is very clumped, which dilutes the effect. Seedling survival was low for new recruits although red maple produces large crops of light seeds (Streng et al.

1989). In addition, red maple has high seed predation by rodents, regardless of the density (Manson et al. 1998). Taken together, the spatial pattern of adult trees, seed predation and survival might be important causes of the density and spatial distribution of new recruits in red maple.

Comparative analyses of the light selection logging at Camp Deerpark forest and the undisturbed forest at the Great Mountain forest in Connecticut, USA (Martin and Canham 2010), indicated that seedling dispersion in red maple is highly localized and that new recruitment entries show a steep decline with increasing distance from parent trees. Without consideration of the age of seedling cohorts, red maple must reach a threshold size before seedling production occurred. Martin and Canham (2010) showed that this also occurs in other native species in northern transition oak-hardwood forests. The effects of single-tree selection management on red maple seedling recruits in my short-term study mimicked the effects found in undisturbed forests. This suggests that the eventual success of canopy recruitment by red maple seedlings at Camp Deerpark will depend on the distance from local parent trees, the size of potential parent trees, wind direction, non-local bath recruitment, site conditions, interannual variation in seedling production, and the negative density-dependent effects of parent trees.

CHAPTER FIVE

A CASE STUDY OF SINGLE-TREE SELECTION SYSTEM AT CAMP DEERPARK

5.1 Why It Is Important to Promote Forest Management on Private Lands?

Private forest lands cover over one-half of all forest lands in the eastern United States (Smith et al. 2004). Representing approximately 430 million acres, or 57% of all forest lands in the United States, these private lands accounted for 92% of all of timber removals in 2001 (Smith et al. 2004). Private owners, including individuals (single persons or family partnerships) and forest industry companies, make up 58% and 13% of U.S. timberland, respectively (Smith et al. 2004). The numbers also show that there were about 10 million private forest landowners in the United States in 2000, although the vast majority, 9.3 million, owned less than 50 acres (Butler and Leatherberry 2004, Fernholz 2004). However, while half of these family landowners have harvested trees, very few of them (3%) have a written forest-management plan (Butler and Leatherberry 2004). Trends in private family forest owners' ages, how they use their lands, and their future land-use intentions suggest sweeping changes in the fate of many of the nation’s forests in the near future (Butler and Leatherberry 2004).

From an economic perspective, timber from private forestland supports local industries and jobs, contributes significantly to the national economy, and is a predominant source of income for many forestland owners. From an ecological perspective, the sound management of 750 million acres of forest in the United States, or

57% of total forestland, exerts a significant influence on forest-dependent plants and wildlife, water quality, carbon sinks, biological diversity, ecological functions, and ecosystem integrity for the 21st century and beyond. Clearly, unless adequate professional assistance and the full range of management options and silviculture tools becomes available to private landowners of the region, landowners are unlikely to receive maximum benefits and minimize negative environmental impacts through appropriate management of their woodlands.

5.2 How Forest Managers Chose and Applied Single-Tree Selection Practice at Camp Deerpark Forest?

Camp Deerpark forest (CDF) is a small privately owned forest of 100 ha. The forest has been managed using a single-tree selection system according to the principles of sustained-yield forestry since 1996. All harvest operations have multiple management objectives that go well beyond the need for income from wood production. Therefore, more than merely achieving sustained yield, important management objectives at Camp Deerpark forest also included aesthetic enjoyment and outdoor recreation opportunities, extending wildlife habitat, maintaining tree vigor, desired species composition, and stand structure and variability across the landscape. This affords an opportunity to educate visiting groups and summer campers about the benefits of good forest management and the responsibilities associated with forest stewardship.

Just as most forest managers throughout eastern North America desire to maintain current levels of oak species (Dey et al. 2004), forest managers at Camp Deerpark favor red oak and black cherry establishment, and want to gradually shift their forest to late-succession, shade-tolerant hardwoods stands. Eastern white pine, a shade intolerant (or mid shade tolerant) species and an indication of colonization in the past disturbed forests, is the most abundant tree species and accounts for over half in tree abundance currently at Camp Deerpark based on the inventory data (see Chapter Two). Forest managers want to remove most of the eastern white pine but still maintain a continuous overstory cover and promote the gradual species shift to the more shade-tolerant species. With the single-tree selection method, foresters remove the mature trees to create small discontinuous openings distributed across the stand for regeneration or the release of younger growing stock. Thus, the forest managers expect eastern white pine in the forest to decline over time under a single-tree selection system, assuming that no catastrophic events such as wildfire and severe hurricane occur beforehand.

By mimicking gap-phase replacement or tree mortality of individuals in unmanaged old-growth, the regulated single-tree selection system needs to take into consideration both age-classes and species, giving rise to a selection system that does not remove a single tree without taking into consideration its reproduction and its relation to the future crop (Miller and Smith 1993a, Nyland 2007). The application of single-tree selection at Camp Deerpak is associated exclusively with natural reproduction instead of planting or artificial regeneration. The major regeneration arises from a combination of new seedlings, advance regeneration (primarily seedlings), and sprouts. Foresters use a reverse-J diameter distribution, which depicts communities with large numbers of small trees and relatively few large-diameter ones as a theoretical ideal to sustain regeneration in a uneven-aged stand (Smith et al. 1997, Nyland 2007). In order to stabilize the forest structure, maintain a good interspersion of diameter classes or age classes through single-tree selection, and optimize volume production over repeated cutting cycles, basic inventory data are required before marking the stand using single-tree selection methods. A10% forest inventory was conducted at Camp Deerpark done by volunteers before harvest. All woody stems ≥ 10.0 cm dbh were identified, recorded, and measured for diameter. Foresters at Camp Deerpark Forest also took tree cores for tree growth analysis. Based on the results of both diameter class distribution and tree growth rate, they calculate how many trees, species and timber volume can be cut for the allowable cut at a time to maintain sustained-yield production. After training, foresters mark stands in a single pass and paint on the bole at breast height for the preferred direction for felling the tree. This can reduce the level of canopy damage to other trees. An appropriate number of the oldest and largest trees were harvested first, partly because they are most susceptible to disease and have large canopy covers that suppress the growth of smaller trees. To minimize canopy disturbance, only one individual tree is removed within tree fall radius of each harvest tree. This creates small canopy openings and further inhibits seedling recruitment in eastern white pine. CDF foresters also make sure to see another individual of the same species from each tree that is marked for felling. And thus, a new age class of appropriate species and density can regenerate and grow in the space previously occupied by mature trees. It also allows unhealthy, defective, non-commercial species to be cut annually in order to maintain healthy and vigorous stands, based on the guideline of Timber Stand Improvement (TSI), which uses either mechanical or chemical treatments of vegetation to improve the species composition, structure, condition, health and growth of either even-age or uneven-age stands (Anderson 1975). Skid trails and landings are carefully laid out to minimize erosion, compaction, and rutting. The cutting cycle for uneven-aged units is set at five-year intervals to attain the desired number of residual trees in each age class. In order to regulate crowding within each age class, the space for each age class, the number of age classes present, and their interspersion (in time and space), growth data is collected and re-calculated at each time to adjust the allowable cut.

Finally, in addition to sustained yield and tree vigor, species composition and variability in stand structure, foresters at Camp Deerpark take wildlife habitat into consideration when they plan harvest operations. They leave nest and den trees in the forest to maintain structural diversity and cavity resource for wildlife habitat. “Heritage” trees, i.e. trees that are usually large, have unique shapes, have unique locations, or rare in some way or another, will be conserved.

5.3 Management Implication of Variation in Sensitivity to Crowding

My results for quantitative estimates of the strength of interspecific competition between pairs of species reveal that most of the individual pairwise interactions were strongly asymmetric in competitive interactions at the Camp Deerpark forest (Table 3.5). Specifically, the asymmetric crowding effects on tree species appeared from a very certain small subset of strong competitors within the guild. The column averages in the matrix shown in Table 3.5 can be used as a ranking of the relative strength of species on crowding competition. I found that two of the most common early- and mid-successional species in the forest, red maple and eastern white pine, had strong crowding effects with high average per capita effects on other species, while all other three oak species (red oak, white oak and chestnut oak) had little effect on them.

Many previous studies have assumed that there is relatively strong competition within conspecific neighbors; this is implicit in most competition theory. I found no evidence to support this assumption in my data, with the exception of the results for red maple (Table 3.5). This relative weak effect via crowding in conspecific neighbors is surprising. Coates et al. (2009) used growth data sampled across a wide range of stand ages, disturbance histories, tree species composition, and competitive neighborhoods in British Columbia. Their results suggested most species had weak intraspecific competition. Other studies found that plant individuals surrounded by conspecific species had lower growth or survival leading these authors to conclude that there was strong intraspecific competition for resources, which further emphasizes the importance of negative density dependence (e.g. (Uriarte et al. 2004a, Queenborough et al. 2007, Comita and Hubbell 2009)). However, as of yet there are no empirical tests that examine variation among species and species abundances for the strength of negative density dependence (Comita et al. 2010). Coates et al. (2009) and my study show that species with fewer individuals experienced very weak intraspecific competition. The value of per cpita competition coefficient λ reflects the competition effect of any given unit of species abundance. Red maple presented strong competition by conspecifics based on my tree growth results with the high value of λ in red maple (Table 3.5).

Contrary to many previous studies of tree competition, I found support for the hypothesis that target trees are more sensitive to crowding when they are smaller rather than when they are larger (γ in Table 3.3). The least sensitive species were also the two most abundant species, red maple and eastern white pine. Furthermore, I found that faster growing trees are less sensitive to neighborhood competition.

My results highlight the strong asymmetries in species and the complexity of the strength of competitive effects and responses within this guild of intermediate shade tolerant and early- and mid- successional species in temperate forests. Moreover, small trees and slow-growing trees have a more pronounced growth response to crowding competition. Relatively low removal rates in the single-tree selection system may be less successful in favoring the growth of regenerating trees for intermediate to shade intolerant species unless careful attention is paid to the spatial distribution of the removed and retained canopy trees (Coates et al. 2003).

5.4 How Will Silvicultural Practice Affect the Forest of Camp Deerpark?

By mimicking gap disturbance or tree mortality of individuals, very small openings in the overstory allow a limited amount of sunlight to reach the forest floor. Generally, this system allows regeneration of only the most shade tolerant species like hemlock, beech, sugar maple, and intermediate shade tolerant speces such as red maple (Smith et al. 1997, Nyland 2007). Red maple is traditionally viewed as only intermediate shade tolerant, but there is accumulating evidence that it is more shade tolerant than widely believed (Canham pers. comm.). My seedling results also support this viewpoint, and the shade-tolerant species red maple is the most abundant tree seedling species. In addition, my seedling results for red maple suggested that the recruitment is determined by site conditions, the availability and location of parent trees, fecundity, and dispersal patterns. Seedling recruitment is significantly correlated with the distribution of parents, and recruitment is severely limited or totally absent when parents are not present (Ribbens 1994). My results also showed that seedling dispersion is local (i.e., short-distance) and tree size in dbh tended to increase with the increasing age of seedling cohort (new recruits to 2-year old seedlings). Martin and Canham (2010) suggested that seedlings produced by larger trees had higher survivorship. They further suggested that "larger trees predominate as the source of successful seedling recruitment (Martin and Canham 2010)."

On the other hand, as Ribbens (1994, p. 1805) pointed out, some species are much more recruitment-limited than others, despite presence of adults. This may be caused by either a low number of recruits or a poor dispersal of recruits. Recruitment limitation can be a common at a stand-level spatial scale and can have substantial and long-lasting effects on community composition and dynamics. It is true in mixed tolerant hardwood-eastern white pine stands at Camp Deerpark forest. In my seedling results, although eastern white pine is the most abundant shade-intolerant tree species there are very few seedling individuals found in the seedling quadrats. This may be because regeneration methods from single-tree selection create only small canopy gaps, which produces very limited understory light levels that are similar to unmanaged, mature hardwood forest structure. Although eastern white pine can germinate under heavy shade, these light levels may be insufficient for their long-term survival. This recruitment limitation situation also occurs in oak species at Camp Deerpark.

Single-tree selection is better suited for seedlings that propagate well in poor light beneath the forest canopy. It is true that seedlings in red maple are the most abundant at Camp Deerpark Forest. However, red maple is poorly regarded as a timber species. Based on my study, both eastern white pine and red maple are the most abundant and least sensitive species to crowding competition, and have strong competition effects to oak species in the neighborhood scale. In addition, my research study showed that seedling recruitment is significantly correlated with the distribution of parents. Based on these findings, it is recommended that both eastern white pine and red maple trees of varying size can be removed gradually to stimulate the growth of the residual oak stock. To meet one mangemnet objective at CDF, removal of mature trees in eastern white pine can decrease seed and seedling abundance and successfully converts mixed tolerant hardwood-eastern white pine stands to shade tolerant species. This can be implemented annually following the principles of TSI to improve the growth and form of oak species and increase the value of the stand.

There were very few oak seedlings during my study years. This might be because the trees were not experiencing a mast year. Temporal variation in reproductive effort can be enormous and have significant effects on the distribution and abundance of regeneration. Many research studies have showed recruitment is severely limited or totally absent when parents are not present (Ribbens 1994). I suggest, therefore, that a selection of mature oak trees be left as seed source in the forest for natural regeneration over several cutting cycles.

5.5 Current Challenges, Opportunities and Future Directions

From a management perspective, my results here are of both theoretical and applied interest in stand-level simulations of "neighborhood" dynamics. Likewise, these results are important for planning the optimal size and shape of single-tree selection silvicultural strategies for forests that are intended to be regenerated naturally and to keep the forest healthy. Neighborhood analyses using inverse modeling are the most economical and powerful method for estimating the parameters of dispersal functions, based on (1) measurements of seed rain or seedling abundance at a set of sample locations and, (2) a map of the spatial distribution and sizes of potential parent trees in the vicinities of the sample locations (Ribbens et al. 1994, Clark and Fastie 1998, Clark et al. 1998, Clark et al. 1999b, LePage et al. 2000, Uriarte et al. 2005, Martin and Canham 2010). Furthermore, my seedling study provides valuable insights on how one should manage regeneration and recruitment process. Forest managers can use these results to help develop detailed stand prescriptions that address the full range of silvicultural systems currently in operation.

Uneven-aged mixed species management is complex in terms of structure and species. Following logging, there is a continuing dynamic competitive balance between one given tree and its neighboring trees in allocation of resources such as light and space (LePage *et al.* 2000, Coates 2002, Coates *et al.* 2003, Canham *et al.* 2004, Canham *et al.*

2006, Papaik and Canham 2006). O'Hara (2002) pointed out that "our biggest challenge in advancing the science and application of uneven-age silviculture is in developing procedures that recognize natural stand dynamics, provide flexibility for different management objectives and provide for long-term sustainability. With new understanding of the importance of disturbances in affecting stand age structures, and the subsequent development of complex mixed-species and multiaged stands, we should recognize this as an opportunity to develop new ways of managing these stands." Forest management at Camp Deerpark Forest is a compromise between many competing objectives and it strives to balance the growth response of residual trees, structural diversity, timber revenues and education objectives. In many of these areas, the management plan has been quite successful. Based on the experience at Camp Deerpark Forest, it would seem to be extremely worthwhile for other private landowners to apply the single-tree selection method to the management of the woodland.

APPENDIX I. R scripts used to examine a series of candidate models for neighborhood competition on tree radial growth rate after selection logging.

I show red maple as an example in the R script. The analyses were done using the R language version 2.6.2.

```
######################################################
#
# Camp Deerpark tree growth
# as a function of (1)tree size,(2)NCI.
# Predicted growth = Maximum growth x Size effect x Neighborhood effect
#
## with a neighborhood calculation and two datasets
## Two forms for the size effect:
##              (1) Power function: Max * DBH^b
##              (2) Lognormal function: Max * exp(-0.5*(log(DBH/Xo)/Xb)^2)
#
##
## give a fixed neighbor trees of types for NCI:
##  NCI = sum(DBH/100)^2 / (distance) of the
```

```
##  neighbors within a 20 meter radius;
##  Parameters: C, Max, b, (Xo, Xb)
##
## Dataset: included targets1 and neighbors1 dataset
##
######################################################


# Set the working directory


#setwd("C:/Sophie/G5010R/CampDP/NCI")
setwd("C:/Documents and Settings/Gradstudent.DA223-
BIOCON7/Desktop/Sophie_ACRU")


# READ IN THE DATA


all.growth <- read.csv("07summer_campDP_tree_updated.csv",header = TRUE)


life.data <- subset(all.growth,(Life=="L") & (DBH != "NA") & (growth.habit=="T"))
core.data <- subset(life.data, pre.harvest!="NA")
acru.data <- subset(core.data, species=="ACRU")
str(acru.data)
```

```
summary(life.data$DBH)

summary(acru.data$pre.harvest)

summary(acru.data$post.harvest)



################################################################################



# scale up growth to avoid problems estimating the variance term

acru.data$growth10 <- acru.data$post.harvest*10


library(neighlikeli)

neighbors1=life.data

targets1=acru.data


################################################################################

#

#   create summary variables for neighbors with fixed alpha and beta

#

################################################################################


neighbors1$dbhm2 <- (neighbors1$DBH/100)^2
```

```
for (i in 1:length(targets1$post.harvest))
{ neighbors1$ndist <-
neighdist(targets1$Xpos[[i]],targets1$Ypos[[i]],neighbors1$Xpos,neighbors1$Ypos)
  neighbors1$dbhm2dist <- neighbors1$dbhm2/neighbors1$ndist
  targets1$ndbhm2[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot == targets1$plot[[i]]
& neighbors1$ndist <=  10 &
                              neighbors1$ndist > 0])
  targets1$ndbhm2dist[[i]] <- sum(neighbors1$dbhm2dist[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                              neighbors1$ndist > 0])


  targets1$ndbhm2gp1[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                              neighbors1$ndist > 0 & neighbors1$groupcode == 1])
  targets1$ndbhm2distgp1[[i]] <- sum(neighbors1$dbhm2dist[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                              neighbors1$ndist > 0 & neighbors1$groupcode == 1])
  targets1$ndbhm2gp2[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                              neighbors1$ndist > 0 & neighbors1$groupcode == 2])
  targets1$ndbhm2distgp2[[i]] <- sum(neighbors1$dbhm2dist[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
```

```
                                    neighbors1$ndist > 0 & neighbors1$groupcode == 2])
  targets1$ndbhm2gp3[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                    neighbors1$ndist > 0 & neighbors1$groupcode == 3])
  targets1$ndbhm2distgp3[[i]] <- sum(neighbors1$dbhm2dist[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                    neighbors1$ndist > 0 & neighbors1$groupcode == 3])
  targets1$ndbhm2gp4[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                    neighbors1$ndist > 0 & neighbors1$groupcode == 4])
  targets1$ndbhm2distgp4[[i]] <- sum(neighbors1$dbhm2dist[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                    neighbors1$ndist > 0 & neighbors1$groupcode == 4])
  targets1$ndbhm2gp5[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                    neighbors1$ndist > 0 & neighbors1$groupcode == 5])
  targets1$ndbhm2distgp5[[i]] <- sum(neighbors1$dbhm2dist[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                    neighbors1$ndist > 0 & neighbors1$groupcode == 5])
  targets1$ndbhm2gp6[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                    neighbors1$ndist > 0 & neighbors1$groupcode == 6])
```

```
  targets1$ndbhm2distgp6[[i]] <- sum(neighbors1$dbhm2dist[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                              neighbors1$ndist > 0 & neighbors1$groupcode == 6])



  targets1$ndbhm2gp.acru.mixed1[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                  neighbors1$ndist > 0 & neighbors1$gp_acru.mixed == 1])
  targets1$ndbhm2distgp.acru.mixed1[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                    neighbors1$ndist > 0 & neighbors1$gp_acru.mixed == 1])
  targets1$ndbhm2gp.acru.mixed2[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                  neighbors1$ndist > 0 & neighbors1$gp_acru.mixed == 2])
  targets1$ndbhm2distgp.acru.mixed2[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                    neighbors1$ndist > 0 & neighbors1$gp_acru.mixed == 2])
  targets1$ndbhm2gp.acru.mixed3[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                  neighbors1$ndist > 0 & neighbors1$gp_acru.mixed == 3])
```

```
  targets1$ndbhm2distgp.acru.mixed3[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                   neighbors1$ndist > 0 & neighbors1$gp_acru.mixed == 3])
  targets1$ndbhm2gp.pist.mixed1[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                 neighbors1$ndist > 0 & neighbors1$gp_pist.mixed == 1])
  targets1$ndbhm2distgp.pist.mixed1[[i]] <- sum(neighbors1$dbhm2dist[neighbors1$plot
== targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                   neighbors1$ndist > 0 & neighbors1$gp_pist.mixed == 1])
  targets1$ndbhm2gp.pist.mixed2[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                 neighbors1$ndist > 0 & neighbors1$gp_pist.mixed == 2])
  targets1$ndbhm2distgp.pist.mixed2[[i]] <- sum(neighbors1$dbhm2dist[neighbors1$plot
== targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                   neighbors1$ndist > 0 & neighbors1$gp_pist.mixed == 2])
  targets1$ndbhm2gp.qupr.mixed1[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                 neighbors1$ndist > 0 & neighbors1$gp_qupr.mixed == 1])
  targets1$ndbhm2distgp.qupr.mixed1[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                   neighbors1$ndist > 0 & neighbors1$gp_qupr.mixed == 1])
```

```
  targets1$ndbhm2gp.qupr.mixed2[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                neighbors1$ndist > 0 & neighbors1$gp_qupr.mixed == 2])
  targets1$ndbhm2distgp.qupr.mixed2[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                  neighbors1$ndist > 0 & neighbors1$gp_qupr.mixed == 2])
  targets1$ndbhm2gp.qupr.mixed3[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                neighbors1$ndist > 0 & neighbors1$gp_qupr.mixed == 3])
  targets1$ndbhm2distgp.qupr.mixed3[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                  neighbors1$ndist > 0 & neighbors1$gp_qupr.mixed == 3])
  targets1$ndbhm2gp.quru.mixed1[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                neighbors1$ndist > 0 & neighbors1$gp_quru.mixed == 1])
  targets1$ndbhm2distgp.quru.mixed1[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                  neighbors1$ndist > 0 & neighbors1$gp_quru.mixed == 1])
  targets1$ndbhm2gp.quru.mixed2[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
```

```
                                        neighbors1$ndist > 0 & neighbors1$gp_quru.mixed == 2])
  targets1$ndbhm2distgp.quru.mixed2[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                           neighbors1$ndist > 0 & neighbors1$gp_quru.mixed == 2])
  targets1$ndbhm2gp.quru.mixed3[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                        neighbors1$ndist > 0 & neighbors1$gp_quru.mixed == 3])
  targets1$ndbhm2distgp.quru.mixed3[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                           neighbors1$ndist > 0 & neighbors1$gp_quru.mixed == 3])


  targets1$ndbhm2gp.family1[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                      neighbors1$ndist > 0 & neighbors1$gp_family == 1])
  targets1$ndbhm2distgp.family1[[i]] <- sum(neighbors1$dbhm2dist[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                          neighbors1$ndist > 0 & neighbors1$gp_family == 1])
  targets1$ndbhm2gp.family2[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                      neighbors1$ndist > 0 & neighbors1$gp_family == 2])
```

```
  targets1$ndbhm2distgp.family2[[i]] <- sum(neighbors1$dbhm2dist[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                   neighbors1$ndist > 0 & neighbors1$gp_family == 2])
  targets1$ndbhm2gp.family3[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                neighbors1$ndist > 0 & neighbors1$gp_family == 3])
  targets1$ndbhm2distgp.family3[[i]] <- sum(neighbors1$dbhm2dist[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                   neighbors1$ndist > 0 & neighbors1$gp_family == 3])
  targets1$ndbhm2gp.family4[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                neighbors1$ndist > 0 & neighbors1$gp_family == 4])
  targets1$ndbhm2distgp.family4[[i]] <- sum(neighbors1$dbhm2dist[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                   neighbors1$ndist > 0 & neighbors1$gp_family == 4])


  targets1$ndbhm2gp.acru.vs.others1[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                       neighbors1$ndist > 0 & neighbors1$gp_acru.vs.others ==
1])
  targets1$ndbhm2distgp.acru.vs.others1[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
```

```
                                     neighbors1$ndist > 0 & neighbors1$gp_acru.vs.others ==
1])
  targets1$ndbhm2gp.acru.vs.others2[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                   neighbors1$ndist > 0 & neighbors1$gp_acru.vs.others ==
2])
  targets1$ndbhm2distgp.acru.vs.others2[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                     neighbors1$ndist > 0 & neighbors1$gp_acru.vs.others ==
2])


  targets1$ndbhm2gp.pist.vs.others1[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                   neighbors1$ndist > 0 & neighbors1$gp_pist.vs.others == 1])
  targets1$ndbhm2distgp.pist.vs.others1[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                     neighbors1$ndist > 0 & neighbors1$gp_pist.vs.others ==
1])
  targets1$ndbhm2gp.pist.vs.others2[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                   neighbors1$ndist > 0 & neighbors1$gp_pist.vs.others == 2])
```

```
  targets1$ndbhm2distgp.pist.vs.others2[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                    neighbors1$ndist > 0 & neighbors1$gp_pist.vs.others ==
2])

  targets1$ndbhm2gp.qual.vs.others1[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                  neighbors1$ndist > 0 & neighbors1$gp_qual.vs.others ==
1])
  targets1$ndbhm2distgp.qual.vs.others1[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                    neighbors1$ndist > 0 & neighbors1$gp_qual.vs.others ==
1])
  targets1$ndbhm2gp.qual.vs.others2[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                  neighbors1$ndist > 0 & neighbors1$gp_qual.vs.others ==
2])
  targets1$ndbhm2distgp.qual.vs.others2[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
```

```
                                     neighbors1$ndist > 0 & neighbors1$gp_qual.vs.others ==
2])

  targets1$ndbhm2gp.qupr.vs.others1[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                   neighbors1$ndist > 0 & neighbors1$gp_qupr.vs.others ==
1])
  targets1$ndbhm2distgp.qupr.vs.others1[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                     neighbors1$ndist > 0 & neighbors1$gp_qupr.vs.others ==
1])
  targets1$ndbhm2gp.qupr.vs.others2[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                   neighbors1$ndist > 0 & neighbors1$gp_qupr.vs.others ==
2])
  targets1$ndbhm2distgp.qupr.vs.others2[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                     neighbors1$ndist > 0 & neighbors1$gp_qupr.vs.others ==
2])
```

```
  targets1$ndbhm2gp.quru.vs.others1[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                        neighbors1$ndist > 0 & neighbors1$gp_quru.vs.others ==
1])
  targets1$ndbhm2distgp.quru.vs.others1[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                          neighbors1$ndist > 0 & neighbors1$gp_quru.vs.others ==
1])
  targets1$ndbhm2gp.quru.vs.others2[[i]] <- sum(neighbors1$dbhm2[neighbors1$plot ==
targets1$plot[[i]] & neighbors1$ndist <=  10 &
                                        neighbors1$ndist > 0 & neighbors1$gp_quru.vs.others ==
2])
  targets1$ndbhm2distgp.quru.vs.others2[[i]] <-
sum(neighbors1$dbhm2dist[neighbors1$plot == targets1$plot[[i]] & neighbors1$ndist
<=  10 &
                                          neighbors1$ndist > 0 & neighbors1$gp_quru.vs.others ==
2])



}
summary(targets1$ndbhm2)
summary(targets1$ndbhm2dist)
```

```
summary(targets1$ndbhm2gp1)

summary(targets1$ndbhm2distgp1)

summary(targets1$ndbhm2gp.family1)

summary(targets1$ndbhm2distgp.family1)


##############################################################################

#

#   (S1)an NCI model using these fixed parameter neighbor sum variables

#      but with species-specific competition coefficients (lambdas)

#          (Mixed)

#          model grouping species which had similar estimated lambda(s)

#

##############################################################################


# power size function with NCI

power.NCIsum.lambda.mixed.model <-

function(Max,b,C,l15,l16,l17,MIX1,MIX2,MIX3,DBH)

{

  ncimix <- l15*MIX1 + l16*MIX2 + l17*MIX3

  (Max * DBH^b) * exp(-1.0* C * ncimix)

}


# par list for the power NCI function
```

```
par<-list(C = 5, Max = 2, sd = 2, b = 1, l15 = 0.5, l16 = 0.5, l17 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, l15 = 0, l16 = 0, l17 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, b = 5, l15 = 1, l16 = 1, l17 = 1)

var <- list(DBH="DBH", MIX1 = "ndbhm2distgp.acru.mixed1", MIX2 =
"ndbhm2distgp.acru.mixed2", MIX3 = "ndbhm2distgp.acru.mixed3")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.power.NCIsum.lambda.mixed <- anneal(power.NCIsum.lambda.mixed.model, par,
var, targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.power.NCIsum.lambda.mixed,"Power_ACRU_NCIsum with
lambda_mixed_R10_output_100000.txt")


######################################################################
#
#   (S2)an NCI model using these fixed parameter neighbor sum variables
#     but with species-specific competition coefficients (lambdas)
```

```
#           with size sensitive (gamma)
#          (Mixed)
#          model grouping species which had similar estimated lambda(s)
#
##########################################################################

# power size function with NCI
power.NCIsum.lambda.mixed.gamma.model <-
function(Max,b,C,gamma,l15,l16,l17,MIX1,MIX2,MIX3,DBH)
{
  ncimix <- l15*MIX1 + l16*MIX2 + l17*MIX3
  (Max * (DBH/30)^b) * exp(-1.0* C * ((DBH/30)^gamma) * ncimix)
}

# par list for the power NCI function
par<-list(C = 5, Max = 2, sd = 2, b = 1, gamma = 0, l15 = 0.5, l16 = 0.5, l17 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, gamma = -10,  l15 = 0, l16 = 0,
l17 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, b = 5, gamma = 10,  l15 = 1, l16 = 1, l17
= 1)

var <- list(DBH="DBH", MIX1 = "ndbhm2distgp.acru.mixed1", MIX2 =
"ndbhm2distgp.acru.mixed2", MIX3 = "ndbhm2distgp.acru.mixed3")
```

```
var$x <- "post.harvest"

var$mean <- "predicted"

var$log <- TRUE


# annealing

result.power.NCIsum.lambda.mixed.gamma <-

anneal(power.NCIsum.lambda.mixed.gamma.model, par, var, targets1,par_lo, par_hi,

        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)


write_results(result.power.NCIsum.lambda.mixed.gamma,"Power_ACRU_NCIsum with
lambda_mixed_gamma_R10_output_100000.txt")



############################################################################

#

#   (S3)an NCI model using these fixed parameter neighbor sum variables

#     but with species-specific competition coefficients (lambdas)

#          with size sensitive (gamma)  and prior growth track (pre)

#         (Mixed)

#         model grouping species which had similar estimated lambda(s)

#

############################################################################
```

```
# power size function with NCI
power.NCIsum.lambda.mixed.pre.gamma.model <-
function(Max,b,C,gamma,pre,l15,l16,l17,MIX1,MIX2,MIX3,DBH)
{
  ncimix <- l15*MIX1 + l16*MIX2 + l17*MIX3
  (Max * DBH^b) * exp(-1.0* C * ((pre*10)^gamma) * ncimix)
}

# par list for the power NCI function
par<-list(C = 5, Max = 2, sd = 2, b = 1, gamma = 0, l15 = 0.5, l16 = 0.5, l17 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, gamma = -10,  l15 = 0, l16 = 0,
l17 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, b = 5, gamma = 10,  l15 = 1, l16 = 1, l17
= 1)

var <- list(DBH="DBH", pre="pre.harvest", MIX1 = "ndbhm2distgp.acru.mixed1",
MIX2 = "ndbhm2distgp.acru.mixed2", MIX3 = "ndbhm2distgp.acru.mixed3")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
```

```
result.power.NCIsum.lambda.mixed.pre.gamma <-
anneal(power.NCIsum.lambda.mixed.pre.gamma.model, par, var, targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.power.NCIsum.lambda.mixed.pre.gamma,"Power_ACRU_NCIsum
with lambda_mixed_pre_gamma_R10_output_100000.txt")



#############################################################################
#
#   (1) an NCI model using these fixed parameter neighbor sum variables
#      (EQUIV) lambda=1
#
#############################################################################

# power size function with NCI
power.NCIsum.model <- function(Max,b,C,NCI,DBH)
{  (Max * DBH^b) * exp(-1.0* C * NCI)   }

# par list for the power NCI function
par<-list(C = 0, Max = 0, sd = 2, b = 1)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01)
par_hi <- list(C = 100, Max = 100, sd = 1000, b = 5)
```

```
var <- list(DBH="DBH", NCI = "ndbhm2dist")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.power.NCIsum <- anneal(power.NCIsum.model, par, var, targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.power.NCIsum,"Power_ACRU_NCIsum_R10_output_100000.txt")

##############################################################################
#
#   (2) an NCI model using these fixed parameter neighbor sum variables
#       (EQUIV) lambda=1
#       with size sensitive (gamma)
#
##############################################################################

# power size function with NCI
power.NCIsum.gamma.model <- function(Max,b,C,gamma,NCI,DBH)
{  (Max * DBH^b) * exp(-1.0* C * ((DBH/30)^gamma)*NCI)   }
```

```
# par list for the power NCI function
par<-list(C = 0, Max = 0, sd = 2, b = 1, gamma = 0)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, gamma = -10)
par_hi <- list(C = 100, Max = 100, sd = 1000, b = 5, gamma = 10)

var <- list(DBH="DBH", NCI = "ndbhm2dist")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.power.NCIsumgamma <- anneal(power.NCIsum.gamma.model, par, var,
targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.power.NCIsumgamma,"Power_ACRU_NCIsum_gamma_R10_outpu
t_100000.txt")



##########################################################################
#
```

```
#   (3) an NCI model using these fixed parameter neighbor sum variables
#       (EQUIV) lambda=1
#          with size sensitive (gamma) and prior growth track (pre)
#
##########################################################################


# power size function with NCI
power.NCIsum.pre.gamma.model <- function(Max,b,C,pre,gamma,NCI,DBH)
{  (Max * DBH^b) * exp(-1.0* C * ((pre*10)^gamma)*NCI)   }


# par list for the power NCI function
par<-list(C = 0, Max = 0, sd = 2, b = 1, gamma = 0)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, gamma = -10)
par_hi <- list(C = 100, Max = 100, sd = 1000, b = 5, gamma = 10)


var <- list(DBH="DBH", NCI = "ndbhm2dist", pre="pre.harvest")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE


# annealing
result.power.NCIsum.pre.gamma <- anneal(power.NCIsum.pre.gamma.model, par, var,
targets1,par_lo, par_hi,
```

```
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.power.NCIsum.pre.gamma,"Power_ACRU_NCIsum_pre_gamma_R
10_output_100000.txt")



###############################################################################
#
#   (4) an NCI model using these fixed parameter neighbor sum variables
#      (EQUIV) lambda=1
#      with size sensitive (gamma)
#      growth ratio
#
###############################################################################

targets1$grratio <- targets1$post.harvest/targets1$pre.harvest

# power size function with NCI
power.NCIsum.gamma.grratio.model <- function(Max,b,C,gamma,NCI,DBH)
{  (Max * DBH^b) * exp(-1.0* C * ((DBH/30)^gamma)*NCI)   }

# par list for the power NCI function
par<-list(C = 0, Max = 0, sd = 2, b = 1, gamma = 0)
```

```
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, gamma = -10)

par_hi <- list(C = 100, Max = 100, sd = 1000, b = 5, gamma = 10)


var <- list(DBH="DBH", NCI = "ndbhm2dist")

var$x <- "grratio"

var$mean <- "predicted"

var$log <- TRUE


# annealing

result.power.NCIsum.gamma.grratio <- anneal(power.NCIsum.gamma.grratio.model,
par, var, targets1,par_lo, par_hi,

        dnorm, "grratio", max_iter=100000, hessian = TRUE)


write_results(result.power.NCIsum.gamma.grratio,"Power_ACRU_NCIsum_gamma_grr
atio_R10_output_100000.txt")



##############################################################################

#

#   (5) an NCI model using these fixed parameter neighbor sum variables

#      but with species-specific competition coefficients (lambdas)

#           Species-specific lambdas

#
```

```
##########################################################################

# power size function with NCI
power.NCIsum.lambda.model <-
function(Max,b,C,l1,l2,l3,l4,l5,l6,G1,G2,G3,G4,G5,G6,DBH)
{
  ncis <- l1*G1 + l2*G2 + l3*G3 + l4*G4 + l5*G5 + l6*G6
  (Max * DBH^b) * exp(-1.0* C * ncis)
}

# par list for the power NCI function
par<-list(C = 5, Max = 2, sd = 2, b = 1, l1 = 0.5, l2 = 0.5, l3 = 0.5, l4 = 0.5, l5 = 0.5, l6 =
0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, l1 = 0, l2 = 0, l3 = 0, l4 = 0, l5 =
0, l6 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, b = 5, l1 = 1, l2 = 1, l3 = 1, l4 = 1, l5 = 1,
l6 = 1)

var <- list(DBH="DBH", G1 = "ndbhm2distgp1", G2 = "ndbhm2distgp2", G3 =
"ndbhm2distgp3", G4 = "ndbhm2distgp4",
  G5 = "ndbhm2distgp5", G6 = "ndbhm2distgp6")
var$x <- "post.harvest"
var$mean <- "predicted"
```

```
var$log <- TRUE


# annealing

result.power.NCIsum.lambda <- anneal(power.NCIsum.lambda.model, par, var,
targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)


write_results(result.power.NCIsum.lambda,"Power_ACRU_NCIsum with
lambda_R10_output_100000.txt")


plot(targets1$ndbhm2dist,targets1$post.harvest)


##################################################





######################################################################
#
#   (5.1) an NCI model using these fixed parameter neighbor sum variables
#      but with species-specific competition coefficients (lambdas)
#           Species-specific lambdas
#
#           * change "post.harvest" to 2*"post.harvest"
```

```
#
##############################################################################

targets1$post.harvest2 <- 2*targets1$post.harvest
# power size function with NCI
power.NCIsum.lambda2.model <-
function(Max,b,C,l1,l2,l3,l4,l5,l6,G1,G2,G3,G4,G5,G6,DBH)
{
  ncis <- l1*G1 + l2*G2 + l3*G3 + l4*G4 + l5*G5 + l6*G6
  (Max * DBH^b) * exp(-1.0* C * ncis)
}

# par list for the power NCI function
par<-list(C = 5, Max = 2, sd = 2, b = 1, l1 = 0.5, l2 = 0.5, l3 = 0.5, l4 = 0.5, l5 = 0.5, l6 =
0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, l1 = 0, l2 = 0, l3 = 0, l4 = 0, l5 =
0, l6 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, b = 5, l1 = 1, l2 = 1, l3 = 1, l4 = 1, l5 = 1,
l6 = 1)

var <- list(DBH="DBH", G1 = "ndbhm2distgp1", G2 = "ndbhm2distgp2", G3 =
"ndbhm2distgp3", G4 = "ndbhm2distgp4",
  G5 = "ndbhm2distgp5", G6 = "ndbhm2distgp6")
```

```
var$x <- "post.harvest2"  #change here!**************

var$mean <- "predicted"

var$log <- TRUE


# annealing

result.power.NCIsum.lambda2 <- anneal(power.NCIsum.lambda2.model, par, var,
targets1,par_lo, par_hi,

        dnorm, "post.harvest2", max_iter=100000, hessian = TRUE)


write_results(result.power.NCIsum.lambda2,"Power_ACRU_NCIsum with
lambda2_R10_output_100000.txt")



################################################################################

#

#   (6) an NCI model using these fixed parameter neighbor sum variables

#      but with species-specific competition coefficients (lambdas)

#          Species-specific lambdas

#          with size sensitive (gamma)

#

################################################################################


# power size function with NCI
```

```
power.NCIsum.lambda.gamma.model <- function(Max,b,C,gamma,
l1,l2,l3,l4,l5,l6,G1,G2,G3,G4,G5,G6,DBH)
{
  ncis <- l1*G1 + l2*G2 + l3*G3 + l4*G4 + l5*G5 + l6*G6
  (Max * (DBH/30)^b) * exp(-1.0* C * ((DBH/30)^gamma)*ncis)
}

# par list for the power NCI function
par<-list(C = 5, Max = 2, sd = 2, b = 1, gamma = 0, l1 = 0.5, l2 = 0.5, l3 = 0.5, l4 = 0.5,
l5 = 0.5, l6 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, gamma = -10,  l1 = 0, l2 = 0, l3 =
0, l4 = 0, l5 = 0, l6 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, b = 5, gamma = 10,  l1 = 1, l2 = 1, l3 = 1,
l4 = 1, l5 = 1, l6 = 1)

var <- list(DBH="DBH", G1 = "ndbhm2distgp1", G2 = "ndbhm2distgp2", G3 =
"ndbhm2distgp3", G4 = "ndbhm2distgp4",
  G5 = "ndbhm2distgp5", G6 = "ndbhm2distgp6")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
```

```
result.power.NCIsum.lambda.gamma <- anneal(power.NCIsum.lambda.gamma.model,
par, var, targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.power.NCIsum.lambda.gamma,"Power_ACRU_NCIsum with
lambda_gamma_R10_output_100000.txt")



##########################################################################
#
#   (7) an NCI model using these fixed parameter neighbor sum variables
#      but with species-specific competition coefficients (lambdas)
#           Species-specific lambdas
#           with size sensitive (gamma) and prior growth track (pre)
#
##########################################################################

# power size function with NCI
power.NCIsum.lambda.pre.gamma.model <- function(Max,b,C,pre,gamma,
l1,l2,l3,l4,l5,l6,G1,G2,G3,G4,G5,G6,DBH)
{
  ncis <- l1*G1 + l2*G2 + l3*G3 + l4*G4 + l5*G5 + l6*G6
```

```
  (Max * DBH^b) * exp(-1.0* C * ((pre*10)^gamma)*ncis)
}


# par list for the power NCI function
par<-list(C = 5, Max = 2, sd = 2, b = 1, gamma = 0, l1 = 0.5, l2 = 0.5, l3 = 0.5, l4 = 0.5,
l5 = 0.5, l6 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, gamma = -10,  l1 = 0, l2 = 0, l3 =
0, l4 = 0, l5 = 0, l6 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, b = 5, gamma = 10,  l1 = 1, l2 = 1, l3 = 1,
l4 = 1, l5 = 1, l6 = 1)


var <- list(DBH="DBH",  pre="pre.harvest", G1 = "ndbhm2distgp1", G2 =
"ndbhm2distgp2", G3 = "ndbhm2distgp3", G4 = "ndbhm2distgp4",
  G5 = "ndbhm2distgp5", G6 = "ndbhm2distgp6")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE


# annealing
result.power.NCIsum.lambda.pre.gamma <-
anneal(power.NCIsum.lambda.pre.gamma.model, par, var, targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)
```

```
write_results(result.power.NCIsum.lambda.pre.gamma,"Power_ACRU_NCIsum with
lambda_pre_gamma_R10_output_100000.txt")



##########################################################################
#
#   (8)an NCI model using these fixed parameter neighbor sum variables
#      but with species-specific competition coefficients (lambdas)
#          (INTERCON)
#          model differentiated between "conspecific" and "heterospecific" neighbors
#
##########################################################################

# power size function with NCI
power.NCIsum.lambda.intercon.model <-
function(Max,b,C,l13,l14,INTERCON1,INTERCON2,DBH)
{
  nciintercon <- l13*INTERCON1 + l14*INTERCON2
  (Max * DBH^b) * exp(-1.0* C * nciintercon)
}

# par list for the power NCI function
par<-list(C = 5, Max = 2, sd = 2, b = 1, l13 = 0.5, l14 = 0.5)
```

```
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, l13 = 0, l14 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, b = 5, l13 = 1, l14 = 1)

var <- list(DBH="DBH", INTERCON1 = "ndbhm2distgp.acru.vs.others1", INTERCON2
= "ndbhm2distgp.acru.vs.others2")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.power.NCIsum.lambda.intercon <- anneal(power.NCIsum.lambda.intercon.model,
par, var, targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.power.NCIsum.lambda.intercon,"Power_ACRU_NCIsum with
lambda_intercon_R10_output_100000.txt")


########################################################################
#
#  (9)an NCI model using these fixed parameter neighbor sum variables
#     but with species-specific competition coefficients (lambdas)
#        (INTERCON)
```

```
#       model differentiated between "conspecific" and "heterospecific" neighbors
#       with size sensitive (gamma)
#
######################################################################

# power size function with NCI
power.NCIsum.lambda.intercon.gamma.model <-
function(Max,b,C,gamma,l13,l14,INTERCON1,INTERCON2,DBH)
{
  nciintercon <- l13*INTERCON1 + l14*INTERCON2
  (Max * (DBH/30)^b) * exp(-1.0* C * ((DBH/30)^gamma)*nciintercon)
}

# par list for the power NCI function
par<-list(C = 5, Max = 2, sd = 2, b = 1, gamma = 0, l13 = 0.5, l14 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, gamma = -10, l13 = 0, l14 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, b = 5, gamma = 10, l13 = 1, l14 = 1)

var <- list(DBH="DBH", INTERCON1 = "ndbhm2distgp.acru.vs.others1", INTERCON2
= "ndbhm2distgp.acru.vs.others2")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE
```

```
# annealing
result.power.NCIsum.lambda.intercon.gamma <-
anneal(power.NCIsum.lambda.intercon.gamma.model, par, var, targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.power.NCIsum.lambda.intercon.gamma,"Power_ACRU_NCIsum
with lambda_intercon_gamma_R10_output_100000.txt")



###########################################################################
#
#   (10)an NCI model using these fixed parameter neighbor sum variables
#      but with species-specific competition coefficients (lambdas)
#          (INTERCON)
#           model differentiated between "conspecific" and "heterospecific" neighbors
#           with size sensitive (gamma) & prior growth track (pre)
#
###########################################################################

# power size function with NCI
power.NCIsum.lambda.intercon.pre.gamma.model <-
function(Max,b,C,pre,gamma,l13,l14,INTERCON1,INTERCON2,DBH)
```

```
{
  nciintercon <- l13*INTERCON1 + l14*INTERCON2
  (Max * DBH^b) * exp(-1.0* C * ((pre*10)^gamma)*nciintercon)
}

# par list for the power NCI function
par<-list(C = 5, Max = 2, sd = 2, b = 1, gamma = 0, l13 = 0.5, l14 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, gamma = -10, l13 = 0, l14 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, b = 5, gamma = 10, l13 = 1, l14 = 1)

var <- list(DBH="DBH", pre="pre.harvest", INTERCON1 =
"ndbhm2distgp.acru.vs.others1", INTERCON2 = "ndbhm2distgp.acru.vs.others2")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.power.NCIsum.lambda.intercon.pre.gamma <-
anneal(power.NCIsum.lambda.intercon.pre.gamma.model, par, var, targets1,par_lo,
par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)
```

```
write_results(result.power.NCIsum.lambda.intercon.pre.gamma,"Power_ACRU_NCIsum
with lambda_intercon_pre_gamma_R10_output_100000.txt")


###########################################################################
#
#   (11) an NCI model using these fixed parameter neighbor sum variables
#        but with species-specific competition coefficients (lambdas)
#            (FAMILY)
#            separate heterospecific neighbors into confamilials of
#            the target species and non-confamilies
#
###########################################################################

# power size function with NCI
power.NCIsum.lambda.family.model <-
function(Max,b,C,l7,l8,l9,l10,F1,F2,F3,F4,DBH)
{
  ncifamily <- l7*F1 + l8*F2 + l9*F3 + l10*F4
  (Max * (DBH/30)^b) * exp(-1.0* C * ((DBH/30)^gamma)*ncifamily)
}

# par list for the power NCI function
```

```
par<-list(C = 5, Max = 2, sd = 2, b = 1, l7 = 0.5, l8 = 0.5, l9 = 0.5, l10 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, l7 = 0, l8 = 0, l9 = 0, l10 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, b = 5, l7 = 1, l8 = 1, l9 = 1, l10 = 1)

var <- list(DBH="DBH", F1 = "ndbhm2distgp.family1", F2 = "ndbhm2distgp.family2",
   F3 = "ndbhm2distgp.family3", F4 = "ndbhm2distgp.family4")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.power.NCIsum.lambda.family <- anneal(power.NCIsum.lambda.family.model, par,
var, targets1,par_lo, par_hi,
          dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.power.NCIsum.lambda.family,"Power_ACRU_NCIsum with lambda
family_R10_output_100000.txt")



##########################################################################
#
#   (12) an NCI model using these fixed parameter neighbor sum variables
#        but with species-specific competition coefficients (lambdas)
```

```
#	(FAMILY)
#	separate heterospecific neighbors into confamilials of
#	the target species and non-confamilies
#	with size sensitive (gamma)
#
########################################################################

# power size function with NCI
power.NCIsum.lambda.family.gamma.model <-
function(Max,b,C,gamma,l7,l8,l9,l10,F1,F2,F3,F4,DBH)
{
  ncifamily <- l7*F1 + l8*F2 + l9*F3 + l10*F4
  (Max * (DBH/30)^b) * exp(-1.0* C * ((DBH/30)^gamma)*ncifamily)

}

# par list for the power NCI function
par<-list(C = 5, Max = 2, sd = 2, b = 1, gamma = 0, l7 = 0.5, l8 = 0.5, l9 = 0.5, l10 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, gamma = -10, l7 = 0, l8 = 0, l9 =
0, l10 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, b = 5, gamma = 10, l7 = 1, l8 = 1, l9 = 1,
l10 = 1)
```

```
var <- list(DBH="DBH", F1 = "ndbhm2distgp.family1", F2 = "ndbhm2distgp.family2",
   F3 = "ndbhm2distgp.family3", F4 = "ndbhm2distgp.family4")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.power.NCIsum.lambda.family.gamma <-
anneal(power.NCIsum.lambda.family.gamma.model, par, var, targets1,par_lo, par_hi,
         dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.power.NCIsum.lambda.family.gamma,"Power_ACRU_NCIsum with
lambda family_gamma_R10_output_100000.txt")


#######################################################################
#
#   (13) an NCI model using these fixed parameter neighbor sum variables
#        but with species-specific competition coefficients (lambdas)
#           (FAMILY)
#           separate heterospecific neighbors into confamilials of
#           the target species and non-confamilies
#           with size sensitive (gamma) & prior growth track (pre)
```

```
#
###########################################################################


# power size function with NCI
power.NCIsum.lambda.family.pre.gamma.model <-
function(Max,b,C,pre,gamma,l7,l8,l9,l10,F1,F2,F3,F4,DBH)
{
  ncifamily <- l7*F1 + l8*F2 + l9*F3 + l10*F4
  (Max * DBH^b) * exp(-1.0* C * ((pre*10)^gamma)*ncifamily)

}

# par list for the power NCI function
par<-list(C = 5, Max = 2, sd = 2, b = 1, gamma = 0, l7 = 0.5, l8 = 0.5, l9 = 0.5, l10 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, b = 0.01, gamma = -10, l7 = 0, l8 = 0, l9 =
0, l10 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, b = 5, gamma = 10, l7 = 1, l8 = 1, l9 = 1,
l10 = 1)

var <- list(DBH="DBH",  pre="pre.harvest", F1 = "ndbhm2distgp.family1", F2 =
"ndbhm2distgp.family2",
   F3 = "ndbhm2distgp.family3", F4 = "ndbhm2distgp.family4")
var$x <- "post.harvest"
```

```
var$mean <- "predicted"
var$log <- TRUE


# annealing
result.power.NCIsum.lambda.family.pre.gamma <-
anneal(power.NCIsum.lambda.family.pre.gamma.model, par, var, targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=25000, hessian = TRUE)

write_results(result.power.NCIsum.lambda.family.pre.gamma,"Power_ACRU_NCIsum
with lambda family_pre_gamma_R10_output_25000.txt")




###########################################################################
#
# (14) an Basic power function model
#
###########################################################################

# Create the basic scientific model function
model.power.size <- function (Max,DBH,b){Max * DBH^b}

# parameter list for model.power.size
```

```
par<-list(Max = 1, sd = 2, b = 1)

par_lo <- list(Max =0, sd=0.000001, b=0)

par_hi <- list(Max= 10000, sd=10000, b=5)

var <- list(DBH="DBH")

var$x <- "post.harvest"

var$mean <- "predicted"

var$log <- TRUE


# annealing

result.power.size <- anneal(model.power.size, par, var, targets1,par_lo, par_hi,

        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.power.size, "Power_ACRU_size_R10_output_100000.txt")





#-----------------------------------------------------------------

#

# LOGNORMAL FUNCTION

#

#-----------------------------------------------------------------

##########################################################################

#
```

```
#   (15)an NCI model using these fixed parameter neighbor sum variables
#      (EQUIV) lambda=1
#
######################################################################


# lognormal size function with NCI
lognormal.NCIsum.model <- function(Max,Xo,Xb,C,NCI,DBH)
{  Max * exp(-0.5*(log(DBH/Xo)/Xb)^2) * exp(-1.0* C * NCI)   }



## Create a place to put our parameters and set single parameter values for
## model


# par list for the power NCI function
par<-list(C = 0, Max = 0, sd = 2, Xo = 30, Xb = 1)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb = 0.1)
par_hi <- list(C = 100, Max = 100, sd = 1000, Xo = 1000, Xb = 1000)

var <- list(DBH="DBH", NCI = "ndbhm2dist")
var$x <- "post.harvest"
```

```
var$mean <- "predicted"
var$log <- TRUE


# annealing
result.power.NCIsum <- anneal(lognormal.NCIsum.model, par, var, targets1,par_lo,
par_hi,
          dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.power.NCIsum,"Lognormal_ACRU_NCIsum_R10_output_100000.t
xt")



##########################################################################
#
#   (16) an NCI model using these fixed parameter neighbor sum variables
#       (EQUIV) lambda=1
#       with size sensitive (gamma)
#
##########################################################################

# lognormal size function with NCI
lognormal.NCIsum.gamma.model <- function(Max,Xo,Xb,C,gamma,NCI,DBH)
{   Max * exp(-0.5*(log(DBH/Xo)/Xb)^2) * exp(-1.0* C * ((DBH/30)^gamma)*NCI)   }
```

```
# par list for the power NCI function
par<-list(C = 0, Max = 0, sd = 2, Xo = 30, Xb = 1, gamma = 0)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb = 0.1, gamma = -10)
par_hi <- list(C = 100, Max = 100, sd = 1000, Xo = 1000, Xb = 1000, gamma = 10)

var <- list(DBH="DBH", NCI = "ndbhm2dist")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.lognormal.NCIsumgamma <- anneal(lognormal.NCIsum.gamma.model, par, var,
targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.lognormal.NCIsumgamma,"lognormal_ACRU_NCIsum_gamma_R1
0_output_100000.txt")


##############################################################################
#
#   (17) an NCI model using these fixed parameter neighbor sum variables
```

```
#       (EQUIV) lambda=1
#         with size sensitive (gamma) and prior growth track (pre)
#
###########################################################################

# lognormal size function with NCI
lognormal.NCIsum.pre.gamma.model <- function(Max,Xo,Xb,C,pre,gamma,NCI,DBH)
{   Max * exp(-0.5*(log(DBH/Xo)/Xb)^2) * exp(-1.0* C * ((pre*10)^gamma)*NCI)   }

# par list for the lognormal NCI function
par<-list(C = 0, Max = 0, sd = 2, Xo = 30, Xb = 1, gamma = 0)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb = 0.1, gamma = -10)
par_hi <- list(C = 100, Max = 100, sd = 1000, Xo = 1000, Xb = 1000, gamma = 10)

var <- list(DBH="DBH", NCI = "ndbhm2dist", pre="pre.harvest")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.lognormal.NCIsum.pre.gamma <- anneal(lognormal.NCIsum.pre.gamma.model,
par, var, targets1,par_lo, par_hi,
          dnorm, "post.harvest", max_iter=100000, hessian = TRUE)
```

```
write_results(result.lognormal.NCIsum.pre.gamma,"lognormal_ACRU_NCIsum_pre_gamma_R10_output_100000.txt")


##########################################################################
#
#   (18) an NCI model using these fixed parameter neighbor sum variables
#       (EQUIV) lambda=1
#       with size sensitive (gamma)
#       growth ratio
#
##########################################################################

targets1$grratio <- targets1$post.harvest/targets1$pre.harvest

# lognormal size function with NCI
lognormal.NCIsum.gamma.grratio.model <- function(Max,Xo,Xb,C,gamma,NCI,DBH)
{  Max * exp(-0.5*(log(DBH/Xo)/Xb)^2) * exp(-1.0* C * ((DBH/30)^gamma)*NCI)   }

# par list for the lognormal NCI function
par<-list(C = 0, Max = 0, sd = 2, Xo = 30, Xb = 1, gamma = 0)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb = 0.1, gamma = -10)
```

```
par_hi <- list(C = 100, Max = 100, sd = 1000, Xo = 1000, Xb = 1000, gamma = 10)


var <- list(DBH="DBH", NCI = "ndbhm2dist")
var$x <- "grratio"
var$mean <- "predicted"
var$log <- TRUE


# annealing
result.lognormal.NCIsum.gamma.grratio <-
anneal(lognormal.NCIsum.gamma.grratio.model, par, var, targets1,par_lo, par_hi,
        dnorm, "grratio", max_iter=100000, hessian = TRUE)


write_results(result.lognormal.NCIsum.gamma.grratio,"lognormal_ACRU_NCIsum_gam
ma_grratio_R10_output_100000.txt")



############################################################################
#
#   (19) an NCI model using these fixed parameter neighbor sum variables
#       but with species-specific competition coefficients (lambdas)
#           Species-specific lambdas
#
############################################################################
```

```
# lognormal size function with NCI
lognormal.NCIsum.lambda.model <-
function(Max,Xo,Xb,C,l1,l2,l3,l4,l5,l6,G1,G2,G3,G4,G5,G6,DBH)
{
  ncis <- l1*G1 + l2*G2 + l3*G3 + l4*G4 + l5*G5 + l6*G6
  (Max * exp(-0.5*(log(DBH/Xo)/Xb)^2)) * exp(-1.0* C * ncis)
}


# par list for the power NCI function
par<-list(C = 5, Max = 2, sd = 2,  Xo = 30, Xb = 1, l1 = 0.5, l2 = 0.5, l3 = 0.5, l4 = 0.5, l5
= 0.5, l6 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb = 0.1, l1 = 0, l2 = 0, l3 =
0, l4 = 0, l5 = 0, l6 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, Xo = 1000, Xb = 1000, l1 = 1, l2 = 1, l3 =
1, l4 = 1, l5 = 1, l6 = 1)

var <- list(DBH="DBH", G1 = "ndbhm2distgp1", G2 = "ndbhm2distgp2", G3 =
"ndbhm2distgp3", G4 = "ndbhm2distgp4",
  G5 = "ndbhm2distgp5", G6 = "ndbhm2distgp6")
var$x <- "post.harvest"
var$mean <- "predicted"
```

```
var$log <- TRUE


# annealing
result.lognormal.NCIsum.lambda <- anneal(lognormal.NCIsum.lambda.model, par, var,
targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)


write_results(result.lognormal.NCIsum.lambda,"Lognormal_ACRU_NCIsum with
lambda_R10_output_100000.txt")



##########################################################################
#
#   (20) an NCI model using these fixed parameter neighbor sum variables
#       but with species-specific competition coefficients (lambdas)
#           Species-specific lambdas
#           with size sensitive (gamma)
#
##########################################################################


# lognormal size function with NCI
lognormal.NCIsum.lambda.gamma.model <- function(Max,Xo,Xb,C,gamma,
l1,l2,l3,l4,l5,l6,G1,G2,G3,G4,G5,G6,DBH)
```

```
{
  ncis <- l1*G1 + l2*G2 + l3*G3 + l4*G4 + l5*G5 + l6*G6
  (Max * exp(-0.5*(log(DBH/Xo)/Xb)^2)) * exp(-1.0* C * ((DBH/30)^gamma)*ncis)
}

# par list for the lognormal NCI function
par<-list(C = 5, Max = 2, sd = 2, Xo = 30, Xb = 1, gamma = 0, l1 = 0.5, l2 = 0.5, l3 = 0.5,
l4 = 0.5, l5 = 0.5, l6 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb = 0.1, gamma = -10,  l1 =
0, l2 = 0, l3 = 0, l4 = 0, l5 = 0, l6 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, Xo = 1000, Xb = 1000, gamma = 10,  l1
= 1, l2 = 1, l3 = 1, l4 = 1, l5 = 1, l6 = 1)

var <- list(DBH="DBH", G1 = "ndbhm2distgp1", G2 = "ndbhm2distgp2", G3 =
"ndbhm2distgp3", G4 = "ndbhm2distgp4",
  G5 = "ndbhm2distgp5", G6 = "ndbhm2distgp6")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.lognormal.NCIsum.lambda.gamma <-
anneal(lognormal.NCIsum.lambda.gamma.model, par, var, targets1,par_lo, par_hi,
```

```
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.lognormal.NCIsum.lambda.gamma,"lognormal_ACRU_NCIsum
with lambda_gamma_R10_output_100000.txt")



##############################################################################
#
#   (21) an NCI model using these fixed parameter neighbor sum variables
#        but with species-specific competition coefficients (lambdas)
#            Species-specific lambdas
#            with size sensitive (gamma) and prior growth track (pre)
#
##############################################################################

# lognormal size function with NCI
lognormal.NCIsum.lambda.pre.gamma.model <- function(Max,Xo,Xb,C,pre,gamma,
l1,l2,l3,l4,l5,l6,G1,G2,G3,G4,G5,G6,DBH)
{
  ncis <- l1*G1 + l2*G2 + l3*G3 + l4*G4 + l5*G5 + l6*G6
   (Max * exp(-0.5*(log(DBH/Xo)/Xb)^2)) * exp(-1.0* C * ((pre*10)^gamma)*ncis)
}
```

```
# par list for the lognormal NCI function
par<-list(C = 5, Max = 2, sd = 2, Xo = 30, Xb = 1, gamma = 0, l1 = 0.5, l2 = 0.5, l3 = 0.5,
l4 = 0.5, l5 = 0.5, l6 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb = 0.1, gamma = -10,  l1 =
0, l2 = 0, l3 = 0, l4 = 0, l5 = 0, l6 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, Xo = 1000, Xb = 1000, gamma = 10,  l1
= 1, l2 = 1, l3 = 1, l4 = 1, l5 = 1, l6 = 1)

var <- list(DBH="DBH",  pre="pre.harvest", G1 = "ndbhm2distgp1", G2 =
"ndbhm2distgp2", G3 = "ndbhm2distgp3", G4 = "ndbhm2distgp4",
  G5 = "ndbhm2distgp5", G6 = "ndbhm2distgp6")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.lognormal.NCIsum.lambda.pre.gamma <-
anneal(lognormal.NCIsum.lambda.pre.gamma.model, par, var, targets1,par_lo, par_hi,
         dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.lognormal.NCIsum.lambda.pre.gamma,"lognormal_ACRU_NCIsum
with lambda_pre_gamma_R10_output_100000.txt")
```

```
######################################################################
#
#   (22)an NCI model using these fixed parameter neighbor sum variables
#      but with species-specific competition coefficients (lambdas)
#          (INTERCON)
#          model differentiated between "conspecific" and "heterospecific" neighbors
#
######################################################################

# lognormal size function with NCI
lognormal.NCIsum.lambda.intercon.model <- function(Max,Xo,
Xb,C,l13,l14,INTERCON1,INTERCON2,DBH)
{
  nciintercon <- l13*INTERCON1 + l14*INTERCON2
  Max * exp(-0.5*(log(DBH/Xo)/Xb)^2)* exp(-1.0* C * nciintercon)
}

# par list for the lognormal NCI function
par<-list(C = 5, Max = 2, sd = 2, Xo = 30, Xb = 1, l13 = 0.5, l14 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb = 0.1, l13 = 0, l14 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, Xo = 1000, Xb = 1000, l13 = 1, l14 = 1)
```

```
var <- list(DBH="DBH", INTERCON1 = "ndbhm2distgp.acru.vs.others1", INTERCON2
= "ndbhm2distgp.acru.vs.others2")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.lognormal.NCIsum.lambda.intercon <-
anneal(lognormal.NCIsum.lambda.intercon.model, par, var, targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.lognormal.NCIsum.lambda.intercon,"Lognormal_ACRU_NCIsum
with lambda_intercon_R10_output_100000.txt")


########################################################################
#
#  (23)an NCI model using these fixed parameter neighbor sum variables
#     but with species-specific competition coefficients (lambdas)
#         (INTERCON)
#         model differentiated between "conspecific" and "heterospecific" neighbors
#         with size sensitive (gamma)
#
```

```
######################################################################

# lognormal size function with NCI
lognormal.NCIsum.lambda.intercon.gamma.model <-
function(Max,Xo,Xb,C,gamma,l13,l14,INTERCON1,INTERCON2,DBH)
{
  nciintercon <- l13*INTERCON1 + l14*INTERCON2
  Max * exp(-0.5*(log(DBH/Xo)/Xb)^2) * exp(-1.0* C *
((DBH/30)^gamma)*nciintercon)
}

# par list for the lognormal NCI function
par<-list(C = 5, Max = 2, sd = 2, Xo = 30, Xb = 1, gamma = 0, l13 = 0.5, l14 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb = 0.1, gamma = -10, l13 =
0, l14 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, Xo = 1000, Xb = 1000, gamma = 10, l13
= 1, l14 = 1)

var <- list(DBH="DBH", INTERCON1 = "ndbhm2distgp.acru.vs.others1", INTERCON2
= "ndbhm2distgp.acru.vs.others2")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE
```

```
# annealing

result.lognormal.NCIsum.lambda.intercon.gamma <-
anneal(lognormal.NCIsum.lambda.intercon.gamma.model, par, var, targets1,par_lo,
par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.lognormal.NCIsum.lambda.intercon.gamma,"lognormal_ACRU_NCI
sum with lambda_intercon_gamma_R10_output_100000.txt")



#########################################################################
#
#   (24)an NCI model using these fixed parameter neighbor sum variables
#      but with species-specific competition coefficients (lambdas)
#         (INTERCON)
#          model differentiated between "conspecific" and "heterospecific" neighbors
#          with size sensitive (gamma) & prior growth track (pre)
#
#########################################################################

# lognormal size function with NCI
```

```
lognormal.NCIsum.lambda.intercon.pre.gamma.model <-
function(Max,Xo,Xb,C,pre,gamma,l13,l14,INTERCON1,INTERCON2,DBH)
{
  nciintercon <- l13*INTERCON1 + l14*INTERCON2
   Max * exp(-0.5*(log(DBH/Xo)/Xb)^2) * exp(-1.0* C *
((pre*10)^gamma)*nciintercon)
}

# par list for the lognormal NCI function
par<-list(C = 5, Max = 2, sd = 2, Xo = 30, Xb = 1, gamma = 0, l13 = 0.5, l14 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb = 0.1, gamma = -10, l13 =
0, l14 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, Xo = 1000, Xb = 1000, gamma = 10, l13
= 1, l14 = 1)

var <- list(DBH="DBH", pre="pre.harvest", INTERCON1 =
"ndbhm2distgp.acru.vs.others1", INTERCON2 = "ndbhm2distgp.acru.vs.others2")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
```

```
result.lognormal.NCIsum.lambda.intercon.pre.gamma <-
anneal(lognormal.NCIsum.lambda.intercon.pre.gamma.model, par, var, targets1,par_lo,
par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.lognormal.NCIsum.lambda.intercon.pre.gamma,"lognormal_ACRU_
NCIsum with lambda_intercon_pre_gamma_R10_output_100000.txt")



###########################################################################
#
#   (25) an NCI model using these fixed parameter neighbor sum variables
#       but with species-specific competition coefficients (lambdas)
#          (FAMILY)
#           separate heterospecific neighbors into confamilials of
#           the target species and non-confamilies
#
###########################################################################

# lognormal size function with NCI
lognormal.NCIsum.lambda.family.model <- function(Max,Xo,
Xb,C,l7,l8,l9,l10,F1,F2,F3,F4,DBH)
{
```

```
  ncifamily <- l7*F1 + l8*F2 + l9*F3 + l10*F4
  Max * exp(-0.5*(log(DBH/Xo)/Xb)^2)* exp(-1.0* C * ncifamily)
}

# par list for the lognormal NCI function
par<-list(C = 5, Max = 2, sd = 2, Xo = 30, Xb = 1, l7 = 0.5, l8 = 0.5, l9 = 0.5, l10 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb = 0.1, l7 = 0, l8 = 0, l9 =
0, l10 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, Xo = 1000, Xb = 1000, l7 = 1, l8 = 1, l9 =
1, l10 = 1)

var <- list(DBH="DBH", F1 = "ndbhm2distgp.family1", F2 = "ndbhm2distgp.family2",
   F3 = "ndbhm2distgp.family3", F4 = "ndbhm2distgp.family4")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.lognormal.NCIsum.lambda.family <-
anneal(lognormal.NCIsum.lambda.family.model, par, var, targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)
```

```
write_results(result.lognormal.NCIsum.lambda.family,"Lognormal_ACRU_NCIsum
with lambda_family_R10_output_100000.txt")



####################################################################
#
#   (26) an NCI model using these fixed parameter neighbor sum variables
#        but with species-specific competition coefficients (lambdas)
#            (FAMILY)
#            separate heterospecific neighbors into confamilials of
#            the target species and non-confamilies
#            with size sensitive (gamma)
#
#####################################################################

# lognormal size function with NCI
lognormal.NCIsum.lambda.family.gamma.model <-
function(Max,Xo,Xb,C,gamma,l7,l8,l9,l10,F1,F2,F3,F4,DBH)
{
  ncifamily <- l7*F1 + l8*F2 + l9*F3 + l10*F4
  Max * exp(-0.5*(log(DBH/Xo)/Xb)^2) * exp(-1.0* C *
((DBH/30)^gamma)*ncifamily)
```

```
}


# par list for the lognormal NCI function
par<-list(C = 5, Max = 2, sd = 2, Xo = 30, Xb = 1, gamma = 0, l7 = 0.5, l8 = 0.5, l9 = 0.5,
l10 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb = 0.1, gamma = -10, l7 =
0, l8 = 0, l9 = 0, l10 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, Xo = 1000, Xb = 1000, gamma = 10, l7 =
1, l8 = 1, l9 = 1, l10 = 1)


var <- list(DBH="DBH", F1 = "ndbhm2distgp.family1", F2 = "ndbhm2distgp.family2",
   F3 = "ndbhm2distgp.family3", F4 = "ndbhm2distgp.family4")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE


# annealing
result.lognormal.NCIsum.lambda.family.gamma <-
anneal(lognormal.NCIsum.lambda.family.gamma.model, par, var, targets1,par_lo,
par_hi,
          dnorm, "post.harvest", max_iter=100000, hessian = TRUE)
```

```
write_results(result.lognormal.NCIsum.lambda.family.gamma,"lognormal_ACRU_NCIsum with lambda family_gamma_R10_output_100000.txt")


##############################################################################
#
#   (27) an NCI model using these fixed parameter neighbor sum variables
#       but with species-specific competition coefficients (lambdas)
#           (FAMILY)
#           separate heterospecific neighbors into confamilials of
#           the target species and non-confamilies
#           with size sensitive (gamma) & prior growth track (pre)
#
##############################################################################

# lognormal size function with NCI
lognormal.NCIsum.lambda.family.pre.gamma.model <-
function(Max,Xo,Xb,C,pre,gamma,l7,l8,l9,l10,F1,F2,F3,F4,DBH)
{
  ncifamily <- l7*F1 + l8*F2 + l9*F3 + l10*F4
  Max * exp(-0.5*(log(DBH/Xo)/Xb)^2) * exp(-1.0* C * ((pre*10)^gamma)*ncifamily)

}
```

```
# par list for the lognormal NCI function
par<-list(C = 5, Max = 2, sd = 2, Xo = 30, Xb = 1, gamma = 0, l7 = 0.5, l8 = 0.5, l9 = 0.5,
l10 = 0.5)
par_lo <- list(C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb = 0.1, gamma = -10, l7 =
0, l8 = 0, l9 = 0, l10 = 0)
par_hi <- list(C = 1000, Max = 100, sd = 1000, Xo = 1000, Xb = 1000, gamma = 10, l7 =
1, l8 = 1, l9 = 1, l10 = 1)

var <- list(DBH="DBH",  pre="pre.harvest", F1 = "ndbhm2distgp.family1", F2 =
"ndbhm2distgp.family2",
   F3 = "ndbhm2distgp.family3", F4 = "ndbhm2distgp.family4")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE

# annealing
result.lognormal.NCIsum.lambda.family.pre.gamma <-
anneal(lognormal.NCIsum.lambda.family.pre.gamma.model, par, var, targets1,par_lo,
par_hi,
         dnorm, "post.harvest", max_iter=100000, hessian = TRUE)
```

```
write_results(result.lognormal.NCIsum.lambda.family.pre.gamma,"lognormal_ACRU_N
CIsum with lambda family_pre_gamma_R10_output_100000.txt")



##########################################################################
#
# (28)an Basic lognormal function model
#
##########################################################################

# Create the basic scientific model function
model.lognormal.size <- function (Max,DBH,Xo,Xb)
{         Max * exp(-0.5*(log(DBH/Xo)/Xb)^2)        }



# parameter list for model.power.size
par<-list(Max = 1, sd = 2, Xo = 30, Xb = 1)
par_lo <- list(Max =0, sd=0.000001, Xo = 0.0001, Xb = 0.1)
par_hi <- list(Max= 10000, sd=10000, Xo = 10000, Xb = 1000)
var <- list(DBH="DBH")
var$x <- "post.harvest"
var$mean <- "predicted"
var$log <- TRUE
```

```
# annealing

result.lognormal.size <- anneal(model.lognormal.size, par, var, targets1,par_lo, par_hi,

          dnorm, "post.harvest", max_iter=100000, hessian = TRUE)

write_results(result.lognormal.size, "Lognormal_ACRU_size_R10_output_100000.txt")



#-----------------------------------------------------------------



##########################################################################

#

# an power size NCI model using varied parameter neighbor sum variables

#     (alpha, beta are varied)

#

#  a more complexed model using "NCI" comong from "sumneigh"

#

##########################################################################


# power size function with NCI

power.NCI.model <- function(Max,b,C,NCI,DBH)

{  (Max * DBH^b) * exp(-1.0* C * NCI)   }
```

```
ncifun <- function (NDBH, alpha, distance, beta) {
  ((NDBH/100)^alpha) / (distance ^ beta)}


# par list for the power NCI function
par<-list(alpha = 2, beta = 2, C = 1, Max = 1, sd = 2, b = 1)
par_lo <- list(alpha = 0, beta = 0, C = 0, Max = 0, sd = 0.000001, b = 0.01)
par_hi <- list(alpha = 4, beta = 4, C = 100000, Max = 1000, sd = 100000, b = 1000)


## Create the place for other data and
## indicate that the "NCI" argument of model comes from sumneigh
var <- list(NCI=sumneigh)


## Set the parameter fors for the function ncifun
var$DBH <- targets1$DBH
var$NDBH <- neighbors1$DBH


## Use neighdist to calculate the distance to the neighbor
var$distance <- neighdist
## Put in the parameters for sumneigh - note that the first four arguments
## are also the parameters for neighdist - note also that the dataset columns
var$targetx <- "Xpos"
var$targety <- "Ypos"
var$neighborx <- "Xpos"
```

```
var$neighbory <- "Ypos"
var$targetsite <- "plot"
var$neighborsite <- "plot"
var$max_radius <- 10
var$sumfun <- ncifun
var$target_data <- targets1
var$neigh_data <- neighbors1

## We'll use the normal probability distribution function - add its arguments
## to our parameter list
## "x" value in PDF is observed value
var$x <- "post.harvest"

## Mean in normal PDF
var$mean <- "predicted"

## Have it calculate log likelihood
var$log <- TRUE

## Calculate likelihood
result <- likeli(power.size.NCI, par, var, targets1, dnorm)

# annealing
```

```
result.power.size.NCI <- anneal(power.size.NCI, par, var, targets1,par_lo, par_hi,
        dnorm, "post.harvest", max_iter=100000, hessian = TRUE)
write_results(result.power.size, "ACRU_Power size varied NCI output_100000.txt")




##############################################################################
#
# an lognormal tree size NCI model using varied parameter neighbor sum variables
#     (alpha, beta vare varied)
#
#  a more complexed model using "NCI" comong from "sumneigh"
#
#
##############################################################################

#model <- function (Max, C, NCI) {Max * exp(-C * NCI)}

lognormal.tree.size.model <- function(Max,Xo,Xb,C,NCI,DBH)
{  Max * exp(-0.5*(log(DBH/Xo)/Xb)^2) * exp(-1.0* C * NCI)   }

## Create the function to be summed over neighbors
```

```
#  NOTE:  to avoid overflow and underflow errors in the calculations,
#     DBH will be in units of meters in the actual calculation
ncifun <- function (NDBH, alpha, distance, beta) {
  ((NDBH/100)^alpha) / (distance ^ beta)}

#ncifun <- function (NDBH, alpha, distance, beta) {
  ((NDBH)^alpha) / (distance ^ beta)}



## Create a place to put our parameters and set single parameter values for
## model

par<-list(alpha = 2, beta = 2, C = 1, Max = 1, sd = 2, Xo = 30, Xb = 1)

par_lo <- list(alpha = 0, beta = 0, C = 0, Max = 0, sd = 0.000001, Xo = 0.0001, Xb =
0.01)
par_hi <- list(alpha = 4, beta = 4, C = 100000, Max = 1000, sd = 100000, Xo = 1000, Xb
= 1000)

#par_hi <- list(alpha = 4, beta = 4, C = 100000, Max = 1000, sd = 100000, Xo = 10000,
Xb = 1000)
```

```
## Create the place for other data and
## indicate that the "NCI" argument of model comes from sumneigh
var<-list(NCI = sumneigh)

## Set the parameters for the function ncifun
var$DBH <- targets1$DBH
var$NDBH <- neighbors1$DBH

## Use neighdist to calculate the distance to the neighbor
var$distance <- neighdist

## We want to exclude trees of type 1 and type=4 from the set of neighbors
# var$min_vals<-list(Type=2)
# var$max_vals<-list(Type=3)

## Put in the parameters for sumneigh - note that the first four arguments
## are also the parameters for neighdist - note also that the dataset columns
## are NOT unique as recommended above, but it still works
var$targetx<-"Xpos"
var$targety<-"Ypos"
var$neighborx<-"Xpos"
var$neighbory<-"Ypos"
```

```
var$targetsite<-"plot"

var$neighborsite<-"plot"

var$max_radius<-20

var$sumfun<-ncifun

var$target_data<-targets1

var$neigh_data<-neighbors1


## We'll use the normal probability distribution function - add its arguments

## to our parameter list

## "x" value in PDF is observed value

var$x<-"post.harvest"


## Mean in normal PDF

var$mean<-"predicted"




## Have it calculate log likelihood

var$log<-TRUE


## Calculate likelihood

result<-likeli(lognormal.tree.size.model, par, var, targets1, dnorm)


result
```

```
## annealing

#acru.result <- anneal(lognormal.tree.size.model, par, var, targets1, par_lo, par_hi,
dnorm, "post.harvest", max_iter=1000, hessian = FALSE)

power.acru.result <- anneal(power.NCI.model, par, var, targets1, par_lo, par_hi, dnorm,
"post.harvest", max_iter=1000, hessian = FALSE)



acru.result <- anneal(lognormal.tree.size.model, par, var, targets1, par_lo, par_hi, dnorm,
"post.harvest", max_iter=5000, hessian = FALSE)



acru.result$best_pars

write_results(acru.result,"ACRU result_tree size.xls")
```

APPENDIX II. Equations used in the dissertion and the original form of each equation and its source from the literature.

#	**Equation in the dissertation**	**Original equation**	**Equation sources**
1	$\mathrm{RG} = \mathrm{PotRG} \times \mathrm{Size\ effect} \times \mathrm{Crowding\ effect}$	$g = g_m \phi_g \delta v$	Uriarte et al. 2004a
2a	$\mathrm{Size\ effect} = e^{-\frac{1}{2}\left[\frac{\ln(\mathrm{dbh}/\delta)}{\sigma}\right]^2}$	$\mathrm{g} = g_m \times \exp^{-\frac{1}{2}\left[\frac{\ln(\mathrm{dbh}/X_0)}{X_b}\right]^2}$	Uriarte et al. 2004a
2b	$\mathrm{Size\ effect} = (\mathrm{dbh})^{\alpha}$		
3	$NCI = \mathrm{dbh}_t \sum_{i=1}^{s} \sum_{j=1}^{n} \lambda_i \frac{\left(\frac{\mathrm{dbh}_{ij}}{100}\right)^2}{\mathrm{distance}_{ij}}$	$SHRUB = \sum_{i=1}^{N} a_i \left[\frac{h_i / D}{O}\right]^2$	Wanger and Radosevich 1998
4	$\mathrm{Crowding\ effect} = e^{-C \times NCI_i}$	$\mathrm{Crowding\ effect} = \exp\left[-\mathrm{C}(\mathrm{NCI})^D\right]$	Canham et al. 2006
5	$C = C' \times (\mathrm{dbh})^{\gamma}$	$C = C' \times \mathrm{dbh}^{\gamma}$	Canham et al. 2006
6	$C = C' \times (prior \times 10)^{\kappa}$		

APPENDIX II (Cont.)

#	Equation in the dissertation	Original equation	Equation sources
7	$F(X_i) = \Sigma(\#\text{recuits per tree}) \times (\text{dispersal kernel of seedlings, } f(d))$		
8	$\#recruits/tree = STR\left(\frac{dbh_k}{30}\right)^{\alpha}$	$STR\left(\frac{dbh}{30}\right)^{\beta}$	Ribbens et al. 1994
9a	$f(d) = \frac{1}{\eta}\exp^{-(\lambda - wind)(dist_i)^{\beta}}$	$\frac{1}{\eta}e^{-Dm^{\theta}}$	Ribbens et al. 1994
9b	$f(d) = \frac{1}{\eta}\exp^{-\frac{1}{2}\left[\frac{\ln\left(\frac{dist_i}{X_0 - wind}\right)}{X_b}\right]^2}$	$f(d) = \frac{1}{\eta}\exp^{-\frac{1}{2}\left[\frac{\ln\left(\frac{d}{X_0}\right)}{X_b}\right]^2}$	Uriarte et al. 2005
10	$wind = p_1 - [(p_2\cos(angle - p_3))]$	$wind = p_1 - [(p_2\cos(angle - p_3))]$	Canham unpublished
11	$R_{im} = bath + STR_m\sum_{j=1}^{n}\left(\frac{dbh_{jm}}{30}\right)^{\alpha} f(d_{ijm})$	$S_i = bath + STR\sum_{k=1}^{n}\left(\frac{D_k}{30}\right)^{\alpha} f(d_{ik})$	Uriarte et al. 2005

LITERATURE CITED

Abrams, M. D. 1998. The red maple paradox. BioScience **48**:355-364.

Abrams, M. D. and M. E. Kubiske. 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: Influence of light regime and shade-tolerance rank. Forest Ecology and Management **31**:245-253.

Abrams, M. D. and S. A. Mostoller. 1995. Gas exchange, leaf structure and nitrogen in contrasting successional tree species growing in open and understory sites during a drought. Tree Physiology **15**:361-370.

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, editors. 2nd International Symposiumon Information Theory. Akademiai Kiado, Budapest, Hungary.

Anderson, W. C. 1975. Timber stand improvement--A entree to forestry for small-tract owners. Journal of Forestry **73**:222-223.

Beaudet, M., C. Messier, and C. D. Canham. 2002. Predictions of understory light conditions in northern hardwood forests following parameterization, sensitivity analysis, and tests of the SORTIE light model. Forest Ecology and Management **165**:235-248.

Berger, U. and H. Hildenbrandt. 2000. A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. Ecological Modelling **132**:287-302.

Bjorkbom, J. C. 1971. Production & germination of paper birch seed and its dispersal into a forest opening. USDA, Forest Service, Northeastern Forest Experiment Station Research Paper NE-209:1-14.

Bliss, J. C. 2000. Public perceptions of clearcutting. Journal of Forestry **98**:4-9.

Braun, E. L. 1950. Deciduous Forests of Eastern North America. Hafner Press, New York.

Bruun H. H., V. K., Kollmann J. & Brunet J. 2010. Post-dispersal seed predation of woody forest species limits recolonization of forest plantations on ex-arable land. Preslia **82**:345-356.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York, New York, USA.

Burns, R. M. and B. H. Honkala. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. U.S. Department of Agriculture, Forest Service, Washington, DC., USA. USDA Agriculture handbook 654.

Buse, L. J., R. G. Wagner, and B. Perrin. 1995. Public attitudes towards forest herbicide use and the implications for public involvement. The Forestry Chronicle **71**:596-600.

Butler, B. J. and E. C. Leatherberry. 2004. America's family forest owners. Journal of Forestry **102**:4-9.

Canham, C. D., A. R. Berkowitz, V. R. Kelly, G. M. Lovett, S. V. Ollinger, and J. Schnurr. 1996. Biomass allocation and multiple resource limitation in tree seedlings. Canadian Journal of Forest Research **26**:1521-1530.

Canham, C. D., J. J. Cole, and W. K. Lauenroth. 2003. Models in Ecosystem Science. Princeton University Press, Princeton, New Jersey.

Canham, C. D., P. T. LePage, and K. D. Coates. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Canadian Journal of Forest Research **34**:778-787.

Canham, C. D., M. J. Papaik, M. Uriarte, W. H. McWilliams, J. C. Jenkins, and M. J. Twery. 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. Ecological Applications **16**:540-554.

Canham, C. D. and M. Uriarte. 2006. Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling. Ecological Applications **16**:62-73.

Carkin, R. E., J. F. Franklin, J. Booth, and C. E. Smith. 1978. Seeding habits of upper-slope tree species. IV. Seed flight of noble fir and Pacific silver fir. USDA Forest Service Pacific Northwest Forest and Range Experiment Station Research Note PNW-312:1-10.

Chave, J. 2004. Neutral theory and community ecology. Ecology Letters **7**:241-253.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics **31**:343-366.

Clark, J. S. 2003a. Uncertainty and variability in demography and population growth: a hierarchical approach. Ecology **84**:1370–1381.

Clark, J. S. 2003b. Uncertainty in ecological inference and forecasting. Ecology **84**:1349-1350.

Clark, J. S., B. Beckage, P. Camill, B. Cleveland, J. HilleRisLambers, J. Lichter, J. McLachlan, J. Mohan, and P. Wyckoff. 1999a. Interpreting recruitment limitation in forests. American Journal of Botany **86**:1-16.

Clark, J. S. and C. Fastie. 1998. Reid's paradox of rapid plant migration. BioScience **48**:13-24.

Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in southern Appalachain forests. Ecological Monographs **68**:213-235.

Clark, J. S. and J. S. McLachlan. 2004. Neutral theory (communication arising): The stability of forest biodiversity. Nature **427**:696-697.

Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. H. J. A. Silander. 1999b. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology **80**:1475–1494.

Coates, K. D., C. D. Canham, M. Beaudet, D. L. Sachs, and C. Messier. 2003. Use of a spatially-explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. Forest Ecology and Management **186**:297-310.

Coates, K. D., C. D. Canham, and P. T. LePage. 2009. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. Journal of Ecology **97**:118-130.

Comita, L. S. and S. P. Hubbell. 2009. Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. Ecology **90**:328-334.

Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. Science **329**:330-332.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive excusion in some marine animals and in rainforest trees. Pages 298-312 *in* P. J. d. B. a. G. R. Gradwell, editor. Dynamics of Populations. Center for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Curtis, R. O. 1998. "Selective Cutting" in Douglas-Fir. Journal of Forestry **96**:40-46.

D'Amato, A. W. and K. J. Puettmann. 2004. The relative dominance hypothesis explains interaction dynamics in mixed species *Alnus rubra*/ *Pseudotsuga menziesii* stands. Journal of Ecology **92**:450-463.

Daniel, T. W., J. A. Helms, and F. S. Baker. 1979. Principles of silviculture. McGraw-Hill, Inc., New York.

Davis, K. P. 1966. Forest management: regulation and valuation. 2nd edition. McGraw-Hill, New York.

Dey, D. C., R. G. Jensen, and M. J. Wallendorf. 2004. Single-tree harvesting reduces survival and growth of oak stump sprouts in theMissouri Ozark Highlands. Proceedings of the 16th Central Hardwoods Forest Conference GTR-NRS-P-24.

Doyon, F., D. Gagnon, and J.-F. Giroux. 2005. Effects of strip and single-tree selection cutting on birds and their habitat in a southwestern Quebec northern hardwood forest. Forest Ecology and Management **209**:101-115.

Edwards, A. W. F. 1992. Likelihood. Expanded edition. Johns Hopkins University Press, Baltimore, Maryland.

Espelta, J. M., P. Cortés, R. Molowny-Horas, and J. Retana. 2009. Acorn crop size and pre-dispersal predation determine inter-specific differences in the recruitment of co-occurring oaks. Oecologia **161**:559-568.

Evans, G. C. 1972. The quantitative analysis of plant growth. Berkeley, University of California Press, Berkeley, California.

Fernholz, K. 2004. Small-scale, private lands forestry in the Lake States. Page 49 *in* B. Palik and L. Levy, editors. Proceedings of the Great Lakes Silviculture Summit. USDA Forest Service GTR-NC-254, Houghton, Michigan.

Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. Ecosystems **1**:96-119.

Freckleton, R. P. and A. R. Watkinson. 2001. Predicting competition coefficients for plant mixtures: reciprocity, transitivity and correlations with life-history traits. Ecology Letters **4**:348-357.

Fujimori, T. 2001. Ecological and silvicultural strategies for sustainable forest management. Elsevier Science, Amsterdam, the Netherlands.

Goffe, W. L., G. D. Ferrier, and J. Rogers. 1994. Global optimization of statistical functions with simulated annealing. Journal of Econometrics **60**:65-99.

Greene, D. F. and C. Calogeropoulos. 2002. Dispersal of seeds by animals and wind. Pages 3-23 *in* J. Bullock, R. Kenward, and R. Hails, editors. Dispersal Ecology. Blackwell Press, Oxford.

Greene, D. F., C. D. Canham, K. D. Coates, and P. T. LePage. 2004. An evaluation of alternative dispersal functions for trees. Journal of Ecology **92**:758-766.

Guevara, S. and J. Laborde. 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. Plant Ecology **107-108**:319-338.

Halkard E. Mackey, J. and N. Sivec. 1973. The present composition of a former oak-chestnut forest in the Allegheny Mountains of western Pennsylvania. Ecology **54**:915-919.

Hall, B., G. Motzkin, D. R. Foster, M. Syfert, and J. Burk. 2002. Three hundred years of forest and land-use change in Massachusetts, USA. Journal of Biogeography **29**:1319-1335.

Hann, D. W. and B. B. Bare. 1979. Uneven-aged forest management: State of the art (or science?). USDA Forest Service General Techical Report INT-50:18.

Helms, J. A. 1998. The Dictionary of Forestry. Society of American Foresters: Bethesda, MD, USA.

Hilborn, R. and M. Mangel. 1997. The Ecological Detective: Confronting Models with Data Princeton University Press, Princeton, New Jersey.

Hobbs, N. T. and R. Hilborn. 2006. Alternatives to statistical hypothesis testing In ecology: A guide to self teaching. Ecological Applications **16**:5-19.

Holthuijzen, A. M. A. and T. L. Sharik. 1985. The red cedar (*Juniperus virginiana* L.) seed shadow along a fenceline. American Midland Naturalist **113**:200-202.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hummel, S. S. 2003. Managing structural and compositional diversity with silviculture. Pages 85-119 *in* R. A. Monserud, R. W. Haynes, and A. C. Johnson, editors. Compatible Forest Management. Kluwer Academic Publishers.

Isaac, L. A. 1956. Place of partial cutting inc old-growth stands of the Douglas-fir region. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station Research Paper No. 16:1-48.

Isaac, L. A. 1967. Douglas fir research in the Pacific Northwest, 1920-1956. Interview by A. R. Regional Oral History Office, Berkey, California: oral history transcript, 1967.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. The American Naturalist **104**:501-508.

Johnson, J. B. and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution **19**:101-108.

Johnson, W. C. 1988. Estimating dispersibility of *Acer*, *Fraxinus*, and *Tilia* in fragmented landscapes from patterns of seedling establishment. Landscape Ecology **1**:175-187.

Jones, T. A. and S. C. Thomas. 2004. The time course of diameter increment responses to selection harvests in *Acer saccharum*. Canadian Journal of Forest Research **34**:1525-1533.

Kimmins, J. P. 1991. The future of the forested landscapes of Canada. The Forestry Chronicle **67**:14-18.

Kimmins, J. P. 2004. Forestry ecology: A foundation for sustainable forest management and environmental ethics in forestry. 3rd edition. Prentice Hall, Upper Saddle River, New Jersey.

Kloeppel, B. D., M. D. Abrams, and M. E. Kubiske. 1993. Seasonal ecophysiology and leaf morphology of four successional Pennsylvania barrens species in open versus understory environments. Canadian Journal of Forest Research **23**:181-189.

Kobe, R. K. and K. D. Coates. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. Canadian Journal of Forest Research **27**:227-236.

Kohm, K. A. and J. F. Franklin. 1997. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington, DC.

Kubiske, M. E. and M. D. Abrams. 1994. Ecophysiological analysis of temperate woody species on contrasting sites during wet and dry years. Oecologia **98**:303-312.

Kubiske, M. E. and K. S. Pregitzer. 1996. Effects of elevated CO_2 and light availability on the photosynthetic light response of tree species of contrasting shade tolerance. Tree Physiology **16**:351-358.

Lambers, J. H. R. and J. S. Clark. 2005. The benefits of seed banking for red maple (Acer rubrum): maximizing seedling recruitment. Canadian Journal of Forest Research **35**:806-813.

Lamont, B. 1985. Dispersal of the winged fruits of *Nuytsia floribunda* (Loranthaceae). Australian Journal of Ecology **10**:187-193.

Leak, W. B. and P. E. Sendak. 2002. Field note - changes in species, grade, and structure over 48 years in a managed New England northern hardwood stand. Northern Journal of Applied Forestry **19**:25-27.

Ledig, F. T. and D. M. Smith. 1981. The influence of silvicultural practices on genetic improvement: height growth and weevil resistance in eastern white pine. Silvae Genetica **30**:30-36.

LePage, P. T., C. D. Canham, K. D. Coates, and P. Bartemucci. 2000. Seed source versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. Canadian Journal of Forest Research **30**:415-427.

Levin, S. A., H. C. Muller-Landau, R. Nathan, and J. Chave. 2003. The ecology and evolution of seed dispersal: A theoretical perspective. Annual Review of Ecology, Evolution, and Systematics **34**:575-604.

Lorimer, C. G. 1984. Development of the red maple understory in northeastern oak forests. Forest Science **30**:3-22.

Manson, R. H., R. S. Ostfeld, and C. D. Canham. 1998. The effects of tree seed and seedling density on predation rates by rodents in old fields. Ecoscience **5**:183-190.

Martin, P. H. and C. D. Canham. 2010. Dispersal and recruitment limitation in native versus exotic tree species: Life-history strategies and Janzen-Connell effects. Oikos **119**:807-824.

Matthews, J. D. 1989. Silvicultural systems. Page 284. Clarendon Press, Oxford.

Mayr, H. 1907. Some fundamental principles of silviculture. Forestry Quarterly **5**:174-189.

Mellanby, K. 1968. The effects of some mammals and birds on regeneration of oak. Journal of Applied Ecology **5**:359-366.

Miller, G. W., Kochenderfer, and J. N. 1998. Maintaining Species Diversity in the Central Appalachians. Journal of Forestry **96**:28-33.

Miller, G. W., T. M. Schuler, and H. C. Smith. 1995. Method for applying group selection in central Appalachian hardwoods. USDA Forest Service Research Paper NE-696.

Miller, G. W. and H. C. Smith. 1993a. A practical alternative to single-tree selection? Northern Journal of Applied Forestry **10**:. 32-38.

Miller, G. W. and H. C. Smith. 1993b. A practical alternative to single tree selection? Northern Journal of Applied Forestry **10**:32-38.

Nathan, R. and R. Casagrandi. 2004. A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen-Connell and beyond. Journal of Ecology **92**:733.

Nathan, R. and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution **15**:278-285.

Nyland, R. D. 1998. Selection system in northern hardwoods. Journal of Forestry **96**:18-21(14).

Nyland, R. D. 2007. Silviculture: Concepts and applications. 2nd edition. Waveland Press, Inc., Long Grove, Illinois.

O'Hara, K. L. 1998. Silviculture for structural diversity: A new look at multiaged systems. Journal of Forestry **96**:4-10.

O'Hara, K. L. 2001. The silviculture of transformation: A commentary. Forest Ecology and Management **151**:81-86.

O'Hara, K. L. 2002. The historical development of uneven-aged silviculture in North America. Forestry **75**:339-346.

O'Hara, K. L. 2009. Multiaged silviculture in North America. Journal of forest science **55**:432-436.

Oliver, C. D. and B. C. Larson. 1990. Forests stand dynamics. McGraw-Hill, New York.

Olsson, K. S. 1981. Soil survey of Orange County, New York. Soil Conservation Service, Cornell University. Agricultural Experiment Station, Ithaca, New York.

Pérez-Ramos, I. M. and T. Marañón. 2008. Factors affecting post-dispersal seed predation in two coexisting oak species: Microhabitat, burial and exclusion of large herbivores. Forest Ecology and Management **255**:3506-3514.

Pacala, S. W., C. D. Canham, J. Saponara, J. A. S. Jr., R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: II. Estimation, error analysis and dynamics. Ecological Monographs **66**:1-43.

Pairon, M., M. Jonard, and A.-L. Jacquemart. 2006. Modeling seed dispersal of black cherry, an invasive forest tree: how microsatellites may help? Canadian Journal of Forest Research **36**:1385.

Palmer, B. 2004. Timber stand improvement: A guide for improving your woodlot by cutting firewood. http://mdc.mo.gov/sites/default/files/resources/2010/10/timber_stand_improvement_10-20-10.pdf.

Papaik, M. J. and C. D. Canham. 2006. Multi-model analysis of tree competition along environmental gradients in southern New England forests. Ecological Applications **16**:1880-1892.

Pedersen, B. S. and J. L. Howard. 2004. The influence of canopy gaps on overstory tree and forest growth rates in a mature mixed-age, mixed-species forest. Forest Ecology and Management **196**:351-366.

Perlin, J. 1989. A forestr journey: The role of wood in the development of civilization. Harvard University Press, Cambridge, Massachusetts.

Phillips, P. D., C. P. de Azevedo, B. Degen, I. S. Thompson, J. N. M. Silva, and P. R. van Gardingen. 2004. An individual-based spatially explicit simulation model for strategic forest management planning in the eastern Amazon. Ecological Modelling **173**:335-354.

Pickett, S. T. A. and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Puettmann, K. J., K. D. Coates, and C. C. Messier. 2008. A critique of silviculture: Managing for complexity. Island Press, Washington, DC.

Queenborough, S. A., D. F. R. P. Burslem, N. C. Garwood, and R. Valencia. 2007. Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. Ecology **88**:2248-2258.

Ribbens, E., J. A. Silander, and S. W. Pacala. 1994. Seedling recruitment in forests: Calibrating models to predict patterns of tree seedling dispersion. Ecology **75**:1794-1806.

Rogers, R. 1990. White oak. Pages 605-613 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America, Vol. 2, Hardwoods. Agriculture Handbook 654. USDA Forest Service, Washington, D.C.

Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of Eastern North America. Ecology **63**:1522-1546.

Russo, S. E., S. Portnoy, and C. K. Augspurger. 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. Ecology **87**:3160–3174.

Russo, S. E., S. K. Wiser, and D. A. Coomes. 2007. Growth-size scaling relationships of woody plant species differ from predictions of the Metabolic Ecology Model. Ecology Letters **10**:889-901.

Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany **82**:399-409.

Seymour, R. S. 2004. Silviculture: Lessons from our past, thoughts about the future. Page 49 *in* B. Palik and L. Levy, editors. Proceedings of the Great Lakes Silviculture Summit. USDA Forest Service General Technical Report NC-254, Houghton, Michigan.

Seymour, R. S., J. Guldin, D. Marshall, and B. Palik. 2006. Large-scale, long-term silvicultural experiments in the United States: historical overview and contemporary examples. Allgemeine Forst und Jagdzeitung **177**:104-112.

Shirley, H. L. 1945. Reproduction of upland conifers in the Lake States as affected by root competition and light. American Midland Naturalist **33**:537-612.

Siegel, J. S. and D. A. Swanson. 2004. The methods and materials of demography. 2nd edition. Academic Press, San Diego, Elsevier.

Smith, B. W., P. D. Miles, J. S. Visage, and S. A. Pugh. 2004. Forest resources of the United States, 2002. General Technical Report NC-241. St. Paul, Minnesota: USDA, Forest Service, North Central Research Station.

Smith, D. M. 1986. The practice of silviculture. 8th edition. John Wiley & Sons, New York.

Smith, D. M., B. C. Larson, M. J. Kelty, and P. M. S. Ashton. 1997. The practice of silviculture: Applied forest ecology. 9th edition edition. John Wiley & Sons, New York.

Spies, T. 1997. Forest stand structure, composition, and function.*in* K. A. Kohm and J. F. Franklin, editors. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington, DC.

Spur, S. H. and B. V. Barnes. 1964. Forest ecology. John Wiley & Sons, New York.

Stoll, P., J. Weiner, and B. Schmid. 1994. Growth variation in a naturally established population of *Pinus sylvestris*. Ecology **75**:660-670.

Stoyon, D. and S. Wagner. 2001. Estimating the fruit dispersion of anemochorous trees. Ecological Modelling **145**:35-47.

Streng, D. R., J. S. Glitzenstein, and P. A. Harcombe. 1989. Woody seedling dynamics in an east Texas floodplain forest. Ecological Monographs **59**:177-204.

Tackenberg, O. 2003. Modelling long-distance dispersal of plant diaspores by wind. Ecological Monographs **73**:173-189.

Toumey, J. W. and C. F. Korstian. 1937. Foundations of silviculture upon an ecological basis. John Wiley & Sons, New York.

Town of Deerpark Town Board, T. o. D. P. B., and Shepstone Management Company. 2003. Town of Deerpark Orange County New York comprehensive plan.*in* Upper Delaware Council.

Uriarte, M., C. D. Canham, J. Thompson, and J. K. Zimmerman. 2004a. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. Ecological Monographs **74**:591-614.

Uriarte, M., C. D. Canham, J. Thompson, J. K. Zimmerman, and N. Brokaw. 2005. Seedling recruitment in a hurricane-driven tropical forest: light limitation, density-dependence and the spatial distribution of parent trees. Journal of Ecology **93**:291-304.

Uriarte, M., R. Condit, C. D. Canham, and S. P. Hubbell. 2004b. A spatially-explicit model of sapling growth in a tropical forest: Does the identity of neighbours matter? Journal of Ecology **92**:348-360.

Vale, T. R. 1982. Plants and people: Vegetation change in North America. Association of American Geographers, Washington, DC.

Vettenranta, J. and J. Miina. 1999. Optimizing thinnings and rotation of Scots pine and Norway spruce mixtures. Silva Fennica **33**:73-84.

Wagner, R. G. and S. R. Radosevich. 1998. Neighborhood approach for quantifying interspecific competition in coastal Oregon forests. Ecological Applications **8**:779-794.

WCED. 1987. Our Common Future. Oxford University Press, New York, NY, USA.

Weiner, J. and S. C. Thomas. 2001. The nature of tree growth and the "age-related decline in forest productivity". Oikos **94**:374.

Wimberly, M. C. and B. B. Bare. 1996. Distance-dependent and distance-independent models of Douglas-fir and western hemlock basal area growth following silvicultural treatment. Forest Ecology and Management **89**:1-11.

Wiser, S. K., R. B. Allen, U. Benecke, G. Baker, and D. Peltzer. 2005. Tree growth and mortality after small-group harvesting in New Zealand old-growth Nothofagus forests. Canadian Journal of Forest Research **35**:2323-2331.

Wright, E. F., C. D. Canham, and K. D. Coates. 2000. Effects of suppression and release on sapling growth for eleven tree species of northern, interior British Columbia. Canadian Journal of Forest Research **30**:1571-1580.

Yahner, R. H. 2000. Eastern deciduous forest: ecology and wildlife conservation. 2nd edition. University of Minnesota Press, Minneapolis, Minnesota.

Yates, F. 1964. Sir Ronald Fisher and the design of experiments. Biometrics **20**:307-321.

Zeide, B. 1993. Analysis of growth equations. Forest Science **39**: 594-616.