Spatial Patterns of Tree Invasion in an Old Field: Implications for Restoration

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revision, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

In north-eastern North America, abandoned agricultural fields typically revert to forest after many decades of spontaneous succession. This process can be influenced in part by nearby available propagule sources and their natural patterns of dispersal. Ecological restoration encompasses understanding this natural process and how it may influence active or passive restoration efforts. This study attempts to determine the spatial and temporal patterns of establishing trees arising in an old field at 10 years post-cultivation and the implications of this process on restoration at rare and other similar sites.

The 0.8 ha field is situated at rare, an ecological reserve in Cambridge, Ontario and is bordered by forest or hedgerow on all sides. Using Environmental Monitoring and Assessment Network (EMAN) protocols, vegetation sampling was completed in the field and adjacent forest and hedgerow. A complete tree inventory was undertaken in the field, followed by a sampling of potential seed sources in the forest and hedgerow. ESRI ArcMap, a Geographic Information System (GIS) was utilized for both spatial representation and spatial analysis. Research revealed that the application of geostatistics to ecological data here and elsewhere in the literature has some specific challenges which need to be overcome for analysis of spatial data.

Currently, the old field shows early signs of woody plant invasion from the nearby forest. Both trees and shrubs have become established, though not yet dominant. The primary dispersal of these species follows spatial patterns based on method of dispersal (wind, nut, fruit and clonal) and there is a higher degree of clustering of all species closer to the forest edge. Invasive species such as *Rhamnus cathartica* and *Rhamnus frangula* have become established in the old field and may influence successional patterns. Implications for restoration include the creation of goals and objectives which incorporate these natural processes into a future management plan. Specific recommendations include:

- Develop a management strategy for invasive species such as Rhamnus spp. which can detrimentally affect restoration goals;
- 2) Continue to monitor EMAN plots for the production of time-series data on the same site;
- 3) Identify sites with good regeneration potential based on spatial patterns identified in this research and collect additional information such as soil conditions, canopy cover, etc.;

4)	Extend the current GIS database created for this thesis to become an inventory of natural and cultural features for the reserve. Advanced spatial analysis required a more extensive data set and/or custom programming.

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My children- Theo, Miranda, and Emily, who fill my life with joy and laughter.

Dedication

This thesis is dedicated to the men in my life: my father, whose love of cultural and natural history was passed down to me and who grew up across the river from Cruickston Park; my husband-without his many hours of dedicated help I would still be at this and whose love and support has pushed me forward; and my first born, Theo; whose entry into this world ten years ago has taught me more than any degree ever could. I love you dearly.

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Chapter 1: Introduction

"The challenge for ecologists is to enhance the integration of scientific knowledge of spontaneous vegetation succession into restoration programs and to ensure effective implementation of theoretical and practical information". (Prach et al. 2001)

For the past 200 years, southwestern Ontario has seen a dramatic decrease (upwards of 90%) in forest cover and wetland habitat. As land was converted to agriculture by European and other immigrants, more and more forests disappeared and the ones remaining were fragmented, selectively logged and reduced in size and function. Only now are we as a society recognizing the value of those habitats and the importance of not just preserving what's left, but also enhancing and creating new ones through ecological restoration. The science of ecological restoration explores the theories and practice of recovering some of the damage humans have created. It can be defined as 'the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed' (SER International Primer 2004). Davis & Slobodkin (2004) go further by integrating the human values associated with restoration into their definition: 'Ecological restoration is the process of restoring one or more valued processes or attributes of a landscape'.

Ecological restoration can be either active through interventions such as plantings, invasives control or prescribed burns, or passive non-intervention. Passive restoration is a crucial first step in ecological restoration (Wissmar & Beschta 1998) in which ecological thresholds can be identified through observing how and when elements of an ecosystem reassemble independent of any direct human attempts of restoration. This can also be referred to as spontaneous succession and much of the literature pertaining to natural regeneration of forests uses this term. Integration of these natural processes into restoration plans can be critical to the outcome and should not be overlooked, particularly at the implementation stage (Prach et al. 2001). Succession is important to restoration because managers have to prevent, enhance or replace natural vegetation and their relevant ecological processes (Pickett et al. 2001).

The research presented here examines one aspect of succession that are especially pertinent to ecological restoration, that of spatial patterns of tree establishment and in particular, the relationship with propagule source(Robinson & Handel 2000). A key concept in this process is 'establishment' which is described by deSteven (1991a) as the germination, emergence, growth and survival of a seedling past the first year of life. Spatial pattern in old fields in early succession is determined in part by the dispersal strategy of a species (Myster & Pickett 1992). These

strategies include wind, bird, mammal, and clonal advance. The surrounding landscape plays a critical role in determining future patterns of tree establishment within the field, particularly in early succession when there are few to no woody propagule sources available in the field itself. An old field abandoned for 10 years and located in Cambridge, Ontario is the study site that provides the source of the collected data.

Research Question

What is the spatial and temporal relationship between establishing woody plants in an old field after 10 years and their likely seed source in the nearby woods?

Null hypothesis: There is no spatial or temporal relationship.

Alternate hypothesis: There is a relationship between mature woody vegetation in the forest and establishing woody vegetation in the field. There is a spatial pattern related to forest edge and method of dispersal. There is a temporal pattern of woody plant invasion into the field after 10 years.

Study of the abandoned field will reveal what stage in succession it has reached after 10 years of no cultivation. After 10 years of no disturbance and with nearby propagule sources in the adjacent forest and hedgerow, it is expected that there would be some establishing trees in the old field. The stage or sere of succession of this field can be determined by the type of herbaceous vegetation, the presence and distribution of woody plants and soil characteristics. More specifically, it will be determined what species of trees are establishing themselves through natural means and their likely seed source. Secondly, spatial distribution of the trees may be evenly distributed through the field, clustered, or concentrated near the forest edges. Even distribution may reflect overall soil and light conditions favouring tree growth, clusters might indicate windborne or clonal dispersal of tree species, or differing localized soil conditions. Concentration of woody species on the perimeter of the field nearest the forest edges may result from clonal reproduction, windborne and gravitational dispersal of seeds, and/or soil conditions more similar to the forest than the field.

It is also expected that the location of tree establishment is highly dependent on several external factors or 'filters' such as the location and composition of nearby propagule sources, the type of seed dispersal (wind, animal, or clonal), microclimate and soil conditions. Prach et al. (2001) have determined that surrounding vegetation in particular, and secondarily, macroclimate, soil moisture, amount of nitrogen and soil texture appeared to have the highest influence on the course of succession. Also, given the recent abandonment of the field (10 years) and the lack of

human activity since then, the earliest stages of forest structure may be there, but vegetation composition would be still closer to old field habitat than young forest.

The motivation for this research stems from a desire to better understand the general ecology of newly abandoned fields at the earliest stage of succession that have not been directly influenced by human activity since abandonment. Aside from personal interests in understanding old field succession, the research is important because the chosen site of study is on an ecological reserve called "rare" located near Cambridge, Ontario. Known simply by its public name of 'rare' since 2004, it was previously referred to as Cruickston Park, and subsequently Cruickston Charitable Research Reserve at the time of its formation in 2001. One of its mandates is on-site scientific research on ecology and restoration and subsequently can directly benefit from research collected on successional processes on its land in future restoration work.

Research Objectives

There were three major research objectives that guided this thesis:

- 1. To develop baseline data on patterns of vegetation over time and space, particularly in a context of old field succession. More specifically, *What is the overall state of woody and herbaceous vegetation in the field and surrounding forest and hedgerow?* These baseline data were collected to be consistent with Environmental Monitoring and Assessment Network (EMAN) protocols and records information in the form of vegetation inventories and tree sampling in the old field and adjacent forest. Two additional questions pertaining to the trees themselves will be addressed: *What are the spatial patterns of field trees (random, regular or clustered)* and how do they differ by dispersal methods, species and height?, and *What are the likely seed sources in the surrounding landscape and how do they influence the spatial distribution?*
- 2. To apply and assess GIS tools of representation and analysis to the spatial data to visualize and measure patterns of tree regeneration, and secondarily, to form the beginning of a centralized storage system of information pertaining to the natural and cultural history of this property. Geostatistics are being increasingly incorporated into ecological studies (see Kent et al. 2006) and applying appropriate analysis tools is a particular challenge as these tools become simultaneously integrated into GIS software. To this end, the following research question is posed: What are the benefits and shortcomings of GIS in this application and how can it best be applied to ecological restoration? In particular, to what extent can the spatial analysis tools offered in ArcMap be most effectively employed to this data set? To this effect, this thesis will apply some of the analytical tools on this data set and assess the outcome

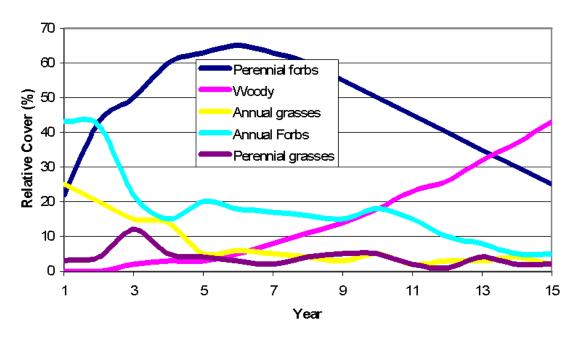
based on the level of knowledge required to appropriately use the tools and the practicality of the output produced.

3. To determine how to best incorporate spontaneous succession into ecological restoration at this study site and others like it. Prach et al. (2001) state the importance of identifying targets for restoration (both structure and function) and that spontaneous succession can be used to achieve them. To that end, *How can the research on the biological legacy (Hobbs & Norton 2004) of this site be used to direct terrestrial restoration of this and other old fields?*

This research included background information in the form of a comprehensive literature review (Ch 2) on forest succession and pertinent theory on ecological restoration of terrestrial ecosystems followed by a description of the study site (Ch 3). Chapters 4 and 5 describe the methods of data collection and analysis and subsequent results of field research undertaken during the summer of 2006. Chapter 6 discusses the findings using GIS applications to represent and analyze the data, and most importantly how knowledge of ecological processes can be effectively integrated into restoration. It discusses many of the challenges of applying geostatistics to ecological data and how this may be overcome. The final chapter (7) summarizes the major findings of this thesis and makes further specific recommendations for future research and restoration both at the **rare** property and towards the more general body of knowledge on spontaneous succession in terrestrial ecosystem restoration.

Chapter 2: Literature Review

Secondary succession in "old fields" (nominally, abandoned agricultural land left in permanent fallow) is the change in species composition and dominance over many years that usually results in a forest ecosystem despite the initial absence of woody vegetation (Lawson et al. 1999; Myster 1993). Studying succession can enhance understanding of the physical and biological processes that affect the recovery of a natural system and how they can be applied to an area in need of restoration. This allows for more appropriate and effective intervention to accelerate natural regeneration. In southwestern Ontario, secondary succession of farmland usually entails a lengthy transition (100+ years) from meadow to a forest comprised of early establishing trees such as Acer saccharum (Sugar Maple), Fraxinus americana (White Ash), Populus tremuloides (Trembling Aspen) and Ulmus americana (American Elm) (Gardescu & Marks 2004; Crowder & Harmsen 1998). In the first years (0-5) also known as early sere, annuals and biennials tend to dominate. These are then replaced in dominance by mid-sere perennials, particularly Solidago canadensis, peaking around 10-20 years, and followed by woody vegetation (Smit & Olff, 1998; Cook et al., 2005) (Figure 1). The expectation is that through succession, a disturbed area will ultimately transform to a forest of similar composition to the surrounding landscape (Wissmar & Beschta 1998; Buckley et al. 2002).



(adapted from Cook et al. 2005)

Figure 1: Old field vegetation change

Major Theories of Succession

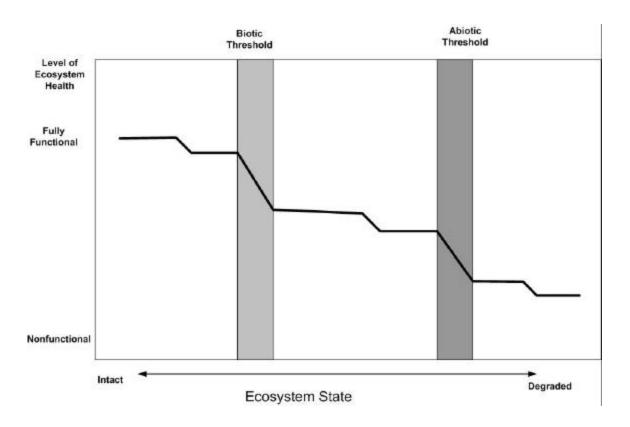
Succession as a biological theory was first proposed by Frederic Clements in 1916 (Cook 1996). This 'Clementsian' theory, as it became known, was based on the observation of a classic progression of vegetation change towards a climax state (forest) and continuing stability thereafter. Disturbance was considered uncommon, and deterministic, unidirectional assumptions were used to explain change in ecological communities. Some contemporaries of Clements disagreed and proposed alternate theories, notably Gleason (1926) and Cooper (1926) emphasizing more unpredictability and individuality in succession. By 1954, Egler proposed the Initial Floristics Model which stated that critical components of a late sere succession can be present right from the beginning. Trees can establish on bare mineral soil, and once present, will become important components of later vegetation community. This also assumed more random, stochastic processes and was in sharp contrast to Clementsian theory.

Eventually, the theories progressed in complexity, such as three models proposed by Connell & Slatyer in 1977. The rate of succession was determined by varying components of 1) the timing of species establishment, 2) competition for space and resources, and 3) species life history characteristics. No steady state was assumed, nor the absence of disturbance. Like Egler's Initial Floristics Model, it recognized that species from all stages of succession can colonize after disturbance. Their models included *facilitation* whereby one species changes conditions to favour other species, *tolerance* (co-existence) with multiple species, and *inhibition* in which one species suppresses another. Of these three models, facilitation seemed to best explain primary succession, and the inhibition model had the most empirical support. Much of the research available in peer reviewed journals observed the facilitation and inhibition relationships. Examples include:

- Shrubs can inhibit tree establishment (Gardescu & Marks 2004)
- Solidago canadensis can inhibit woody plant invasion (Myster 1993; Crowder & Harmsen 1998; Dickie et al. 2007)
- Grasses can inhibit woody plant invasion (Maycock 1963; Myster 1993; Scholes & Archer 1997; Dickie & Reich 2005)
- Predation on seeds and seedlings through herbivory can inhibit establishment of woody vegetation (Howard & Lee 2003)
- Herbs can facilitate germination of tree seeds (Gill & Marks 1991)

- Shrubs can facilitate establishment of trees through the provision of perches (seed dispersal), less predation and improved microsite suitability (Myster 1993; Battaglia et al. 2002; Li & Wilson 1998)
- Proximity to other trees can facilitate tree establishment, most likely from increased ectomycorryizal infection (Dickie et al. 2007)

Other theories that relate specifically to succession abound, but it is the advent of the science of ecological restoration in the 1980s that is transforming the nature of research today. Assembly rules described in Halle & Fattorini (2004) entail the understanding of not just the parts of a system to be reassembled, but how they function individually and integratively and in what order they should be re-introduced or "re-assembled". Assembly theory focuses on factors such as the natural disturbance regime of a system, recruitment dynamics, plant interactions, mycosymbionts, decomposers, pollinators and seed dispersers. In some of the more recent research (Bartha et al. 2003; Hobbs & Norton 2004; Reidel & Epstein 2005), this is incorporated as the existence of thresholds with filters such as drought and invasive species which can alter the succession rate and composition of communities. Hobbs & Norton's (2004) conceptual framework of transition thresholds (Figure 2) can serve as a template from which to identify where a system is currently and what constitutes a desired end state. Abiotic filters such as climate, substrate and landscape structure represent the first hurdle (threshold) to be overcome for a system to become higher functioning. Biotic filters include relationships between species, biological legacy, propagule availability and disturbance regimes.



(Hobbs & Norton 2004)

Figure 2: Transition thresholds and their effect on ecosystem recovery

An over-riding challenge of ecological restoration, whether it is active or passive, is in identifying which filters are more important than others for the specific goals that restoration is trying to achieve and subsequently finding a way to incorporate them into restoration. Ultimately, it entails determining when intervention is desirable at a site and to what degree and when to leave it alone.

The study of landscape ecology has also influenced research on succession, with attention focused on spatial processes and the matrices of land use (Jacquemyn et al. 2003; Benjamin et al. 2005). Interestingly, some of the most progressive ideas about succession are based somewhat on relatively neglected past theories as a basis. W.S. Cooper's idea of vegetation change from 1926 has been adopted by Anand (2000) in which the analogy of ecosystem change is like a complex braided stream incorporating both elements of predictability and randomness. Most importantly, ecosystems are seen to possess a certain amount of inertia - systems which are relatively stable tend to stay that way unless a drastic event pushes them far from their equilibrium. A non-stable system requires only small influences for there to be large effects (Anand 2000).

These big-picture concepts are important in presenting a context in which change happens and as a holistic perspective that incorporates many different areas of ecology. Nevertheless, as indicated above, many studies continue to focus on smaller scales using a narrow range of variables which still lend themselves to the traditional models of succession, particularly that of facilitation and inhibition. In Hobbs & Norton's (2004) paradigm, descriptions of thresholds are essentially these processes of facilitation and inhibition. It is from this context that much of the research in this chapter is presented.

Major Studies on Succession

Currently, there are several North American studies on the succession of old fields to forest which focus on temporal and spatial patterns through time series data (long term permanent plot studies) and chronosequences (space for time studies). Some of the most well known include the following:

- Tompkins County, New York State (Stover and Marks 1998)
- Cedar Creek Natural History Area, Minnesota (Inouye et al. 1987), and
- Buell-Small Successional Study, Hutcheson Memorial Forest Centre, New Jersey (Bartha et al. 2003; Meiners et al. 2001)
- Queens University Biological Research Station, Ontario, (Crowder & Harmsen 2005, Blatt et al. 2003)

Many of these studies on old field succession have primarily focused research on forest edge effects (Coffin et al. 1996; Dickie and Reich 2005; Riedel & Epstein, 2005), soil conditions, particularly nitrogen levels and effects on grasses, forbs and woody vegetation (Wilson and Tilman 1991; Wilson and Tilman 2002), and herbivory and seed dispersal (Manson et al. 2001; Meiners et al. 2000; Myster 1993). These studies and others (Gill and Marks 1991) indicate that forest establishment is often inhibited by a number of factors including: high mortality of germinated tree seeds, competition from dense forbs and grasses, herbivory (mammalian and insect), drought, invasive species, and low available nitrogen and absence of mycorrhizal fungi in soil. Perhaps most importantly, forest establishment on old fields is often limited by proximity to seed sources (Holl & Crone, 2004; Myster 1993).

Seedling invasion and establishment of woody species has been an important part of major investigations into old field succession in eastern deciduous forests (Myster 1993). Tree establishment is defined as a seedling's dispersal, germination and survival past the first year

during which mortality is very high (Gill & Marks 1991; Desteven 1991b; Myster 1993; Meiners et al. 2000). Tree establishment is highly dependent on local seed sources and the opportunity to invade a suitable location with sufficient resources and then to survive predation, physical damage and harsh environmental conditions. Table 1 summarizes the primary causes of tree mortality under natural conditions.

Table 1: Causes of tree mortality during the first year

Seed Predation	75-100%
Emergence	6-12%
Competition	0-100%
Seedling Predation	34-100%
Frost Heaving	0-23%
Physical Damage	5-15%
Drought, Insects	0-2%

(Myster 1993)

Seed and seedling predation represents the largest cause of mortality, although most causes were highly variable depending on local site conditions and the nature of the studies. Although my thesis only examines tree seedlings that have survived past the first year, knowledge about possible causes of mortality may help explain abundance or absence of particular species noted during field work.

Temporal Factors: Recovery Rates and Influences

Because old-field succession is first and foremost a time-dependent process, studies typically involve recording permanent plots over many years, where the location and presumably most of the processes remain constant (Bartha et al. 2003; Meiners et al. 2001; Crowder & Harmsen 1998). Other studies (Howard & Lee 2003; Lawson et al. 1999; Foster & Tilman 2000) have substituted or 'swapped' time for space and examined many fields in many different stages in a minimal time period. This is also known as a chronosequence and has the benefit of gathering a great deal of information of different successional stages in similar vegetation communities within a more realistic time frame. Neither type of study was practical for this thesis, but because the temporal patterns are so important, findings of other research are discussed and applied here where appropriate.

In the southern Ontario temperate climate, agriculture has been the main reason why so much land is devoid of the original native species. Abandoned agricultural fields are somewhat like early successional meadows and can be expected to eventually revert to forest cover (Buckley et al. 2002; Wissmar & Beschta 1998). This process takes many decades or centuries and the speed of succession depends mainly on soil conditions (Blatt et al. 2005), existing vegetation (Gardescu & Marks 2004), proximity to seed sources (Battaglia et al. 2002; Gill & Marks 1991, Oosterhorn & Kappelle 2000), previous land use (Stover & Marks 1998) and human interference (Wilcox 1998). Both the initial and the ultimate species composition of the reestablished forest are dependent on these same factors. Egler's theory of Initial Floristic Composition (1954) argues that in the very earliest stages of revegetation, the earliest establishing species will direct the trajectory of succession. Even in the first few years post-disturbance, woody species can become established and influence later stages (Bartha et al. 2003; K Buschert personal observation).

Transition of a field to a forest begins with invasion of woody vegetation. Natural systems can reassemble in multiple ways depending on biotic/abiotic filters that influence them at any given time (Halle & Fattorini 2004; Dickie & Reich 2005; Blatt et al. 2005). For instance, in prairie ecosystems, trees and shrubs exist but tend to remain a minor component because of abiotic filters such as fire and/or drought which favour a prairie community. When these filters are reduced or disappear, the system may cross the threshold responsible for the status quo and it then has potential to reassemble into something different (eg. prairie to savanna). In the case of a cultivated field, it is the cultivation which functions as a filter. The abandonment of the field releases the system past that threshold, presenting opportunities for plant invasion. After that, the speed of woody plant invasion is affected by multiple factors that either inhibit or accelerate the process (Table 2).

Table 2: Factors affecting recovery rates of field to forest transitions

Slower	Faster
xeric and nutrient poor soil conditions (Davis et al. 2005; Inouye et al.1994; Crowder & Harmsen 1998; Prach & Pysek 2001)	mesic soil conditions (Blatt 2005; Druckenbrod 2005; Prach & Pysek 2001)
large area (but see (Cook et al. 2005))	small area (Buckley 2002; Prach & Pysek 2001)
isolated (>100 m) from forest (Gardescu 2004; Jacquemyn, 2003)and lack of connectivity (Holl 2004)	nearby propagule souce (forest) (Riedel 2005; Crowder & Harmsen 1998; Cook 2005; Battaglia 2002; Lawson et al. 1999; Harmer & Kerr 1995; Wissmar & Beschta 1998; Holl 2004; Gill & Marks 1991; Oosterhorn & Kapelle 2000; Gardescu & Marks 2004)
establishment of exotic species, perennial species (Smit & Olff1998; Crowder & Harmsen 1998; Myster 1993), or general plant competition (Harmer et al. 1995; Prach & Pysek 2001)	invasive weed control (Bakker & Wilson 2004), herbaceous and shrub facilitation (Myster 1993; Battaglia 2002)
doing no restoration (Bell 1997)	revegetation (Wilcox 1998)
herbivory (early succession only) (Cadenasso et al. 2002; Manson 2001; White & Jentsch 2004; Harmer 1995; Gill & Marks 1991; Myster 1993; Howard & Lee 2003)	soil restoration (Harris & Hill 1995) including mycorrizal inoculation (Dickie & Reich 2005; Halle & Fattorini 2004; but see Hedlund 2002), and pit and mound creation (White & Jentsch 2004)
prior agricultural uses, crops (Stover & Marks 1998; Myster 1993)	perches for bird-dispersed seeds (McClanahan & Wolfe 1993) and hedgerows (McCarthy 1994)

Expected recovery times for forest regrowth have been estimated at 30-50 years for a young forest (Maycock 1984; Buckley & McLachlan 2002) to over 100 years for old growth (Wissmar & Beschta 1998). Accelerated woody vegetation establishment is highly dependent on proximity to a nearby propagule source such as a forest or hedgerow. Many of the sources listed above agreed that this is the primary factor in effective natural regeneration of forests. Soil conditions such as nutrient levels, moisture levels and the presence of mycorrhizae are important but at the microtopographic scale (White & Jentsch 2004; Dickie & Reich 2005). In fact, Mou (2005) stresses that regeneration is far more dependent on the nature of disturbance and regeneration strategies such as seed dispersal methods and species effects than on soil conditions and resources. Likewise, herbivory through seed predation is crucial to tree establishment but becomes less important over time. Competition from other species, particularly invasive ones, appears to inhibit recovery rates (Holl & Crone 2004; Davis et al. 2005), but can be addressed

with some moderate intervention such as exotic species removal and weed control (Bakker 2004).

There is a lack of consensus as to the role of soil in the process of succession. Some research indicates that wet areas are likely to succeed faster than dry areas because of better soil conditions (Inouye et al.1994; Crowder & Harmsen 1998; Perrow & Davy 2002; Blatt et al. 2005; Druckenbrod et al. 2005; Davis et al. 2005), although Messaoud & Houle (2006) did not find this to be true in their studies. Conversely, Smit & Olff (1998) and Harmer & Kerr (1995) observed faster woody vegetation establishment on the poorest soil, albeit mostly pioneer species. Prach & Pysek's studies of Central Europe (2001) observed that spontaneous succession as measured by the regrowth of woody vegetation was faster in sites with moderate moisture and soil conditions and slower in extreme conditions such as xeric soil and/or toxic substrates.

Nutrient levels in the soil have a mixed effect. Available nitrogen was considered to facilitate tree and shrub establishment (Li & Wilson 1998; Prach 2001), though Davis et al. (1999) found that oak seedling survival was lower in nitrogen enriched plots and Lawson et al. (1999) found no relationship to tree abundance and density. Because nitrogen mainly concentrates in the upper soil layer, it may not alter the course of succession so much as increase the biomass and density of existing vegetation (Huberty et al.1998). The role of potassium and phosphorous seemed to be minimal except in their association with fertilizers (Romermann 2005). The absence of ectomycorrhyzal infection on tree root systems may reduce establishment potential in trees far from the forest edge (Dickie & Reich 2005), but research is lacking and inconclusive (Burton & Bazaaz 1995; Crowder & Harmsen 1998). Clearly the role of soil in forest establishment is complex and aside from the role of moderate to high moisture levels accelerating forest regeneration, soil is too highly variable to conclusively predict how succession will proceed.

Time clearly influences the process of forest establishment and combinations of the previously mentioned factors play a role in recovery rates and successional trajectories. By far the overwhelming consensus in the literature for predicting future forest composition assuming no human interference seems to be nearby propagule sources and their composition (Gill & Marks 1991; Harmer & Kerr 1995; Crowder & Harmsen 1998; Wissmar & Beschta 1998; Lawson et al. 1999; Oosterhorn & Kapelle 2000; Battaglia et al. 2002; Holl & Crone 2004; Gardescu & Marks 2004; Riedel 2005; Cook et al. 2005). Whether this is a result of being a commonly studied phenomenon or whether it represents a true major influence cannot be answered here but may be an interesting area of study using methods such as the Akaike Information Criterion (Akaike 1973) in which various factors are measured for their impact on a given phenomenon. In addition to the temporal component, propagule sources have strong influence on spatial patterns such as the edge effect which in turn influence the future outcome of old field successions.

Spatial Factors of Tree Establishment

There are patterns of tree establishment in old fields which are most evident in early to mid succession and become less significant over time (Myster & Pickett 1992). Succession is highly contingent on local spatial patterns (Pickett et al. 2001). In particular, it has been observed that trees in old fields are more likely to establish close to the edge of a forest or hedgerow and that these trees are influenced by the surrounding landscape (Gill & Marks 1991; Pickett & Cadenasso 1995 and others). This is referred to as the edge effect.

Edge Effects

In the literature, spatial data relating to old field succession are often studied in the context of edge effects, particularly in ecosystems that have clear, well defined boundaries (Matlack 1994; Burke & Nol 1998; Meiners et al 2002). The rate of change in environmental conditions and vegetation composition is greatest in the transition area between the two communities and can be observed as effects penetrating into the forest and/or into the field. Because environmental conditions such as light levels, humidity, soil moisture and nutrient levels change drastically from the forest to the field (Burke & Nol 1998), the edge effect phenomenon is easier to observe than many other factors and this is reflected in the abundance of literature that examine it (Burke & Nol 1998; Meiners et al. 2000; Manson et al. 2001; Gardescu & Marks 2004; Reidel & Epstein 2005; Cook et al. 2005). Change is strongest within 5-10 m of the forest edge (Burke & Nol 1998; Meiners et al. 2000), but edge effects can still be evident up to 40 m into the forest or field (Matlack 1994; Meiners et al. 2002).

The edge effect on a forest-field boundary is strongest early in the successional process and at closer proximity to the boundary. Trees spread into a field faster near the forest edge (Cook et al. 2005) and the canopy closes over at the edges first (Crowder & Harmsen 1998; Reidel & Epstein 2005) with closure recorded at approximately 8-30 cm per year (Matlack 1994). Nonetheless, the edge effect can persist for many decades, even after the canopy has closed (Matlack 1994; Lawson et al. 1999). Herbivory has been observed more often at the forest edge (Myster & Pickett 1993; Meiners et al 2000; Manson et al. 2001). Additionally, the edges provide openings for invasive species such as *Rhamnus spp.* and *Alliaria petiolata* to penetrate into the forest and alter forest understory composition (Burke & Nol 1998; Harper et al. 2005). Even ectomycorrhyzal fungi are influenced by the edge (Dickie & Reich 2005). However, one aspect of tree establishment which is most evidently influenced by the edge is the seed dispersal patterns of various species in the adjacent landscape

Seed Dispersal Patterns

Seed dispersal from forests into adjacent fields or forests is a widely documented phenomenon affecting ecosystem reassembly (Pickett & Cadenasso 1995; Oosterhorn & Kappelle 2000). These nearby seed sources greatly influence species composition and spatial patterns of woody plants (Gill & Marks 1991). Making predictions about specific parent-offspring relationships is difficult because of patterns of dispersal and the challenges of identifying parents with their offspring. Nonetheless, two generalizations can be made about seed dispersal and distance: first, seed deposition is greater near the forest edge and decreases exponentially, even for bird-dispersed species (McDonnell & Stiles 1983), and secondly, heavy-seeded trees such as *Quercus & Carya* deposit seeds closer to the edge (Cook et al. 2005) while wind-dispersed trees (*Acer, Fraxinus*, *Ulmus*) deposit their seeds at a wider range of distances away from the edge (Myster 1993). Specific distances are indicated in Table 3 below. In Johnson (1988), *Fraxinus* had the furthest dispersal and *Tilia* the shortest (nothing past 21 m). Clonal advance is also widely observed among certain species, particularly *Populus tremuloides* and also proceeds closest to the forest edge.

Table 3: Eastern tree species and their dispersal potential

Species	Method of Dispersal	Dispersal Distance	Time of Dispersal
Acer rubrum	Wind	Most <40m, up to 120m ²	Apr-Jun ¹
Acer saccharum	Wind	Most <15m, up to 100 m ⁹	Sept-Oct ⁹
Fraxinus americana	Wind	Most <40m, up to 120m ²	Sept-Oct ¹
Pinus strobus	Wind	Most <20 m, up to 210m ⁷	Aug-Sept 7
Quercus rubra	Mammal, Bird	5-45 m ^{4,5}	Sept-Oct ¹
Rhamnus	Bird, Clonal	0.35 m/year advancement 8	September-April ¹
Carya	Mammal, Bird	More than Quercus rubra 4	
Populus tremuloides	Clonal, Wind	Up to 1.5 m year (clonal) ³	
Tilia	Wind	Most within 15 m 5,6	

 $^{^1}$ Gill & Marks 1991, 2 Wagner et al. 2004, 3 Barnes 1966, 4 Li & Zinnel 2003, 5 Olsson 1987, 6 Johnson 1988, 7 Dovciak et al. 2005, 8 Frappier et al. 2003, 9 Tirmenstein 1991.

In many successional studies, patterns were noted between establishing trees and their seed dispersal method (Olsson 1987; Stover & Marks 1998; Crowder & Harmsen 1998; Howard & Lee 2003). Colonization was similar for species of similar dispersal mechanisms, implying that

dispersal mechanism can be applied across several species (Olsson 1987). These dispersal methods included wind, bird (fruit), mammal (nut) and clonal. In many cases, a tree can be dispersed more than one way such as *Populus tremuloides* which has longer-distance reproduction and dispersal via wind, but more often reproduces clonally (near-distance reproduction and dispersal). This was also true of many fruit and nut trees which are typically dispersed by both birds and mammals and for which dispersal can't always be clearly determined based on establishment pattern alone. Some clear trends emerged from the literature:

- 1) Wind dispersed trees and fleshy fruited shrubs/trees tended to colonize and dominate early on (Maycock 1984; Myster 1993; Stover & Marks 1998; Howard & Lee 2002; Cook et al. 2005), particularly when soil is bare and exposed.
- 2) Dry nut trees such as *Quercus* and *Carya* tend to show up slightly later (Maycock 1984; Myster 1993; Crowder & Harmsen 1998), but rapidly achieve co-dominance (Maycock 1984).
- 3) Clonal advance of *Populus tremuloides* is more common than seed-germinated trees of the same species except where soil is thin and nutrient poor (Barnes 1966).
- 4) Tree and shrub density declines dramatically with increased distance from the forest edge (10-20 m into field), even for wind and bird-dispersed species (Lawson et al.1999; Rigg & Beatty 2004). This effect remains strong, even after decades of succession (Lawson et al.1999).

Another distinct spatial pattern relating to tree establishment is the tendency to cluster. Establishing trees cluster more at the edges and this is especially evident on a species-specific level in early succession (McDonald et al. 2003; Jiri et al. 2004; Druckenbrod et al. 2005). Trees are more likely to cluster if they are found close to the edge and reproduce clonally or through wind-dispersed seeds. Over time, trees self-thin and clustering is less evident. This phenomenon is less studied than the edge effect and has more frequently been applied to gaps within forests rather than old field succession (Aldrich et al. 2003; Druckenbrod et al. 2005). Shade-intolerant species are especially likely to aggregate in early succession, while shade-tolerant species become more aggregated as conditions become favourable (Aldrich et al. 2003). Because tree densities fluctuate over time with patterns typically changing from highly aggregated to random or regular as a forest matures, this concept is worth further exploration and analysis, in its application in successional studies, and by extension, ecological restoration at sites like rare and others.

The Role of Ecological Restoration in Old Field Succession

Ecological restoration can be used in abandoned old fields at **rare** to expand and reconnect adjacent forest patches that have been fragmented and isolated, thereby restoring structure and function that historically existed. It may especially facilitate the migration of populations, individuals and gene pools that would otherwise remain isolated and face local extinction. These populations in turn can act as vectors for secondary dispersal, multiplying the effects of early restoration. Declining bird populations would experience particularly strong benefits. Interior bird species such as *Seiuris aurocapillus* (Ovenbird), *Hylocichla mustelina* (Wood Thrush) and *Certhia americana* (Brown Creeper) have been recorded at **rare** (Table 6, Larson, 2002) and would ultimately benefit by an increase in their habitat, particularly if it reduces the edge effect of small and fragmented forest patches. In the meantime, the old field habitat itself is valuable for declining grassland bird species (Larson, 2002). Over time, different species of birds would utilize different successional seres of old fields (Lanyon 1981).

Restoration can also be used to favour native forest vegetation and discourage the establishment of invasive exotic species. Invasion of aggressive non-native species in the first few years of abandonment can adversely affect woodland and restored habitats and create a 'reverse' edge effect (Burke & Nol 1998; Holl & Crone 2004) into the forest interior. There is some evidence that native species such as *Sanguinaria canadensis* restored in the proper conditions and densities can suppress invasions of *Alliaria petiolata* (Murphy 2005) and ecological restoration should be implemented in experimental areas to further test this theory.

The comparatively new body of research related to restoration (vs. more traditional succession) is currently lacking in a variety of areas. According to Prach et al. 2001, research into the prediction of spontaneous successional changes is needed and can be made in the following ways: 1) detailed case studies, particularly relating to vegetation ecology, 2) field experience and observation, particularly by local experts, and 3) comparative studies of larger areas and involving different successional seres (chronosequence). From there, succession can be 'directed' to cross otherwise impassable thresholds beginning with some simple interventions such as the appropriate introduction of desired species for maximal survival and/or the elimination of invasives (Prach et al. 2001).

Ecological processes which influence the reassembly of one ecosystem into another have been well studied, particularly the edge effect, the role of soil and the availability of nearby propagule sources in influencing future composition of a site. These are all important processes that need to be better understood for the design of effective interventions in ecological restoration (Pickett et al. 2001). Restoration plans should be ecologically appropriate through the inclusion of local

genotypes of plants and establishing corridors to facilitate immigration and connect landscapes (Quon et al. 2001). Ecological restoration at its best should be a version of environmental triage through the prioritization of sites based on ability to recover naturally. From there, intervention can take place where it's most needed and/or where it will have the best results.

Conclusion

In the research conducted in the 1900's, science has broadened in focus from a reductionist perspective (as seen in the early work by Clements and Egler, for example) to more holistic paradigms such as Holl & Crone (2004) and Halle & Fattorini (2004). Succession has become less a study of which species comes in and when to how and why is a system changing through its internal and external influences. All theories seem to concur that change happens in predictable ways much of the time and the purpose of the science is to understand the underlying mechanisms that influence it. The major factors that influence succession appear to be most importantly the availability of and distance to propagule sources (Gill & Marks 1991; Harmer & Kerr 1995; Wissmar & Beschta 1998; Crowder & Harmsen 1998; Lawson et al. 1999; Oosterhorn & Kapelle 2000; Battaglia et al. 2002; Holl & Crone 2004; Gardescu & Marks 2004; Riedel & Epstein 2005; Cook et al. 2005) and secondly, environmental conditions such as soil, light, and nutrients (Inouye et al.1994; Crowder & Harmsen 1998; Prach & Pysek 2001; Blatt et al. 2005; Davis et al. 2005; Druckenbrod et al. 2005).

In light of the objectives outlined in the introduction and the research gathered here, I have drawn the following conclusions:

- 1. In old field succession, rapid vegetation change occurs in the first few decades after abandonment and typically results in forest establishment after about 40 years;
- 2. Forest regeneration depends first and foremost on what species exist nearby and that seeds generally don't travel farther than 40 m from their source;
- 3. The edge effect in extreme border transitions, such as a forest-field gradient, on tree establishment is a well studied phenomenon and likely is a result of proximity to seed sources and moderate environmental conditions; and
- 4. Some spatial patterns of tree establishment have been observed, mainly in the context of the edge effect (see above), gap regeneration, and seed dispersal of individual trees, but not in the context of a whole field and including all establishing tree species. Representation and analysis of these patterns generally follows traditional methods of data collection through plot samples and statistical techniques.

Chapter 3: Site Description

Formerly known as the Cruickston Charitable Research Reserve until 2005, "rare" is a charitable research reserve approximately 370 ha (913 acres) in size located at the confluence of the Grand and Speed Rivers in Cambridge, Ontario (Figure 3). It is located at 43° 20′ west longitude and 80° 20′ north latitude, lying in the eastern temperate forest bioregion of North America. Its geology was influenced by the last ice age (10 000 years BP) and it has numerous soil types originating from the bulldozing effects of glaciers. Generally, the soil is loamy, well drained, and of moderate to low fertility (Presant 1971). Because of the moderating effects of the Great Lakes, it contains the northern-most limits of Carolinian forest that extends well into the mid-eastern United States and as a result, has a number of species that are uncommon or endangered in Canada.

Eastern deciduous forests such as that found at **rare** are subject to numerous disturbance events that include wind (storms, tornados), drought and disease. These result in naturally occurring gaps, and turnover rates in these forests range between 0.5-2% (Buckley et al. 2002). Human disturbance in these same ecosystems include clearcutting for agriculture and development, and selective logging for wood harvesting.

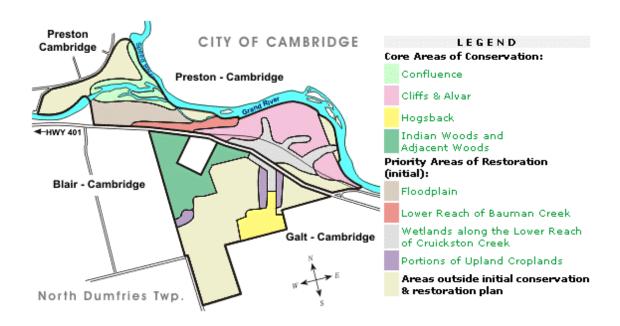


Figure 3: Map of rare property

Rare is a significant part of Waterloo County cultural history and it dates back to the original European settlement of southern Ontario. It was historically known as Cruickston Park and was owned privately for much of this time. Aside from land clearing for agriculture that was typical in the mid-1800's, it has escaped much of the timber harvesting that was done in other local wooded areas. As a result, it has healthy old growth forests unusual for the region, as well as a wealth of diverse ecosystems that include regionally significant cliffs and alvars, Grand River floodplains, several creeks and wetland complexes, hedgerows and old field habitats. The property has seen a number of land uses typical of Waterloo Region, including conventional agriculture, pasturing and human settlement. It has secured protection within an Environmentally Sensitive Landscape (ESL) Policy Area and it has 2 Environmentally Sensitive Policy Areas (ESPA) and one Provincially Significant Wetland (PSW) (Cruickston Park Management Plan 2002).

The field which is the focus of this thesis is located in an area known as the Hogsback, on the south-east portion of the property (See Figure 3). It is approximately 0.8 ha and was taken out of cultivation in 1995, mainly due to the difficulty in maneuvering large farm equipment in a relatively small area (Bill Wilson, personal communication). It is not unique in this aspect, other small fields are abandoned for similar reasons (Benjamin et al. 2005). It lies almost entirely within the Hogsback forest which borders it on three sides, and has an old, well established hedgerow on the fourth side (see Figure 4). In fact, this hedgerow is very likely untilled land as there is the remains of an old stump fence (pre-1900) and several large old stumps within it. The field is rectangular, about 180 m long and 40 m wide located on an undulating hillside (nicknamed The Hogsback) within 50 m of a wetland depression and creek (Figure 5). The site was chosen for this research because it has had no human intervention since abandonment either through disturbance or rehabilitation and therefore any processes which are observed can be assumed to be natural. Because all its edges are bordered by trees either from the forest or hedgerow, the influence of woody vegetation and potential for invading the field is quite high. As a result, this area is targeted for passive restoration in rare's management whereby one of the goals is to increase interior forest habitat along the borders of the Hogsback forest plan (Recommendation 7.5, Larson 2002).

The establishment of a site-appropriate species list should include native vegetation adapted to local conditions and a thorough understanding of the reference composition. In 1817, survey notes described Indian Woods on the western boundary of the property as containing *Acer saccharum*, *Fagus grandifolia* and *Ulmus americana* as the dominant trees (from Larson, 2002). Today, that composition has been altered since the arrival of Dutch Elm disease in this area in the 1970's killed all the large elm. The current dominant trees are *Acer saccharum* (> 50% basal area), *Fraxinus americana* and *Fagus grandifolia*, with secondary species consisting of *Acer*

rubrum, Quercus rubra, Quercus alba, Pinus strobus and Prunus serotina (Ministry of Natural Resources 2004). Also notable are the appearance and increasing presence of several aggressive exotics, notably *Rhamnus cathartica* and *Rhamnus frangula*. Both species, particularly *Rhamnus frangula*, have been recorded as abundant on this property since at least the early 1970's (Lothian 1976).





Figure 4: Aerial maps of study field showing open gaps on western boundary in 1962 (left) and in 2003 (right)

Although no details were found on what was cultivated in the study field or for how long, the field has been there since at least the 1950s. The western forest edge was considerably more uneven and more open in the past than it is now, whether from cultivation or pasturing. Species found there today include large vines (mainly *Vitus riparia*) and shade intolerant trees such as *Populus tremuloides*, *Prunus serotina* and *Cretaegus crus-galli*. These species are typically shade intolerant (ie. they grow best in open areas) so the now-closed canopy likely was more open when these species originally established.

The **rare** management plan (Larson & Wilson 2002) states that one goal is to foster scientific research within the property. That goal, combined with their goal of restoring much of their property to historical ecosystems has been incorporated into this thesis and provides an ideal study site that has not been disturbed for ten years which is likely to remain in long term protection. Baseline information is needed about successional patterns on its newly abandoned farmland and recommendations as to the future restoration and management of this exceptional property.



Figure 5: Field in 2006 taken from the southeast corner facing north

Chapter 4: Methods

Research Design and Data Collection:

The design of this study was influenced by the spatial and temporal questions outlined in Chapter 1 and utilized many existing techniques in ecological studies. Research was undertaken with several assumptions in mind. First, all processes observed were natural and were not directed by humans although they may at one time have been influenced by human activities. Second, all trees appearing in the field had established themselves through wind, gravity or animal dispersal or vegetative propagation and were not planted by humans. Lastly, most of the trees had their genetic origins in the surrounding forest or hedgerow.

Three major types of data were collected: 1) transects containing square plots which recorded all background vegetation, 2) all establishing trees in the field in the form of spatial data with GPS northings and eastings which recorded all field tree locations and 3) point-quarter plots of the 10 metres of the forest bordering the field which recorded all mature tree specimens. The rationale for collecting transect data was to examine the edge effect between forest and field which is widely described in the literature, and also to collect baseline data to describe all vegetation, not just woody plants. The field tree data recorded all species, their height and GPS locations as of the summer of 2006. These data have the potential to be analyzed with standard statistical tests and also with the newer spatial tools offered in the GIS. The third type of data collection sought to identify potential parent trees in the surrounding forest and hedgerow and their subsequent influence on spatial patterns of establishing trees. Temporal data were also considered, but because of the short time span of this research and the challenges in accurately dating tree specimens, could only be included as contextual observations.

1. Background Vegetation

Background vegetation studies were employed to give an indication of current overall vegetation composition and associations. The types of vegetation sampled included trees, shrubs, and all non-woody plants. Although useful in giving a broad understanding of how the field has regenerated in the decade since abandonment, transect data may be especially useful in the future if further studies follow up on this baseline research.

Background Temporal Data

The field targeted for study has been abandoned for 10 years, but there is no comprehensive information about previous years' vegetation composition. Therefore, these data are the first of their kind at this location and can be considered a starting point for future monitoring of this site. Specific temporal data within the time frame of abandonment to the present were hard to collect because of the challenges of determining the age of young establishing trees. Height was not a good indicator because of the evidence of browsing on some samples. Core sampling was likewise not possible because of the small trunk diameters. Stem diameter was also discounted because of variability in growth between species and under different environmental conditions. Ultimately, although exact dating of establishment of the sampled trees was not possible, it was reasonable to assume that all the samples dated to within a 10 year period starting from abandoned cultivation in 1995. Since succession is such a long term process, these trees are now permanently recorded as being present at the earliest stage of this forest regeneration. As with the collection of background vegetation data, these data will have further application if follow up studies are conducted in the future.

Transect Vegetation Sampling

Surrounding vegetation in the adjacent forest and hedgerow was sampled via three transects running perpendicular from the forest across the field, hedgerow and into an adjacent field. This sampling followed the terrestrial vegetation sampling protocols (Roberts-Pichette & Gillespie 1999) of the Environmental Monitoring and Assessment Network (EMAN) created by Environment Canada and the Canada Centre for Inland Waters. Its application for this thesis was intended to provide background information on species composition, dominant vegetation, and transitions between habitat types. EMAN was chosen because it not only represented standardized methods in ecological research, but was being utilized elsewhere on the rare property and throughout Ontario, thus enabling research on a more comprehensive basis than on the research site alone.

Three transects labeled T, M and E ran roughly perpendicular to the forest-field boundary starting 30m into the forest and across the field and hedgerow, and 20 m into a surrounding field (Figure 4). The transects were 110m in length with 5x5m plots in which tree sampling and ground vegetation were recorded. Each 5m² plot was assigned a unique identifier based on transect and location along the transect. For example, T01 was the first plot located at the beginning of transect T in the forest, and T22 was the last plot located in the newer field at the end of transect T. Four different habitat types were included: forest, transition (forest edge and hedgerow), old field and recent field. Depending on the nature and abundance of ground vegetation, the plots

were subdivided into one or two 1m² quadrats and were kept consistent through each habitat type.

Vegetation was recorded as stem count within the plot and recorded in the data sheet. When high stem density made counting difficult, conversion to cover (cm²) was done by estimating ground cover in the field when possible, or alternatively from the data provided in the '# stems' column and comparing to abundance of other plants in the quadrat. Plants that were abundant were placed in one of 10 categories that equaled percentage and converted to the proper units in cm² (1000, 2000, 3000 cm² etc.). Plants that were few in number were assigned either 100 cm² for a solitary plant, or 600 cm² for a few.

For each plot, a clear plexiglass stake was inserted in the south-east corner and a retractable tape measure laid out the boundaries of the 5 x 5m and the 1 x 1m quadrat (where relevant). Selected plots were recorded with the GPS unit to provide an alternate means of location in the event of a stake being removed. Although EMAN outlines detailed procedures for mapping all trees within the 5 x 5m plot, this was too time-consuming for the purpose of this research. Instead, a systematic recording of the vegetation and tree layers beginning nearest the stake and continuing clockwise around the plot was substituted. Common names of all species were entered along with their Latin names and coding as indicated in the Ontario Plant List (Newmaster, 1998). Additional aids for identification included Newcomb's Wildflower Guide (1977), Shrubs of Ontario (Soper & Heimburger 1990), and Trees in Canada (Farrar 1995).

2. Field Tree Data

Spatial patterns of old fields have generally been studied in the context of edge effects using methods such as straight transects that run perpendicular to the forest edge (Burke & Nol 1998; Dickie & Reich 2005) or stratified random plot sampling (Bartha et al. 2003; Gardescu & Marks 2004; Blatt et al. 2005;) and employing traditional statistical techniques in the analysis. As previously described, these methods have been employed here and provide much useful information. However, they are not as useful in capturing trends that may not be detectable within the transect plots such as patterns relating to seed dispersal. To account for this, this study incorporates a few spatial analysis tools in GIS, to capture isotropic (directional) patterns as described in the following chapter.

Old Field Sapling Inventory

There were over 100 trees establishing in the field that were greater than 50 cm in height, making a complete sampling of them easy to complete in a field season. Trees less than 50 cm in height

were not measured because of the difficulty in identifying all possible seedlings in the field. Although it is highly probable that seedlings of this height may be more than 2 years old (DeSteven, 1991b), they also are more vulnerable to physical damage and herbivore predation and their long-term survival is much lower. Species, height, dbh (where possible), evidence of browsing, and surrounding ground cover were recorded in a field notebook. Crown cover was considered as an additional variable, although in the end it was not recorded because of time constraints, browsing effects and because of the still-minimal influence on ground vegetation.

Spatial analysis of tree establishment was undertaken by first inventorying locations of all the establishing trees in the old field. Latitude and longitude were recorded on a Trimble GeoExplorer 3 GPS unit for each tree or cluster of trees (2 or more within 2x2m area) using UTM, NAD 83, Zone 17. In most cases, over 200 positions were logged for each data point. For those points with fewer, it was because of time, inclement weather or low battery power. The unit was placed as close to the tree or transect marker as possible, either on the ground or in a tree branch. For cluster points (GPS points where there were more than one tree for the same location), each tree was randomly reassigned a different northing and easting within 4m² of the original point to allow representation of all the trees at the cluster point. An error margin of roughly 6 metres was estimated based on the stated precision of the GeoExplorer. To minimize this error, roughly 200 positions were recorded at each location and then differentially corrected with a base station in Johnstown, PA.

GPS Data Transferral

Data were downloaded to a PC from the GeoExplorer within 4 hours of recording in the field. GPS Pathfinder Office was used for downloads and for differential correction with the Johnstown base station. Corrected data were saved as a dbf file and exported as a shapefile to facilitate viewing and analysis in ArcMap. Data from the dbf file were imported and edited in Excel with the additional field data entered manually into a separate file and later merged together.

All spatial data were imported into ArcMap and overlaid on an aerial photo of the field taken in the spring of 2003 (see Figure 6). The spatial locations of the trees were represented by species (colour) and height (size of dot) to give an initial indication of what the spatial patterns might be. The GIS allowed for many different representations of the data, which showed obvious spatial patterns even before analysis was attempted.

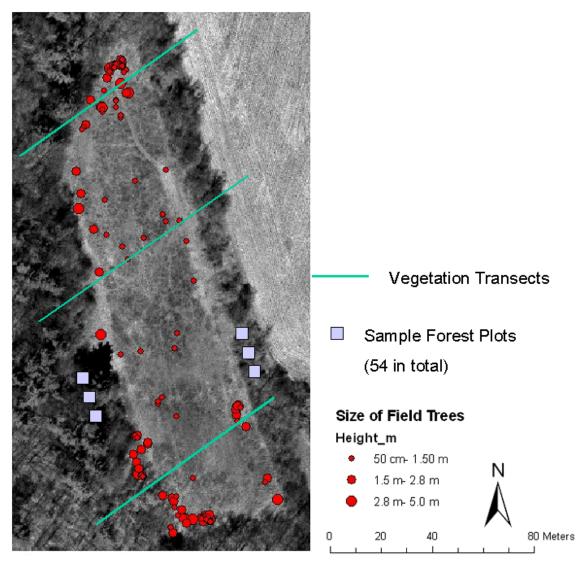


Figure 6: Location and size of field trees

3. Seed Source Inventory

The surrounding forest and hedgerow was assumed to be the most likely seed origin of the establishing trees but a complete sampling of possible parent trees in these areas was not feasible. Instead, a modified point-quarter method (Barbour et al., 1980) was undertaken to identify likely seed sources. The point-quarter plots were based on a centre point with four 5m X 5m quadrants, each labeled a, b, c, or d. The c and d quadrants were closest to the field side and the a and b quadrants were further in to the forest/hedgerow. The plots ran parallel to the forest-field boundary and the centre points were located 10 m apart. Within each quadrant, all species with a dbh of over 10 cm were recorded since this implied the trees were large enough to be

reproductively mature and tall enough to potentially disperse its seed into the field, particularly for wind-borne seed (see Gardescu & Marks 2004). Dbh was not specifically recorded because of the time restrictions, however relative size differences were noted by categorizing each tree as small (10-25 cm), medium (25-50 cm) and large (>50 cm). No attempt was made to distinguish dioecious (separate gendered) trees such as *Fraxinus americana* since the trees were not yet in fruit during the time of data collection. For the two *Rhamnus* species, the size criteria had to be altered since most of them were small but likely reproducing before reaching the minimum size of the other trees. In this case, the size criterion was 4 cm.

Additional incidental information was also collected. Surrounding vegetation type near the establishing trees in the old field was recorded as a rudimentary method in determining whether trees were more likely to be present in certain types of vegetation over others. Evidence of deer browse on establishing trees was also recorded.

One omission from data collection was soil sampling. Because of the additional time required to do the sampling and analysis and also the uncertain consensus in the literature on the role of soil in the establishment of seedlings (see Chapter 2), this was not evaluated. Likewise, other environmental conditions such as light and soil moisture levels were not considered. These factors likely contribute to tree establishment, but for this thesis, the emphasis remains on the proximity to seed source as the dominant factor in the spontaneous succession process of this field. These missing variables are planned to be studied by future students beginning in 2008 (SD Murphy pers comm.).

Analysis

A number of analyses were applied based on their anticipated relevance to answer the research objectives and questions 1) comparison of baseline data of adjoining habitats along the sampled vegetation transects, and 2) spatial representation and analysis (where appropriate) of tree populations in the forest and field. Vegetation analysis followed commonly used techniques to summarize the current composition of the vegetation communities at the study site. Selecting appropriate spatial analysis tools was considerably more challenging because of the sparse applications in terrestrial ecology and the newly evolving applications of GIS analysis.

1. Vegetation Transects

As part of the original data collection, the sampled plots had to be characterized according to community type and assessed for the total area of plots. Plot size for vegetation sampling was dependent on the type of community sampled along the transects as per EMAN guidelines. For

woodland habitat, the entire 5×5 metre plot was sampled for both vegetation and trees. The old field vegetation samples had single 1x1 m quadrats within the plot, and the transition habitat, the hedgerow and the new field had $2 \times 1x1$ quadrats within each plot (Table 4). Although all three transects were 110 m in length with a total of $22 \times 5m^2$ plots in each transect, the area of each community varied somewhat from transect to transect.

Table 4: Community types

Community Type	Number of Plots	Area of Quadrats Within Plot	Total Area of Plots
Forest	20	5m ²	500m ²
Old Field	25	1m ²	25m ²
New Field	6	2m ²	12m ²
Transition (Edge)	5	2m ²	10m ²
Hedgerow	10	2m ²	20m ²
Total	66		567m ²

Importance Value

Using the community types described above, dominant vegetation was determined using Importance Value calculations outlined in the EMAN guidelines (Roberts-Pichette & Gillespie 1999) for each type of vegetation in each habitat. Importance value calculations were based on a sum of relative density, relative dominance (as measured by basal area and % cover) and relative frequency. For each stratum of vegetation, the three species with the highest importance values were considered the dominant species for that habitat. The strata were defined as follows:

- 1) canopy-dbh >=4 cm
- 2) small tree and shrub- woody vegetation > 50 cm in height and < 4cm dbh
- 3) ground vegetation- woody vegetation < 50 cm in height or herbaceous vegetation

The rationale of recording importance values for the various canopy layers is to provide a baseline of data for both EMAN and rare. Over time, the old field may become more like the forest and hedgerow and further data collection should reflect that. A turnover in species dominance will also be easy to note as local extinctions and invasions change composition over time.

Jaccard Index of Similarity

Another method, the Jaccard Index of Similarity (Bray & Curtis 1957; Booth et al. 2003), compares populations over time or in different locations to see how similar they are. The formula used to calculate this index is $C_j = j/(a+b+j)$, where j is the number of species found in both locations, a is the number of species found only in one location and b is the number of species found in the other location. The more similar two communities are, the higher the number is, with 1 being completely similar and 0 being completely different. The distinctive community types of forest, old field and hedgerow within the 3 transects were compared using this measure.

Measures of diversity were also considered but were not included because in this case they cannot reveal much about the current state of succession. If anything, the measure can be misleading if assumed that high diversity is related to the health and stability of a forest ecosystem, for species diversity first increases, peaking around 40 years, and then typically decreases as succession proceeds (Howard & Lee 2003). In the case of early succession, there is high species turnover and high species diversity resulting in the brief coexistence of many transitory species.

2. Field Tree Spatial Representation and Analysis

Studying the spatial pattern of a species is useful because it can give insight on its reproductive and dispersal behaviour (Miller & Franklin 2002). Studies that examine distribution patterns of vegetation typically map them on xy co-ordinates and use density per hectare or plot to show concentrations in the field (Battaglia et al. 2002; Dovciak et al. 2005). Using similar methods, the xy coordinates of individual trees were transferred into ArcMap version 9.2 by ESRI which then plotted the points overlaid on a 2003 aerial map of the field and surrounding area digitally georeferenced as NAD_1983_UTM_Zone17N. This was effective, other than a slight offset from the aerial map where some trees appeared growing in the forest boundary. This may have been an actual offset from the true location in space or may have been a result of the camera's southwest perspective when the air photo was taken was taken in 2003. The aerial map served only as a representation tool to provide context, while any analysis performed was done on the point locations and a field edge polyline/polygon added based on a rough approximation of the forest dripline.

Spatial analysis was done using several tools provided in the GIS package, namely Ripley's K, and density mapping. *The ESRI Guide to GIS Analysis: Volume 2* (Mitchell 2005) and *Using ArcGIS Geostatistical Analyst* by Johnson et al. (2001) were used as a consultative resource for explaining various spatial techniques and how to apply them to a data set. Several techniques in

the ArcGIS spatial analyst extension were applied to the data set with varying degrees of success, including kriging, nearest neighbour, Ripley's K and density mapping. A species distribution can be random, regular or clustered, but can change at different scales of analysis (Miller & Franklin 2002). On initial observation of the field tree data set, there appeared to be patterns of clustering at the field scale. To further analyze this, several techniques of kriging were applied on the vector data using height as a continuous variable. This proved unsuccessful because there was not a clear enough relationship of height to location in the field and/or the data set was too small and variable. Similarly, nearest neighbour analysis was done on a small subsection of the data and once again, results were not clear, most likely from the sample set having too few points. To measure the clustering patterns that seemed obvious even without analysis, Ripley's K statistic (K-function) was attempted. Ripley's K statistic is a measure of spatial autocorrelation that can determine the uniformity or aggregation of a population distribution and has been applied in the study of forest gaps (Dolezal et al. 2004; Druckenbrod et al. 2005) as well as spatial distributions of trees over time (Mast & Veblen 1999; McDonald et al. 2003; Wolf 2005). Ripley's K summarizes spatial dependence over a range of distances (bands). It determines clustering patterns in tree species throughout the field by counting pairs of features (trees) within defined distances within the perimeter of the field. Density surfaces show where point features (trees) are concentrated over a given area and was utilized here to depict the concentration of trees throughout the field, in particular, any 'hot spots' of regeneration. This was done using the estimated field polyline as the boundary and required the point data (vector) to be converted to a raster format to a resolution (cell size) of 0.377 m, using a radius of 3.14, both the default settings provided by the program when applied to this particular data set. All points were equally weighed. Density mapping visually represented the concentration of trees throughout the field, whereas Ripley's K defined the extent of clustering via chart format.

3. Seed Source Inventory

While doing mapping on GIS, queries performed by species revealed that forest composition changed considerably by location. The hedgerow (eastern edge) composition was different than the western edge, as were the north and south boundaries. To capture this difference, the areas were subdivided into four sections by orientation towards the field consisting of the hedgerow and the north, south and west sectors of the forest bordering the field. Using Excel, pie charts illustrated the composition of the forest sector by species. In GIS, each plot was approximated and marked as a separate layer on the aerial map. Information about the plot could be readily retrieved along with their approximate x and y coordinates. This proved especially useful in locating species that were not regenerating in the field, such as locations of all *Fraxinus nigra* specimens. For other species that were establishing in the field, it was possible to merge locations of possible parent trees in the forest with potential offspring in the field into additional

map layers. More detailed analysis did not take place at this time because of the uncertainty of identifying specific parents with offspring, a question that can likely only be resolved through genetic tests and further population sampling.

Chapter 5: Results

From a successional standpoint, the results from these analyses confirmed spatial patterns observed by other studies, particularly the edge effect. Vegetation composition was harder to gage because most successional studies on eastern deciduous forests were done further away in differing soil and climactic conditions. There were no nearby research sites with which to compare data, but neither were there any unexpected species or community types encountered for this area during this research.

1. Description of Community Types Along Transects

In total, 103 different plant species were recorded in all transects and across all vegetation types. There were 58 species recorded in the forest community, 30 in the hedgerow, and 47 in the old field. There was also a transition (edge) community between the forest and old field and also a 'new field' on the other side of the hedgerow. Neither the edge nor the new field community was included in the results section. The edge was highly variable, in some places it was a smooth transition between community types and other places it was a hard edge of about 5 m, making it hard to discern which plots to include for analysis. In the case of the new field, there were too few plots (only 6) to make a reasonable analysis on vegetation composition.

Importance Value

Importance value calculations assign a number to each species within a specific vegetation community and strata type based on its relative dominance, density and frequency. The higher the number, the greater the importance, with a maximum score of 300. Table 5 below is a summary of the three most dominant species in each stratum for each vegetation community.

Table 5: Importance Value (IV) of dominant species in each habitat (Maximum 300)

Strata	Forest	IV	Old Field	IV	Hedgerow	IV
Canopy	Acer saccharum	73			Tilia americana	92
	Pinus strobus	43			Acer saccharum	67
	Quercus rubra	25			*Rhamnus cathartica	62
Shrub	Fraxinus americana	93	*Rhamnus frangula	188	*Rhamnus cathartica	134
	*Rhamnus frangula	45	Fraxinus americana	76	Prunus virginiana	57
	Acer saccharum	41	*Rhamnus cathartica	35	*Rhamnus frangula	41
Ground	Erythronium americanum	58	Solidago canadensis	66	*Alliaria petiolata	45
	Fraxinus americana	46	Potentilla recta	33	*Dactylis glomerata	40
	Arisaema triphyllum	24	Rubus idaeus	32	Erythronium americanum	27

^{*}non-native species

The three dominant trees in the forest transects in 2006 were *Acer saccharum* (Importance Value 73), *Pinus strobus* (42) and *Quercus rubra* (24). This differs from original surveys of this area from the early 1800s (see Larson & Wilson 2002) which include *Ulmus americana* and *Fagus grandifolia* as co-dominants with *Acer saccharum*. *Ulmus americana* has been decimated by Dutch Elm disease which explains an almost complete absence in this data set, and *Fagus grandifolia* was not present in great numbers in this particular site although it is elsewhere at **rare**. Non-native vegetation was a significant component in all habitats, particularly both species of *Rhamnus*, which were found in all the habitat types. *Fraxinus americana* was dominant in the small tree & shrub layer in both the forest and old field habitats but was a very small component of the canopy layer of the forest (Importance Value of 4.8).

Rubus idaeus, though woody, was recorded in the vegetation layer where it was an important component in the old field because it will not ever form a canopy much higher than 1m like most other shrubs. Further, although Solidago canadensis, Rubus idaeus and Potentilla recta were codominants, they were typically found in separate microsites throughout the field. Potentilla recta dominated on the sun-baked knolls and Rubus idaeus grew in lower patches and near the forest edge, often to the exclusion of most other vegetation. Solidago canadensis did not form pure colonies but was intermixed with other species.

Jaccard Index of Similarity

The Jaccard Index was used in this case to compare three vegetation community types: forest, hedgerow and old field. Ten plots from each were selected for comparison by location within the community type. To avoid edge effects of the forest and old field being considered more similar than they really are because of transitional plots between the community types, only those closer to the centre (ie. most representative of the community) rather than the periphery were chosen. The hedgerow was too narrow to record internal plots so all plots were included for this community type.

Table 6: Jaccard index of similarity

Similarity	Forest	Hedgerow	Old Field
Forest	1.00	0.33	0.08
Hedgerow	0.33	1.00	0.22
Old Field	0.08	0.22	1.00

The results of Table 6 show that there is great variation between all vegetation communities, with none of them being more than 0.33 or 33% similar. At this point in time, the forest is least similar to the field (0.08) and the edge is most similar to the hedgerow (0.33). This analysis may have even greater application if future studies repeat this methodology at the same location, giving a comparison of habitats over time that may show convergence (increased similarity) or divergence (increased difference) in vegetation composition. It is expected that future studies of these same plots should show the old field increasing in similarity to the forest and hedgerow as succession proceeds, indicating a convergence of communities.

Both Importance Value and the Jaccard Index of Similarity show distinct communities across the transects. The forest is representative of a climax eastern deciduous forest at this latitude, but with some evidence of past clearing and secondary succession from the presence of species such as *Prunus serotina*, *Rhamnus frangula*, *Vitus riparia* and *Cretaegus crus-galli*. The hedgerow shows a community distinctly different from the forest, with a higher proportion of *Rhamnus cathartica*, *Quercus rubra* and *Carya cordiformis*. The old field is dominated by perennials such as *Solidago canadensis* and *Rubus idaeus* and with abundant woody vegetation at the edges near the forest.

2. Field Tree Spatial Pattern Analysis

Proximity to Edge

There are some general spatial patterns to tree establishment in the field. Over 75% of trees have established within 10 m of the forest-field edge (see Figure 7). There is a clear edge effect, with the number of trees proportionally decreasing as distance from the edge increases, a phenomenon also observed by Myster & Pickett (1992) and Lawson et al. (1999).

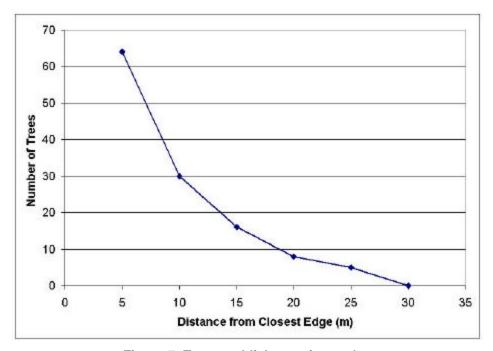


Figure 7: Tree establishment from edge

Tree Size

The average height of establishing trees in this field after 10 years was 1.69 m and they were fairly evenly distributed in size with most of them between 0.5 and 2 m tall (Figure 8 below). The tallest trees were only found at the edge, whereas shorter trees were found throughout the field (Figure 9). Species type also seemed to be somewhat randomly distributed by height. *Fraxinus*, *Rhamnus*, *Carya* and *Populus tremuloides* were found at varying heights, although *Quercus* was mainly short and stubby, possibly as a result of browsing by deer. The tallest trees were *Rhamnus frangula* and *Rhamnus cathartica*.

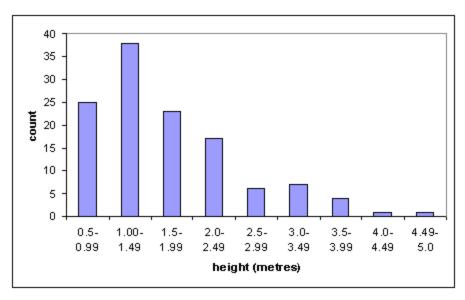


Figure 8: Height of field trees

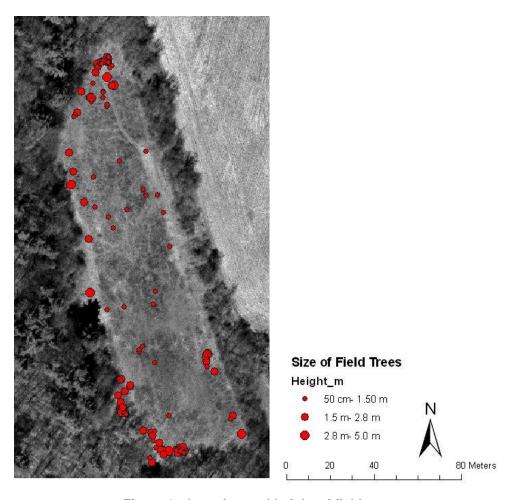


Figure 9: Location and height of field trees

Density

Although trees were distributed throughout the field, clustering occurred at the perimeter. There were 2 areas near the forest edge containing a high density of tree seedlings (Figure 10). The species composition of these two clusters differs, with the north cluster comprised mainly of *Fraxinus americana* seedlings and the south cluster a combination of several different species (*Rhamnus cathartica*, *R. frangula*, *Acer saccharum*, *Carya cordiformis* and *Fraxinus americana*). It is not clear what might be causing these 'hot spots', although it is likely a combination of close proximity to abundant seed sources and favourable environmental conditions (moderate moisture, soil nutrients and light levels). Further study examining these variables may yield answers that could help with the identification of other areas of high regeneration potential.

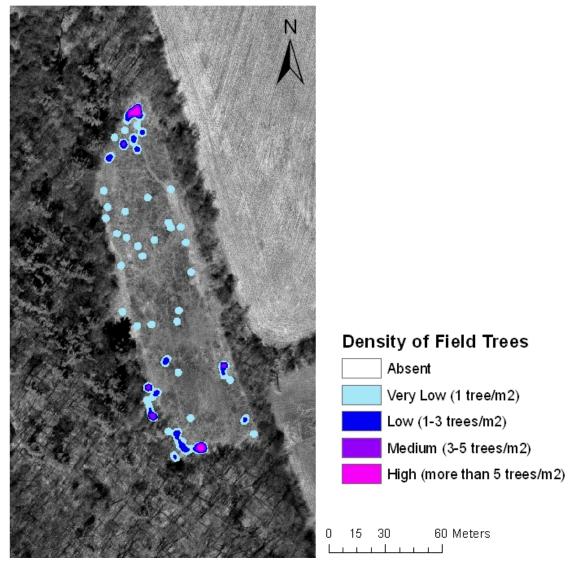


Figure 10: Density map showing concentrations of. establishing trees in the study field

Species

Species type also influenced the degree of clustering, with *Populus tremuloides* exhibiting the highest clustering tendencies (Figure 11) and was likely the result of clonal advance. *Fraxinus* and the two *Rhamnus* species had dispersed farther distances but were also moderately clustered. The other species were too sparse to make any generalizations.

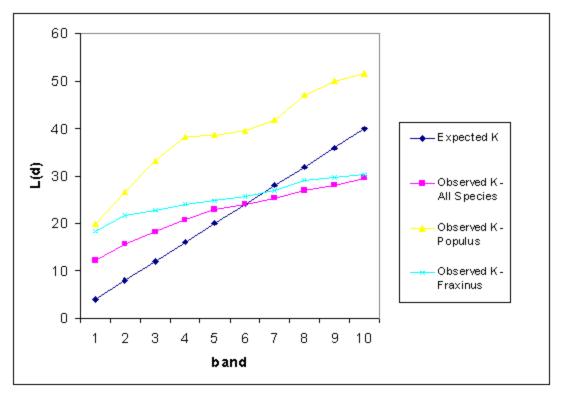


Figure 11: Ripley's K demonstrating the clustering tendencies of trees at close distances.

Observed K lines above the expected K (blue line) show clustering, below the expected K, random dispersal. The term 'band' signifies regular distance calculations between points. L(d) is the transformation of the K-function where the expected result with a random set of points is equal to the input distance.

Clustering seems to be associated with early tree recruitment and establishment (Wolf 2005). Young trees tend to be found in clusters, most likely from an aggregation of seed rain leading to high germination and survival in localized conditions. As trees grow and mortality thins out the clusters, trees become more evenly distributed. MacDonald et al. (2003) identify respective factors favouring uniform distributions as density-dependent competition (ie. too many trees

eventually self thin) whereas clumping could be the result of gaps or environmental heterogeneity (eg. good light conditions or proximity to seed sources lead to clusters of young trees).

Dispersal Type

The nine species of field trees could be divided into four main dispersal types: nut (*Carya cordiformis* and *Quercus rubra*), fruit (*Rhamnus cathartica* and *Rhamnus frangula*, *Celtis occidentalis*, *Crataegus crus-galli*), wind (*Acer saccharum*, *Populus tremuloides* and *Fraxinus americana*) and clonal (*Populus tremuloides* and possibly *Rhamnus spp*) as done similarly in a recent study by Howard & Lee (2003). Each dispersal method had unique spatial distributions influenced by its method of dispersal and proximity to source trees. The following maps illustrate the establishment patterns of forest-field trees based on their dispersal method (Figure 12 to Figure 15). Wind-dispersed species such as *Acer* and *Fraxinus* dispersed over the widest area in the field, and to a lesser degree, the fruit-dispersed species (*Rhamnus*). The nut species both dispersed shorter distances away from the edge and did not exhibit clustering other than along a north-south line in parallel to the hedgerow.

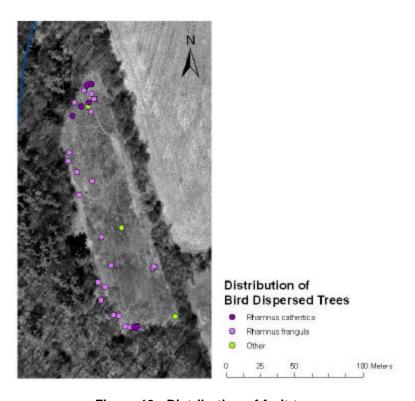


Figure 12: Distribution of fruit trees

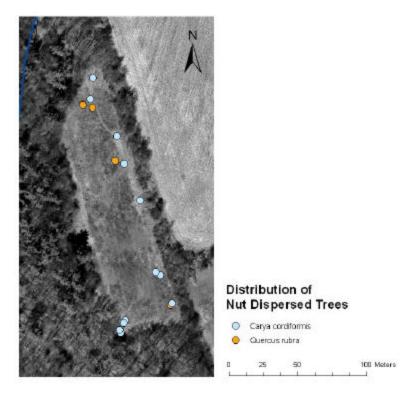


Figure 13: Distribution of nut trees

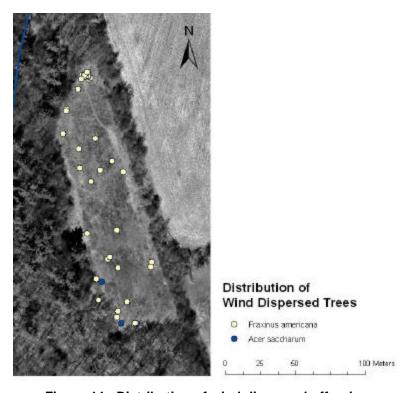


Figure 14: Distribution of wind-dispersed offspring

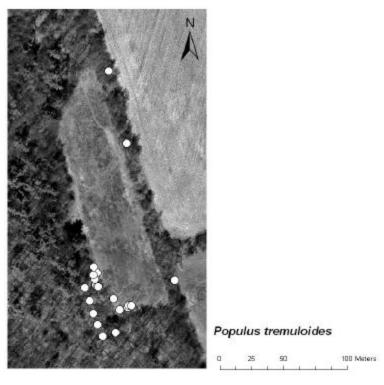


Figure 15: Distribution of probable clonal-dispersed offspring (*Populus tremuloides*) and mature specimens in the adjacent forest.

Wind represented the most successful dispersal method, with almost 40% of establishing trees being of this type (Figure 16 below). *Populus tremuloides* was excluded from this category, however, because other research indicates that it is much more likely to reproduce clonally than by seed (Barnes 1966), and the pattern of establishment of this species in the study field showed it highly clustered around mature aspen at the forest edge, suggesting probable clonal reproduction (Figure 15 above). With this species alone representing clonal advance, it still comprised 11% of establishing trees. Fruit-dispersed species were also abundant at 36%, while nut trees which are primarily dispersed by small mammals were 14%. Interestingly, very similar results were reported from an experimental study of natural recruitment over 5 years on a landfill site in New Jersey, with 36% avian-dispersed, 10% clonal and the remainder wind (Robinson & Handel 2000). Dispersal type seems to have influenced not just the spatial pattern of field trees, but also composition, in this case by favouring wind and fruit-dispersed woody species establishment early in the successional process.

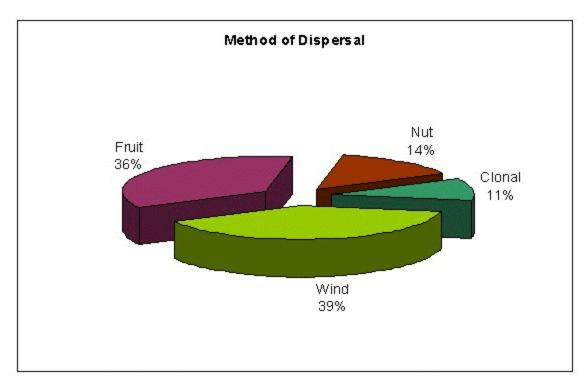


Figure 16: Method of dispersal of field trees

Other Patterns

During field work, two other easily collected variables were noted when recording tree data: vegetation association near sampled trees and evidence of deer browse.

Vegetation Association

As data were being collected, it became apparent that trees grew in some areas of the field and not others. The presence of certain types of vegetation seemed to coincide with the existence of young saplings, with trees rarely being found in grassy or poorly vegetated areas but more likely in *Rubus idaeus* and *Solidago canadensis*. Ninety percent of trees were establishing in areas with *Rubus idaeus or Solidago canadensis*, and less than 10% in areas where these species were not also present. Although it is possible that somehow *Rubus idaeus* and *Solidago canadensis* facilitate the survival and establishment of trees (Myster 1993), once again, other research suggests competition (Myster 1993; Crowder & Harmsen 1998; Gardescu & Marks 2004; Dickie et al. 2007). In this case, the edge effect may be predominating in influence, that is, the trees are establishing close to the forest edge regardless of the type of vegetation they are competing with and that *Rubus idaeus* and *Solidago canadensis* also prefer edge habitat. Also, favourable soil conditions may be a contributing factor, although it was not studied here.

Deer Browse

Some trees were clearly browsed by deer, as evidenced by thick trunks, missing branches and short height. Thus, during field data collection, a note was made if a tree appeared browsed. Table 7 displays the results:

Table 7: Evidence of browsing by deer

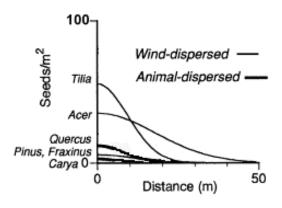
	Not Browsed	Browsed	Total
Malus pumila	1		1
Carya cordiformis	12		12
Crataegus crus-galli	1		1
Rhamnus cathartica	12		12
Rhamnus frangula	28	1	29
Celtis occidentalis	1		1
Quercus rubra	2	3	5
Acer saccharum	4		4
Populus tremuloides	12	1	13
Fraxinus americana	35	9	44
Morus alba	1		1
Total	109	14	123

It was found that of the 123 trees, over 10% were browsed and of those, all but 1 were native species. In this field study area, deer seem to prefer native species over the non-native buckthorns and they also seem to avoid *Carya cordiformis*. Deer did not appear to be discouraged from browsing by the presence of *Rubus idaeus* since many of the browsed trees were located in *Rubus idaeus*. Other studies have shown that trees especially prone to herbivore damage include *Quercus alba, Acer rubrum*, and *Fraxinus americana* (Myster 1993).

3. Seed Sources

Forest and Hedgerow

The surrounding forest represents the most likely dispersal source of seeds germinating in the field. Although trees have the potential to disperse seed up to 100 m (wind-dispersed in particular), most seeds tend not to go much farther than 20 m (Wagner et al. 2004) regardless of the amount of seeds produced (Figure 17).



adapted from Clark et al. 1998

Figure 17: Seed dispersal of several tree genera

Only one species in the field (*Morus alba*) could not also be found in the forest and was likely bird-dispersed from elsewhere. The composition of the forest varied depending on orientation to the field and was most likely the result of varying microclimates, site relief (proximity to wetland) and past land use (possible pasturing in distant past). The hedgerow contained 16 potential seed-bearing species, of which the 3 most abundant were *Rhamnus cathartica*, *Quercus rubra* and *Carya cordiformis* (Figure 18). The northern and southern edges contained the fewest species, with 12 and 15 respectively, but whereas *Acer saccharum* was highly dominant in the southern edge (32%), it was less common (7%) in the northern edge. Incidentally, the reverse was true with *Quercus rubra*, with the proportions being 32% in the northern edge vs. 7% in the southern edge. The western edge had the highest number of species (19), perhaps because of the higher number of sampled plots, but also because there was evidence of some clearing and/or possible pasturing in previous decades, which encouraged shade intolerant species such as *Prunus serotina* and *Crataegus crus-galli* to become intermingled alongside 'climax' forest species such as *Acer saccharum* and *Ostrya virginiana*.

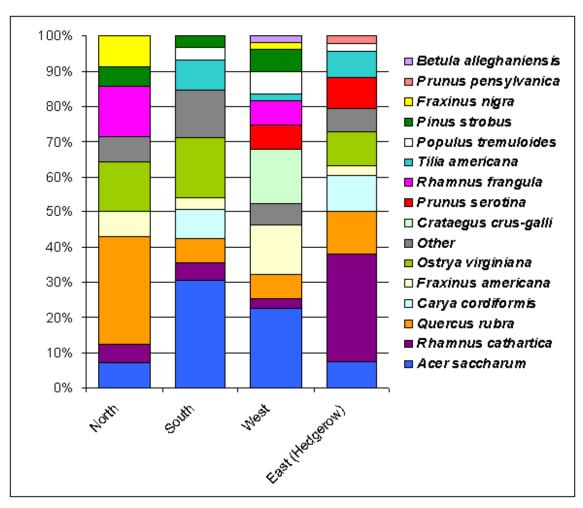


Figure 18: Forest and hedgerow composition (reproductive size)

Source vs. Field Tree Composition

In comparing the composition of the forest/hedgerow with the establishing trees in the field, a different though not unexpected pattern is evident. *Fraxinus americana*, *Rhamnus frangula* and *Populus tremuloides* are the most abundant in the field, comprising 35, 24 and 11% respectively. (Figure 19) *Fraxinus americana* is present throughout the forest, particularly as young seedlings; however, there are a few mature specimens bordering the western edge of the field and are likely doing the most of the dispersal into the field where it is the most abundant tree species. *Acer saccharum* has a high presence in the south and west sectors, but a surprisingly low presence in the field. *Quercus rubra* is highly abundant in the north and east sectors, but similarly scarce in the field. Invasive species such as both species of *Rhamnus* are establishing a fairly significant presence in the field and will likely persist, if not increase in abundance. What is noticeably

absent in the field but common in the forest and hedgerow are some early pioneering species such as *Prunus serotina*. *Tilia americana*, and *Pinus strobus*.

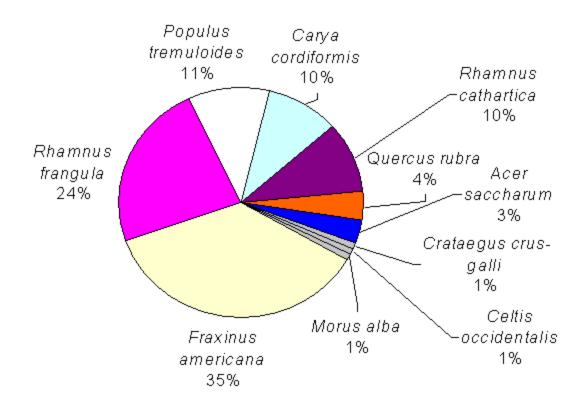


Figure 19: Field tree composition

Overall, these results indicate that the strongest spatial pattern was the edge effect, i.e. the tendency for trees to establish close to the forest edge. This effect was strongest at 5m or less, where over half of establishing trees less than 10 years old were recorded. Taller (possibly older) trees were also found at this distance, as were clusters of multiple trees. Perhaps the most surprising was the distinctive spatial patterns related to dispersal methods, particularly the nut trees dispersing in such a specific zone within 10 m of the edge. *Fraxinus americana* was the only species likely to be found anywhere in the field and in any height category. The strong presence of *Rhamnus spp* and *Alliaria petiolata* is worrisome for future restoration because of their allelopathic (suppressive) effects on nearby species. On the other hand, the healthy populations of *Quercus rubra* and *Carya cordiformis* are encouraging because these species seem to be maintaining a solid (though not necessarily dominant) presence in both the forest and the old field and together with *Fraxinus* will likely form the basis for the future canopy in the field.

Chapter 6: Discussion

The three main research objectives during this research were: 1) to develop baseline ecological data on the current state of the vegetation communities in the field, forest and hedgerow at the rare reserve; 2) to apply and evaluate GIS tools for the visual representation and analysis of spatial data; and 3) to recommend how spontaneous succession processes can be incorporated into future plans for ecological restoration at **rare** and other similar sites. Since much of the research consisted of traditional ecological studies and was centered on collection and analysis of data, the first objective comprises the bulk of this thesis. The challenges of incorporating GIS were primarily in the application of representation and analysis tools from the ESRI ArcMap package to my collected data. This technical issue will be discussed in detail. Lastly, determining how this information can be used in future restoration here and elsewhere is perhaps the most applicable lesson from this thesis and is highlighted here (section 3) and in Chapter 7 (Recommendations).

1. Baseline Ecological Data

The overall vegetation composition of the plots that were sampled were consistent with a southern Ontario mixed deciduous forest ecosystem such as that observed by Crowder & Harmsen (1998) and Burke & Nol (1998). One decade into the successional process, field vegetation composition showed some signs of becoming a future forest. *Rubus* species can be prominent in early successional vegetation of the northern hardwood forest (Crowell & Freedman 1994), and this study field was no exception with about 40% coverage (personal observation). The driest areas had the fewest woody plants, an observation that was also made by Crowder & Harmsen (1998) in a similar habitat.

There was a transition zone from the forest to the field where there was a mixture of co-existing plants from both communities. This zone varied from about 5 m to about 20 m depending on how abrupt the forest-field edge was. Recent research has indicated that when a field is under cultivation, there is more of an influence of dispersal from the cultivated field into the forest than the reverse, but that the edge can act as a barrier of species dispersing into the forest past 3 m (Devlaeminck et al. 2005). Once cultivation ceases, the influence will reverse over time as woody vegetation invades an old field and changes environmental conditions to favour forest.

The two introduced species of *Rhamnus* have become well established both in the forest and the field, and may pose a threat to native species' establishment if left alone (Frappier et al 2003).

Frappier et al. (2003) discuss lag-phase behaviour (Cousens & Mortimer 1995) in which *Rhamnus frangula* shows initial sparse population, but expands quickly after a period of time. This will prove an interesting barrier to overcome for future restoration efforts and its persistence and aggression may detrimentally affect regenerating forest potential.

Field Tree Spatial Analysis

There were clear patterns of tree establishment relating to proximity to a forest edge, height, species type and method of dispersal. Processes affecting forest structure vary in importance over time (Wolf 2005) and the spatial pattern of the trees establishing in this field appear to be strongly influenced by one process in particular, the edge effect. Tree establishment is undeniably influenced by edges, not just the spatial pattern of seed dispersal (Meiners et al. 2000). This effect could be due in part to factors such as soil conditions and mycorrhyzal associations, particularly in the case of oak species (Dickie & Riech 2005), but even more so from distance to propagule source. There is a greater effectiveness of establishment when the seed source (forest or hedgerow) is on more than one side of the field (Myster 1993) and this may partly explain the clustered 'hot spots' in the density map (Figure 10) which are both located less than 10 m from two distinct forest edges. Height, which was closely tied with proximity to edge, was most likely related to age, though it could also be influenced by environmental conditions and browsing by deer.

Seed Sources

Almost all tree species in the field could also be found in the forest as mature specimens and consequently possible seed sources. At this level of study, it was not possible to determine exact parent matches, only possible connections based on distance to the forest edge and/or presence of mature (presumably reproducing) individuals of the same species. Based on this, several observations can be made:

- some species exhibit a dense spread in or near the forest edge (*Populus tremuloides*, *Acer saccharum*, *Rhamnus cathartica*)
- some species are more widely distributed throughout the field (*Fraxinus americana*, *Rhamnus frangula*)
- there is the presence of the occasional single individual of other species (*Morus alba*, *Celtis occidentalis*, *Crataegus crus-galli*), all of which are bird dispersed.

Not all mature forest species are found in the field, most notably Tilia americana, Prunus serotina, Ulmus americana, and Pinus strobus. There are a few possible reasons for this which are: 1) poor dispersal potential; 2) unsuitable moisture or nutrient conditions for these species which results in low emergence; 3) herbivory; and 4) competition from existing vegetation (Olsson 1987; Johnson 1988; DeSteven 1991a; Harmer & Kerr 1995). Pinus strobus appears to be limited by growing conditions rather than seed dispersal. It tends to grow slowly and compete poorly in extremes of high and low light, and tends to regenerate the best in poor soil where competition is low (Dovciak et al. 2005). The germination stage is also a significant filter on tree establishment in old fields during which there is large variability in species performance (DeSteven 1991a). McEuen & Curran 2004 suggest that recruitment limitation is a major barrier to species such as Acer rubrum, Ostrya virginiana, Betula alleghaniensis, and Ulmus americana, despite having abundant seed dispersal. This can be observed at the landscape scale, with few recruits occurring between forest fragments > 300 m apart. Furthermore, there seems to be a distance limitation to proximity to seed sources that results in a maximum density of tree establishment up to 10 m from a parent tree for many species. This is true not only for old field regeneration where there is a hard boundary (Matlack 1994; Meiners et al. 2002), but also into the forest interior (Burke & Nol 1998), and in canopy gaps (Messaoud & Houle 2006).

At this point in time, the field shows early signs of woody plant invasion from the nearby forest. Both trees and shrubs are establishing, though not yet dominant. The primary dispersal of these species follows spatial patterns based on method of dispersal (wind, nut, fruit and clonal) and there is a higher density of saplings of all species closer to the forest edge. Conservation and management goals should be based on these natural patterns and can either enhance areas that are already regenerating well naturally or target areas that are not regenerating. This point will be further addressed in the Conclusions.

Patterns of Tree Establishment by Dispersal Methods and Seed Sources

There are distinctive patterns relating to dispersal methods and differences between wind, mammal, clonal and bird-dispersed species. Colonization patterns are similar for species of similar dispersal mechanism, implying that the establishment patterns could be generalized across several species of the same dispersal mechanism, an observation also made by Olsson (1987) in northern European forest ecosystems with related species.

Wind-dispersed: Wind-dispersed trees can quickly dominate in old crop fields because of the exposed soil and mass distribution of seeds (Stover & Marks 1998). The first abundant pioneer trees in eastern deciduous forests are usually wind-dispersed, particularly *Fraxinus americana* (Crowder & Harmsen 1998, Benjamin 2005). This was true in the old field, with *Fraxinus*

americana the most abundant and most widespread establishing tree species (36%). In contrast, Acer saccharum was very sparse and was only found in the south-west portion of the field despite being highly abundant in the nearby forest (Figure 20). At this stage, Fraxinus americana is the most abundant and most widely dispersed, making it a current dominant in the old field woody vegetation (Figure 21).

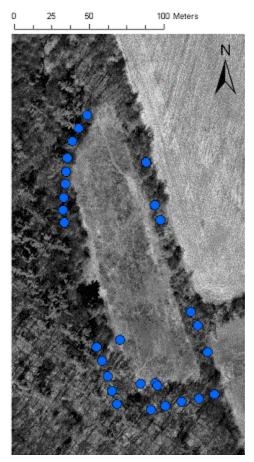


Figure 20: Acer saccharum distribution

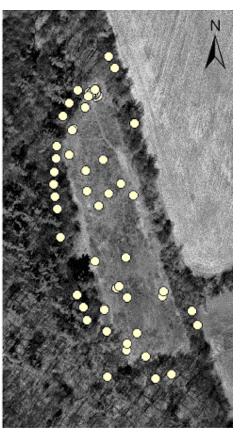


Figure 21: Fraxinus americana distribution

Mammal-dispersed: Most nut trees (*Quercus rubra* and *Carya cordiformis*) are establishing within 10m along the hedgerow. Their dispersal by squirrels and chipmunks is the primary factor in the spatial patterns of future establishment (Garcia & Houle 2005), which is a result of the tendency of the dispersal agents (mammals) to stick to the near-forest edge when storing their food. In Li & Zinnel (2003), the dispersal distances of most nuts were within 20 m. *Carya spp.* have a greater mean distance of dispersal than *Quercus spp.* (Sork 1983,from Barnett 1976) but that pattern was not evident here because of the small study area and few samples. Nut trees tend to be found in caches away from the forest edge (Crowder & Harmsen 1998), a finding

which is consistent with the patterns of establishment of these species in the study field (Figure 22 and Figure 23). Additionally, *Carya spp.* have been found to regenerate faster in hedgerow habitats than in forest (McCarthy 1994), which was also observed in the hedgerow adjoining the old field where there were numerous young saplings interspersed with more mature ones (personal observation).

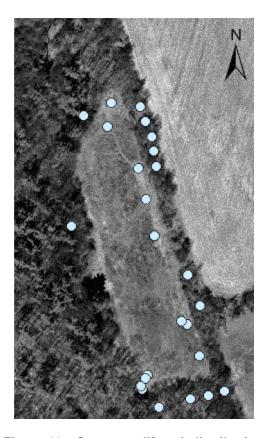


Figure 22: Carya cordiformisdistribution

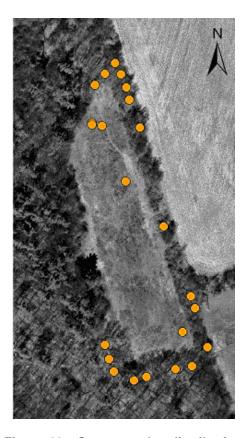


Figure 23: Quercus rubra distribution

Bird-dispersed: Bird dispersed vegetation establishment is more likely in structurally complex old fields than in younger, more uniform fields (ie more perches, more bird dispersed seeds) (McDonnell & Stiles 1983). However, it has also been observed that bird-dispersed vegetation dominates in early succession (Cook et al. 2005; Howard & Lee 2002; Robinson & Handel 2000). Bird-dispersed vegetation did comprise a significant proportion of the vegetation in the study field (36% of tree seedlings/saplings), with species such as *Rubus*, and *Rhamnus spp.* becoming well established only a decade after field abandonment. Though the patterns of establishment differed between these species, they both showed greater establishment at the edges than the interior (Figure 24 and Figure 25). Interestingly, *Rhamnus cathartica* was abundant in the hedgerow but did not seem to be reproducing into the field from there. Both *Crataegus crus-galli* and *Celtis occidentalis* showed solitary trees in the field occuring nowhere near the possible parent

population (Figure 26). It is likely that bird dispersal is more random than the mammaliandispersed seeds arising from carefully selected caches of squirrels and chipmunks or winddispersed seeds that show a 'seed rain' pattern.

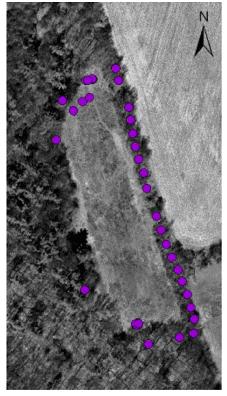


Figure 24: *Rhamnus cathartica* distribution

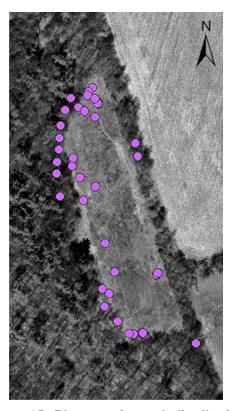


Figure 25: Rhamnus frangula distribution

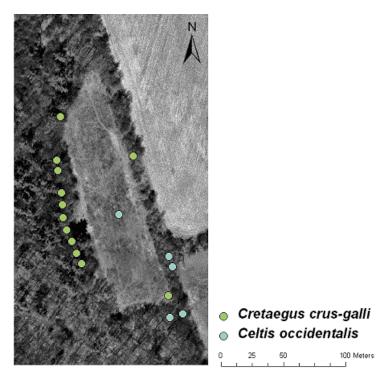


Figure 26: Crataegus and Celtis distribution

2. Application of GIS to Collected Data

GIS proved to be a valuable tool in visualizing patterns in the tree data mainly through effective presentation of maps and easy querying capabilities applied to subsamples. Spatial analysis was a great deal more complicated and posed some interesting challenges discussed further in section 'Problems With Spatial Analysis in Ecology'.

Representation of Data

Spatial patterns in nature are abundant, but the study of ecology using traditional statistical techniques often ignores or understates their significance. Since spatial patterns were a significant part of this research, I attempted to incorporate Geographic Information Systems into the representation and analysis of my data. For the most part, this was successful, though some shortcomings made this task more complicated than expected. I developed a greater appreciation for simple, robust and well-tested methodologies and a better understanding of the complexities of modern technology in the form of Global Positioning Systems (GPS) and Geographic Information Systems (GIS).

Because the location of establishing trees in the old field was a major focus of this research, I chose to utilize a GPS Trimble unit to give accurate locations of trees for later spatial analysis. The alternative was to use a compass and tape measure to determine locations from a central point, but as I had no field partner for much of the time, the former method was preferrable. The manual method would still have required calculations and conversions to x-y coordinates for incorporation into GIS and ultimately would have taken longer. The major downfall of the Trimble unit was in acquiring readings, particularly in the forest where cover interfered with satellite communication. It was also time-consuming to wait for logged points (15-20 minutes for each location) and then to download them to a networked computer in time for differential correction. A third problem was that precision could only be achieved to within 6 m on the Trimble unit which is a moderate degree of error for the scale that was being studied. Once the points were plotted, it was relatively straightforward to incorporate them into GIS (see Chapter 4 Methods, Field Tree Data, GPS Data Transferal).

The shortcomings of the GPS were to a large degree surmountable. Once the GPS unit was able to locate a minimum of 4 satellites, it could be left alone to record points while other data were being collected. As for precision, consulting the aerial map underlay acted as a double-check in confirming whether the points were where they should be based on the field observations. Only one point seemed to be in the wrong spot (in the hedgerow vs. about 10 m into field) and it may have been a result of low battery power and too few logged positions at that point. This was easily corrected by retroactively moving it in the GIS program.

The application of GIS for the representation of data was straightforward. GIS can greatly facilitate the storage, updating, retrieval and display of spatial data that were previously maintained on paper (Klosterman 1995). The flexibility and range of options for the production of maps was perhaps its biggest strength. Data were easily manipulated and specific questions were straightforward to answer, often only through simple queries. The data set were easy to update, which is an important factor if future monitoring of the site is done. Many patterns were analyzed even without using the spatial statistics options. The ArcGIS program was easy enough for a beginner to fairly quickly grasp the basics, and with some additional training, utilize its representation features for most desired outcomes.

Problems with Spatial Analysis in Ecology

Many times during analysis there were difficulties in performing tests that were appropriate for the data and that could give straightforward answers to the research questions. Spatial representation was chosen as the primary means of determining patterns using mostly traditional statistics (linear regression) for much of the analysis over geostatistical techniques (kriging,

cellular automata) which were not an ideal fit for the nature of my data. The best studies I encountered from the standpoint of measuring overall spatial patterns of trees used Ripley's K. This method identified patterns of clustering, random or regular spatial distributions and was frequently employed in forest studies. In particular, research published by Wolf (2005), Dolezal et al. (2004), Druckenbrod et al. (2005) and McDonald et al. (2003) followed similar research strategies of determining spatial patterns of trees based on species, age, mortality or time. This method can be employed relatively easily through the spatial analysis extension in ArcMap, as was done in my research. It is important to note however, that the scale being studied will influence the patterns. Clustering at one scale may become random or regular at another. Sites should be chosen with the scale that is most appropriate to the goal of the research: in this case, restoration at a 1 ha site basis proved to be adequate to illustrate patterns of clustering within the field using representation, but not for GIS-based spatial analysis.

Despite some progress noted in the literature, there is still a gap between ecological studies and the application of appropriate geostatistical analysis tools. As mentioned in the second research objective (see Introduction), geostatistics is a new and growing field that has many applications in a variety of research areas. Ironically, it is the field of geography itself that is only recently beginning to use such analysis. Biologists, geologists and ecologists have been using these techniques for years (see Legendre & Fortin 1989; Kent et al. 2006), whereas geographers have been focusing their work mainly on visual output and map production. The study of ecological systems poses many challenges for researchers, not only from the field of ecology itself, but also from the methods used for research and analysis. There are many spatial analysis techniques that have been applied in plant ecology to date which include tests such as Moran's I and Geary's C, Mantel tests, various forms of ordination such as principle components analysis and canonical correspondence analysis, detrended correspondence analysis (DCA), interpolation, and kriging (Kent et al. 2006).

Researchers repeatedly emphasize that the strongest assumptions of geostatistical tests (second order stationarity and isotropy) are likely to be violated when applied to ecological theories (Thomson et al. 1996; Miller & Franklin 2002; Jensen et al. 2006; Kent et al. 2006). The problem is that the significance of spatial patterns affecting ecological processes and vice versa is inherent in most ecological studies. Additional factors such as patchy distributions, heterogeneity, scale issues and physical and/or biological barriers further complicate analysis, making it difficult to determine random error from actual relationships. Current studies tend to restrict analysis to very specific criteria in univariate analysis (eg. stem densities) most likely because spatial variables can be dependent on so many factors that identifying significant patterns becomes too difficult. McDonald et al. (2003) raise a similar issue in their conclusions by identifying a need for more sophisticated spatial analysis techniques for multi-variate analysis. Modeling methods such

as kriging and cellular automata are also being widely experimented with, particularly in riparian and marine environments (Bulit et al. 2003; Fonseca et al. 2004; Jensen et al. 2006); however, these systems are somewhat easier to model because they are more of a closed system with more definable boundaries than terrestrial environments (Miller & Franklin 2002). Taking directionality into account can (and should) also be done which will lead to better predictions (Wagner et al. 2004), but the quality of the data must be very high. In short, the best studies tended to examine a narrow range of variables, restricted the study area to a highly definable system such as an aquatic environment, and incorporated directionality into predictive modeling using a high quality data set.

Geostatistical analysis must incorporate statistical tests of linear correlation and regression with spatial autocorrelation, which by their very nature violate the others' assumptions. For example, the concept of isotropy states that distance and direction are unimportant in determining the relationship between two points in space. Basic statistical techniques assume the importance is only in separation, not distance and location (Kent et al. 2006); however, most environmental data are anisotropic. That is, distance and direction are important, perhaps more so than other studied variables, but traditional statistical analysis can only model anisotropy as random error. The study of geostatistics relaxes the assumption of independence and allows spatial autocorrelation in the residuals (Peterson & Urquhart 2006). Euclidean distance is also assumed in many geostatistical models, but relationships are not always direct and concepts such as patchiness, time-distance on flow, dispersal and asymmetry are often present in stream systems, hilly terrain or across other barriers (Jensen et al. 2006). Another assumption that is violated is the idea of second-order stationarity (spatial constancy of mean and variance), particularly in the case of environmental gradients (Jensen et al. 2006) such as a trend in mean plant density along a forest-field transect.

Finding spatial patterns that are statistically significant can be a matter of determining the right scale to examine a phenomenon. For example, research conducted by Benjamin (2005) did not determine any spatial patterns, but instead found abiotic factors to be the most significant factor in how succession proceeds in old fields. This could be because the scale was too large to identify smaller-scale spatial patterns, but sufficiently large to capture abiotic ones. Likewise, in Cook et al. (2005), there were not any strong spatial patterns of woody species and their dispersal methods. However, this research was based on experimental plots which may not fully capture spatial patterns, merely a presence/absence. Tree establishment can be influenced primarily by local seed source and elevation (Battaglia et al 2002), although this effect may be very site specific (Cook et al. 2005). To determine significant spatial relationships in tree establishment, research has to be on a scale that can measure those patterns. In my research, this meant studying patterns on a scale of meters and centimeters such as the distance of trees

from edge or height of establishing trees. The GPS technology utilized in this study was still unable to accurately georeference to less than 6 m which is probably too great an error for confident analysis. Nonetheless, using the field observations and the aerial map as a cross-reference, the patterns that were generated by the georeferenced locations did correspond accurately enough to draw some conclusions.

Kriging was attempted on the spatial data set of establishing trees, but in the end did not reveal any more information than the density map. It may have had better application in interpolating canopy cover using height as a continuous variable, but when this was attempted, the data set was too small and/or too variable to make reasonable predictions. Although tall trees were consistently near the edges, the presence and abundance of short trees throughout the field complicated the predictions and could not give an accurate semivariogram from which to do the kriging. Converting data from vector to raster would likely have improved results as well, particularly in determining future concentration of trees. The density map produced in Chapter 5 was the first step and was adequate for illustrating the current state of the field, but it did not show how tree clustering might change in the future. The other drawback, and a concern expressed by several spatial experts during consultations, was the 'black box' approach for running tests on data. Spatial analysis tools in the GIS package are somewhat generic and often require customizing through short programs or scripts to provide the best results. The knowledge of the user should be sufficient enough to understand the data set and to account for assumptions that may be violated which may give erroneous results. Results in this research were most reliable when using the simplest analysis methods such as the density mapping and trend analysis. To do this type of analysis well with the tools I attempted on the ArcMap program involved learning its limitations and how to customize it to the data set. In my opinion, application of GIS analysis still requires the user to be highly proficient in spatial analysis techniques and somewhat knowledgeable on the data set itself in order to make custom alterations for the most accurate results.

3. Incorporation of Ecological Processes into Restoration Plans

All ecological restoration should begin with a basic knowledge of the site that is being restored and of the ecological processes that play major roles in the site. Successful ecological restoration entails integrating ecological knowledge such as vegetation succession in particular into restoration programs (Prach et al. 2001). In fact, the field of ecology is arguably most important during the implementation stage of restoration, when ecological knowledge and understanding are necessary before manipulating the system to achieve the desired goals (Davis & Slobodkin 2004).

This can be achieved by first determining the goals and objectives of restoration, then carefully studying the environmental site characteristics, formulating a restoration plan that includes monitoring and evaluation, and lastly, generalizing to other similar sites. Perhaps the biggest obstacle in this regard is spending the time to understand a particular site targeted for restoration well enough to predict what may happen there in the future. Because it is imperative that ecological processes affecting a site are incorporated in to implementation and monitoring programs at the beginning of the planning process, a few important steps should be followed. These are:

- 1. knowing what the processes are through research and observation
- 2. incorporating these processes when selecting achievable goals for restoration
- implementing restoration practices to enhance or discourage these processes in order to direct succession toward that goal

Regarding the first point, although each site is unique, many ecological processes tend to be somewhat predictable. As examples, it has been observed that *Populus tremuloides* tend to clonally advance when given the opportunity (Barnes 1966), that wind-dispersed trees will establish early (Stover & Marks 1998), that *Rhamnus spp.* will invade and suppress establishment of other species (Frappier et al. 2003; Fagan & Peart 2004; Johnson et al. 2006; Heneghan et al. 2006). Any one of these processes will direct succession in a particular direction unless other threshold events (disturbance) interfere, sending the system on a different pathway (Lockwood & Samuels 2004).

In the case of an old field abandoned by agriculture, it begins as a 'degraded state' with few species at the start of succession and with multiple possibilities of future states (Lockwood & Samuels 2004). This concept is being integrated into ecological research, such as that done by Dovciak et al. (2005) in which they outline three potential pathways of succession to describe the invasion of *Pinus strobus* into a field. They reiterate the potential of temporal changes that alter direction and 'mediate switches' which in turn can affect spatial variation. In the study field at rare, one possible scenario is the invasion and subsequent domination of *Rhamnus spp.* which may consequently prevent or delay the return of a forest ecosystem and result in stabilization at a desired end point, a simplified version of the system that has the potential to be more highly complex. Intervention to keep *Rhamnus spp.* invasion minimized may then allow other species to become established and form a more diverse forest structure than it might otherwise without the added 'disturbance'.

Hobbs & Norton (2004) expand on Lockwood's model in the sense that they define specific filters that can restore or inhibit function of the ecosystem, thus also affecting the successional pathway. Using the old field again as an example, the specific filters examined in this research include propagule availability, order of species arrival and competition. The first two represent facilitating thresholds, which have a positive effect on creating a higher functioning ecosystem. Competition, in this case, the presence of *Rhamnus*, will most likely have an inhibiting effect on other vegetation and can potentially send the system back to a lower state of function. To fully apply this concept to the research site, consider the mature forest ecosystem as the fully functioning desired end state. The hedgerow and old field are at separate transitional stages based on their biological filters. The abiotic filter in the old field has been crossed with the cessation of cultivation, which now no longer inhibits the establishment of herbaceous perennials and woody vegetation that were otherwise kept suppressed.

To carry this concept one step further towards ecological restoration, there are several filters for which direct observations have been made in this research which need to be directly understood in the context of this specific research site. These filters include: propagule availability, predation-trophic interactions, order of species arrival, and substrate. Below is a summary of these observations and how they can potentially be incorporated into restoration goals for the **rare** site.

Biotic Filter: Propagule availability

Observation: Most seeds will disperse naturally within 40 m, with most (75%) establishing at 10 m or less. This includes all methods of dispersal, but is especially true for nuts and heavy samaras (*Tilia americana, Acer spp*)

Implication for restoration: Interior areas of old fields that are greater than 40 m away from a seed source will have delayed sapling establishment resulting in longer forest regeneration times (40+ years) and may depend to a greater extent on secondary dispersal when the initially established trees begin reproducing.

Incorporation into goals: If short-term forest establishment is a goal, then intervention will be required by planting or seeding desired species in these isolated areas. On the other hand, if old field habitat is a desired goal (for grassland bird habitat as an example), then leaving these interior field areas to slowly regenerate may be a preferred option.

Biotic Filter: Predation-trophic interactions

Observation: Herbivory from deer and small mammals is a potential threat to woody plant regeneration (Rooney & Waller 2003). Browse from deer is most likely on highly palatable

saplings such as Quercus rubra and Acer saccharum and less so on Carya cordiformis and Rhamnus spp.

Implication for restoration: Although desirable species may establish naturally in a site, interactions with other species may increase or decrease that species' dominance. Intervention may be required to ensure the survival of desired species and the minimal presence of undesirable ones, particularly *Rhamnus spp*.

Incorporation into goals: If encouraging certain species (usually native) and discouraging others is a goal, protecting desired species from browse with chicken wire until they reach a size where they are less vulnerable is one means of directing ecological restoration. Conversely, actively removing undesirable species such as *Rhamnus* by applying herbicide or by manual pulls, neither of which are ideal solutions, can also change the successional pathway by preventing *Rhamnus* from increasing in dominance at the expense of other species more palatable to deer.

Abiotic/Biotic Filter: Substrate/ Order of species arrival

Observation: Clusters or 'hotspots' of establishing trees in old fields are likely to be found close to forest edges and can include multiple species and ages. This may be a direct result of environmental conditions favourable to establishment, particularly in the soil and/or proximity to good seed sources.

Implication for restoration: These areas should be considered ideal spots to allow natural regeneration, thereby targeting other areas for more intensive restoration.

Incorporation into goals: If identifying areas of high natural regeneration potential is a goal, more detailed research and monitoring of areas of high and low regeneration should be done to determine which factors are contributing to the favourable outcome (eg. good soil, highly abundant seed source nearby, shelter from extreme weather). Once again, targeting plantings in sites with some of these characteristics (e.g. good local soil conditions) may improve survival and establishment of transplants if for some reason natural regeneration is not occurring.

Two other points are important to consider at the implementation stage of an old field restoration project: with the passage of time, interactions within the field become more dominant than those outside it (Myster & Pickett 1992) and that an ecosystem will tend to stabilize in the absence of disturbance (Anand 2000). If restoration goals can enable processes within a site to continue to naturally regenerate and with minimal human intervention, then so much the better. Once greater stability has been reached in a system, it will (in theory) take a larger disturbance to change it (Anand 2000). The 10 year field which is the subject of this study is still highly dependent on

exterior interactions (seed sources) and sensitive to changes which make it harder to predict an eventual 'stable' state. For example, the abundance of *Fraxinus americana* implies eventual forest cover with that species as a likely dominant. However, the threat of disease such as the Emerald Ash borer may change that trajectory if it reaches this area and destroys this component of the ecosystem. This would in essence provide opportunity for other species to increase in abundance, desired or not. Perhaps the best measure of success will be in the secondary dispersal of new trees further into the field once the initial establishing trees have matured and reproduced. This will be a very long term goal given that most trees will not begin reproducing before 20 years of age. In the short term, changes in vegetation composition will be slow compared with changes in spatial pattern (Wolf 2005) as clusters thin out and new ones are created.

Ecological restoration has concentrated on planting site-appropriate species in prepared soil and in desired locations. What is still missing is the incorporation of spatial patterns and processes that direct spontaneous succession and how they fit into overall management plans. Some of these processes include seed dispersal and seedling survival and establishment, microtopographic variations in the landscape such as pits-and-mounds and forest-field edge effects. Those involved in ecological restoration need to incorporate these processes into their management plans. For example, in fields where recent abandonment has occurred and forest cover is desired, management strategies should try to determine when and where passive forest regeneration is most likely and when intervention may be required. Restoration efforts can then target specific areas based on original goals by: 1) accelerating edge succession by incorporating practices that aid the process (eg. planting trees, eliminating invasive non-natives), or 2) concentrating on the rehabilitation of non-edge areas where succession will be slowest (eg. planting new hedgerows) to provide a future secondary seed source. However, jump-starting basic ecological processes such as by recruiting secondary woody vegetation via directed plantings can be successfully implemented into restoration goals, but only with moderate expectations (Robinson & Handel 2000), particularly in regard to realistic timelines. Secondary succession cannot be expected to happen before the sources of natural dispersal or directed plantings reach maturity in a minimum of 20 years and many conditions can change before that, making predictions difficult.

Chapter 7: Conclusion and Recommendations

Conclusions

Many studies have researched the phenomenon of vegetation succession in abandoned fields (Crowder & Harmsen 1998; Meiners et al. 2001; Bartha et al. 2003 and others). Many ecological studies incorporate spatial analysis techniques to measure vegetation population distributions (Legendre & Fortin 1989; Miller & Franklin 2002; Druckenbrod et al. 2005; Peterson & Urquhart 2006). There were none that I encountered that examined overall spatial patterns of trees establishing in old fields (other than the edge effect or beyond one or two species) and the subsequent influence of nearby propagule sources. This thesis is an attempt to bridge the gap between science and the practical realities of restoration by explaining what vegetation arises in an old field after one decade and some of the reasons, and most importantly, how this knowledge can assist in restoration efforts at **rare** and other sites like it. Below is a summary of the most important findings:

Vegetation

- Old field and forest communities at this research site are typical of deciduous forests of this
 area containing dominant species such as Acer saccharum, Quercus rubra, Ostrya virginiana
 and Fraxinus americana. In addition, they contain significant populations of some Carolinian
 species at the northern limits of their range, specifically Carya cordiformis and Celtis
 occidentalis.
- There are several introduced and invasive populations in the forest, hedgerow and old field that have become dominant components of these communities, namely the 2 species of *Rhamnus*, *Dactylis glomerata* and *Alliaria petiolata*. The presence of these species may delay the timeline of recovery and alter future vegetation composition unless adequately managed.
- There was evidence of deer browsing on 10% of old field trees, with the highest incidence on Fraxinus americana (20%) and the least on Rhamnus spp. (2%) and Carya cordiformis (none).
 Deer are a major presence at the rare property and may be affecting nearby forest understory populations as well.

Field Tree Spatial Patterns

- After 10 years of spontaneous succession, there are still hard edges in the forest-field transition areas, but most edge areas have a higher concentration of saplings and woody shrubs than in the interior of the field. This effect is strongest less than 10 m from the forest boundary and decreases proportionally with distance away from this edge.
- Of all the trees sampled in the field that were assumed to be less than 10 years old, height was evenly distributed from 0.5 m to 5 m; however, trees over 2.8 m were only found within 10 m of the forest edge and not in the centre of the field. This may be because of better environmental conditions favouring growth, or in may be a function of age, with the oldest saplings having established earlier nearest the forest-field boundary.
- Establishing trees exhibited clustering patterns by species and proximity to edge. Populus
 tremuloides was most highly clustered, possibly from clonal reproduction, and the nut trees
 were the least clustered. Two dense clusters containing multiple species were located on
 opposite edges of the field and both were within 5 m of an edge.
- Spatial patterns varied by dispersal type, with wind-dispersed trees (primarily *Fraxinus*) being the most abundant (39% of establishing trees) and widely distributed across the field. Mammal-dispersed trees (*Quercus* and *Carya*) were concentrated in a band about 5 m from the hedgerow. Bird-dispersed trees (36% of establishing trees) were also abundant, consisting mainly of *Rhamnus spp.* and showed greatest advancement on the western and northern edges.

Forest and Hedgerow Composition

Canopy forest species varied in composition on the different sides of the field (north, south, east or west edges), with some species as probable seed sources for the field (*Fraxinus americana*, *Acer saccharum*, *Carya cordiformis*, *Quercus rubra*) and other species not reproducing at all (*Fraxinus nigra*, *Tilia americana*, *Prunus serotina*, *Pinus strobus*). Based on the data collected here, it was not possible to pinpoint exact parent trees, only the likely origins of seedlings. This may serve as a good starting point for further research into these relationships, including more detailed spatial analysis which could not be accomplished here.

The Application of GIS to Determine Spatial Patterns

Advances in spatial statistics and geographic information systems have been made in the past several decades, but the challenges of applying them to ecological studies remain onerous. Spatial statistics remains an area of specialized expertise that does not lend itself easily to application by anyone who is not adept at mathematics. Though ArcMap had numerous spatial analysis tools and they were attempted at various stages in my own analysis, inevitable problems arose that required customizing the programs that were beyond my general capabilities. These issues are best tackled by a team of experts from each discipline who can apply their expertise to maximum effectiveness rather than attempting a one size fits all approach.

Having said that, there are many good studies that have successfully incorporated geostatistics for analyzing data. The best studies I found on discerning spatial patterns of trees had a narrow range of criteria such as species, age, and mortality (McDonald et al. 2003; Dolezal et al. 2004; Wolf 2005; Druckenbrod et al. 2005). Incorporating directionality could also be done, effectively addressing the issue of isotropy (Wagner et al. 2004), but with the caveat that a high quality data set is required.

Unquestionably, GIS is a highly valuable tool for data recording and representation. The flexibility and ease of producing maps of any number or combination of attributes means that information can be quickly and effectively disseminated for any number of applications. That certainly proved true in my application. Although some training is required for a typical user, it is manageable given good support systems through a university or tech-support business.

Recommendations

The scientific perspective is one of many that influence the management of natural areas and cannot work in isolation from the social or political dynamics of decision making (Davis & Slobodkin 2004). The following recommendations entail both site specific and general comments on incorporating the specifics of this research into future research and/or restoration projects. It should be noted that the very first step that management at **rare** should do is to determine goals and priorities for restoration interventions at the old field and at other old field habitats at **rare** through a restoration master plan. It should outline overall goals for restoration (eg. expansion of forest into abandoned old fields) and the degree of intervention they are willing to undertake to achieve those goals. The following suggestions can potentially be incorporated into a master plan.

Site-Specific Recommendations

Ecological restoration depends on the activity of nearby natural populations which can enhance or even rescue restoration attempts (Robinson & Handel 2000). Because of the extensive forests and alvar habitats at **rare**, there is great potential for collecting seeds and seedlings for propagation and using those for future ecological restoration.

1. Continue to monitor EMAN plots and incorporate into province-wide databases. Using the same techniques outlined in this study, repeat the study of both the field trees and the EMAN vegetation plots in 5 or 10 years to mark changes in the population such as size, composition, mortality, canopy cover, etc. This will be the beginning of long term data collection at this site and can be extended to other areas at rare for comparison.

The measurement of species diversity through such techniques as the Shannon-Wiener diversity index has frequently been employed in ecological studies related to succession (Crowell & Freedman 1994; Huberty et al. 1998; Howard & Lee 2003 and others). Though it was not implemented in this research, the main benefit of employing this method is in examining trends in the number and abundance of plant species in an area over time or space. Most studies of this nature seemed to agree that diversity peeks around 10-25 years, long enough for many species of plants to move in but not yet succumb to competition for light and soil resources (Crowell & Freedman 1994; Howard & Lee 2003). Future studies of this research site should incorporate such a measure in order to track changes in such diversity over time. This has pertinent application because of the high presence of *Rhamnus spp.*, which has been observed to reduce plant diversity in areas where it has established.

- 2. Develop a management strategy for the control of both Rhamnus species to limit their effect on spontaneous succession. Rhamnus spp. has been observed to have negative effects on native trees, even to the point of altering soil conditions and creating long term effects that inhibit seedlings and saplings nearby (Frappier et al. 2003; Fagan & Peart 2004; Johnson et al. 2006; Heneghan et al. 2006). As such, invasive species such as Rhamnus spp. have the potential to significantly alter the direction of succession (Reidel & Epstein 2005) and its control and management should therefore be addressed in any subsequent restoration plan.
- 3. Extend the current GIS database created from this thesis to become an inventory of natural and cultural features for all of the rare property. Although it is a site of exceptional natural and cultural features with an extensive historical context, rare does not yet have a comprehensive data storage and retrieval system. One way to do this is the creation of an 'expert system' as described by Prach & Pysek (1999) which combines intuitive and anecdotal

knowledge with quantitative (scientific) information. It would function as an archive for historical information, compiling and storing anecdotal data from field experts who may not always be available for consultation. Just as importantly, it would be a clearing house for scientific data that can be retrieved and added to by others for further research. In essence, it would answer the questions of most anecdotal information such as what was found where, when and by whom and would also store scientific data based on studies carried out there. This has the benefit of creating a comprehensive source of information that has value to a wide range of users from someone giving a historical talk to the public to highly advanced research carried out by a local university. GIS has the benefit of providing features such as archiving, querying and visualizing data even for a user with limited spatial analysis training.

- 4. Based on spatial patterns of woody plant recruitment that were observed in the field, identify sites with good regeneration potential (i.e. clusters) and do further research on environmental conditions of those sites, particularly soil. Use that information to identify other sites with good (or poor) regeneration potential elsewhere at rare. Restoration can direct the spatial patterns of woody plant recruitment, particularly avian dispersed, through experimental plantings though they will not likely serve well as recruitment sources in the short term (Robinson & Handel 2000).
- 5. Enhance native populations of trees and herbaceous vegetation by starting an on-site nursery for stock to be transplanted at rare and/or sold commercially. Rare has a few Carolinian species at the northern limit of their range. If the genetic and phenotypic variation is large, then the populations likely will survive and thrive in situations that benefit growth, i.e. regional impacts of global climate change (though models are not yet specific to the scale of rare and its environs so whether precipitation and temperatures will favour Carolinian species is not established). This has ramifications on a greater landscape scale because the outer ranges of species such as Carya cordiformis and Celtis occidentalis may be significantly affected by the effects of climate change, leading to possible northern expansion. Changes in tree dominance over time towards favouring these more Carolinian species may stem from climate warming and this change will be most noticeable in areas where northern and southern species co-exist, such as the site at rare. At the very least, testing this hypothesis at a localized scale can be done at this site to measure such compositional changes in relation to climate change. In addition to protecting these somewhat 'elastic' tree populations, it may be worth propagating them. One likely candidate species is Carya cordiformis. It is deer-resistant, it can grow in varying soil and light conditions when mature (Farrar 1995), it is easier to transplant than other Carya species (Waldron 2003) and it is relatively disease-free.

Consider the creation of a deer-proof, in-situ forest nursery for propagation through the removal of populations of *Convallaria majalis* (Lily-of-the-valley), (personal observation outside of recorded transects), and other invasives and replacing them with native understory vegetation such as *Trillium grandifolium*, *Asarum canadense* (wild ginger), and *Sanguinaria canadense* (bloodroot). This has the dual benefit of simultaneously reducing the invasive populations and increasing natives that can then be transplanted elsewhere. It may even be possible in some cases to suppress the establishment and spread of invasives through carefully planned native species re-establishment (Murphy 2005). Weiher (2005) discourages the over-emphasis of manipulating vegetation in terrestrial systems, ascribing it the characteristics of being a glorified gardening activity; however it has direct application to this site where restoration is an immediate concern and has excellent tie-in with the public perception of landscape preservation using native species. Furthermore, it addresses such biotic filters (Hobbs & Norton 2004) as competition, predation-trophic interactions, propagule availability and biological legacy which are necessary components of a highly functioning ecosystem.

General Recommendations

Restoration theorists and practitioners have many recommendations on advancing the science of restoration ecology. Specifically they suggest a focus on seed ecology, such as sources and patterns of transport in fragmented landscapes (Prach et al. 2001), more comparisons of spontaneous vs. controlled succession and also examining the course of succession in more extreme environments (very dry or wet, contaminated soils) (Prach & Pysek 2001). Weiher (2005) recommends the use of more multi-variate studies in restoration science and going beyond mere demonstration science (controlled experiments). Last but not least, further spatial analysis of patterns of tree establishment on a larger scale may contribute to this field of research in a way that has not been possible until recently.

Based on the current literature and on the research carried out in this thesis, I recommend further research at the site on other variables that were not incorporated in this research. An expanded data set with additional variables and/or more data points recorded at similar sites should be considered to test other hypotheses relating to forest regeneration. Other types of studies could incorporate measures of diversity and experimental vs. control areas. Specific research questions should address:

- how soil and/or light conditions affect growth of establishing trees (multivariate studies)
- patterns of crown cover and canopy formation (application of kriging, cellular automata)

- changes in species composition and diversity over time, particularly any trends towards oakhickory vs maple/beech dominated canopy species.
- incorporation of other similar sites but at different successional stages
- specific experiments involving the control and/or removal of Rhamnus (see reaction-diffusion model in Frappier et al. (2003)
- changes in spatial patterns of establishing trees over time such as decreased clustering as trees mature and self-thin.

The research presented here reiterates to a large degree what has been observed by others regarding the phenomenon of old field succession. Edge effects and proximity to seed sources have consistently been found to be important components in forest regeneration and this study proves no exception. It differs in that no study to date has focused on the northern edge of the Carolinian forest where possibilities for successional trajectories are much different than in the mid-zones of the eastern United States where much existing research has taken place. This study also goes beyond the description of what species are establishing and in what number to the identification of spatial patterns of tree establishment and their potential propagule sources. Incorporation of GIS can aid in the collection, storage and retrieval of important data relating to the site and can greatly assist in the spatial analysis of these patterns. Visual representation and density mapping was the best method of analyzing this particular data set at this scale. Armed with a better understanding of local forest regeneration through research into the most relevant ecological processes, **rare** and other sites like it can target specific restoration outcomes through the recommendations listed here.

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Appendix

Glossary

abiotic/biotic filter non-living/living factors that contribute positively or negatively to the health of an ecosystem.

assembly rules (Halle & Fattorini 2004) A theory of how ecosystems assemble themselves based on interactions between living and non-living features.

biological legacy (Hobbs & Norton 2004) The past and present features and events that contribute to the current state of an ecosystem.

EMAN Environmental Monitoring and Assessment Network. A system of standardized collection and analysis methodologies for biological data.

establishment The successful germination, survival and growth of a tree seedling past the first year during which mortality is highest.

importance value A method of identifying which species are structurally dominant in a study site based on the sum of their relative density, relative dominance and relative frequency within and between plots.

isotropy Distance and direction are not important. An assumption of most basic statistical techniques.

kriging A predictive geostatistical method of analysis based on measuring pairs of points in space and their relationship to one another, from which a modelling map can be produced.

Moran's I A spatial analysis method that measures clustering of a phenomenon in relation to another feature.

Ripley's K A spatial analysis method that measures clustering of a phenomenon at various distances apart. (in relation to each other)

second-order stationarity Spatial constancy of mean and variance. The assumption that mean and variance are not affected by location.

Terminology

Latin Name (based on Newmaster 1998)

Acer rubrum L.

Acer saccharum Marshall ssp. saccharum Alliaria petiolata (M. Bieb.) Cavara &Grande Amelanchier arborea (Michx. F.) Fern.

Anemone americana (DC.) H. Hara

Anemone canadensis L.

Apocynum cannabinum L. var. cannabinum Arisaema triphyllum (L.) Schott ssp. triphyllum

Articum minus (Hill) Bernh. ssp. minus

Asarum canadense L. Asclepias syriaca L. Aster novae-angliae L.

Aster pilosus Willd. var. pilosus

Berberis vulgaris L.

Betula alleghaniensis Britton

Bromus tectorum L.

Cardimine diphylla (Michx.) Alph. Wood

Carex laxiflora Lam.

Carpinus caroliniana Walter ssp. virginiana (Marshall) Furlow

Carya cordiformis (Wangenh.) K. Koch Carya ovata (Mill.) K. Koch var. ovata

Caulophyllum giganteum (Farw.) Leconte & Blackwell

Celtis occidentalis L.

Chenopodium album L. var. album Chrysanthemum leucanthemum L.

Circaea lutetiana L. ssp. canadensis (L.) Aschers. & Magnusson

Cirsium arvense L.Scop.

Cirsium discolor ((Muhlenb. ex Willd.) Spreng.

Cirsium vulgare (Savi) Ten.

Convallaria majalis L.

Conyza canadensis (L.) Cronquist

Cornus alternifolia L. f.

Cornus foemina Miller ssp. racemosa (Lam.) J.S. Wilson

Crataegus crus-galli L. Dactylis glomerata L. Daucus carota L.

Dipsacus fullonum L. ssp. sylvestris (Hudson) Clapham

Epilobium strictum Muhlenb. Ex Spreng.

Epipactis helleborine (L.) Crantz

Equisetum arvense L. Erigeron annuus (L.) Pers.

Erythronium americanum Ker Gawl. ssp. americanum

Euphorbia esula L. Fagus grandifolia Ehrh.

Fragaria vesca L. ssp. americana (Porter) Staudt

Fraxinus americana L.

Common Name

Maple, Red Maple, Sugar Garlic Mustard Serviceberry

Hepatica, Round-Lobed Anemone, Canada Indian Hemp Jack-in-the-Pulpit Burdock, Common Ginger, Wild

Milkweed, Common Aster, New England Aster, White Heath Barberry, Japanese Birch, Yellow

Grass, brome
Toothwort
Grass, Wood
Blue-beech
Hickory, Bitternut
Hickory, Shagbark
Cohosh, Blue
Hackberry
Lamb's Quarters
Oxeye Daisy

Nightshade, Enchanter's

Thistle, Canada Thistle, Field Thistle, Bull Lily of the Valley Horseweed

Dogwood, Alternate-leaf

Dogwood, Gray Hawthorn, Cockspur Grass, Orchard Queen Anne's Lace

Teasel Willow Herb

Helleborine, Common Horsetail, Common Fleabane, Daisy

Trout lily Leafy Spurge Beech, American Strawberry, Wood

Ash, White

Fraxinus nigra Marshall
Galium mollugo L.
Geranium maculatum L.
Geranium robertianum L.
Geum canadense Jacq.
Geum virginianum L.
Hamamelis virginiana L.
Hypericum perforatum L.
Impatiens capensis Meerb.

Lactuca serriola L.
Lapsana communis L.
Linaria vulgaris Miller
Lonicera tartarica L.
Lotus corniculatus L.

Maianthemum canadense Desf.

Maianthemum racemosum (L.) Link ssp. racemosa

Malus pumila Miller Medicago lupulina L. Melilotus officinalis (L.) Pall.

Monarda fistulosa L. Morus alba L.

Ostrya virginiana (Mill.) K. Koch

Oxalis acetosella L. ssp. montana (Raf.) Hulten

Oxalis stricta L.

Parthenocissus inserta (A. Kern.) Fritsch

Pinus strobus L.
Plantago major L.
Polygonum persicaria L.
Populus tremuloides Michx.

Potentilla recta L.
Prenanthes alba L.
Prunus americana Pursh
Prunus pensylvanica L. f.
Prunus serotina Ehrh.

Prunus virginiana L. ssp. virginiana

Pteridium aquilinum (L.) Kuhn var. latiusculum (Desv.) L. Underwl

ex A. Heller Quercus alba L. Quercus rubra L. Rhamnus cathertica L. Rhamnus frangula L. Rhus typhina L. Ribes cynosbati L. Ribes triste Pall.

Rubus idaeus L. ssp. melanolasius (Dieck) Focke

Rubus odoratus L.
Rumex crispus L.
Sambucus canadensis L.
Sanguinaria canadensis L.
Setaria viridis (L.) P. Beauv.
Silene vulgaris (Moench) Garcke
Smilax hispida Muhlenb. Ex Torr.

Ash, Black Wild Madder Geranium, Wild Herb Robert Avens, White Avens, Rough Witchhazel

St. John'swort, Common

Jewelweed
Lettuce, Prickly
Nipplewort
Butter-and-eggs
Honeysuckle, Tartarian
Trefoil, Bird's-foot
Canada Mayflower
False Solomon's Seal

Apple

Medick, Black Sweet Clover, Yellow

Monarda Mulberry, White Ironwood

Wood Sorrel, Common Wood Sorrel, Yellow Virginia Creeper Pine, White Common Plantain Lady's Thumb Aspen, Trembling Cinquefoil, Rough-fruited

Lettuce, White Plum, Wild Cherry, Pin Cherry, Black Chokecherry Bracken fern

Oak, White Oak, Red

Buckthorn, European Buckthorn, Glossy Sumac, Staghorn Gooseberry, Prickly Currant, Red

Currant, Red Bramble

Raspberry, Purple-flowering

Dock, Curly-leaf Elderberry Bloodroot Grass, Foxtail Bladder Campion Greenbriar, Bristly Solanum dulcamara L. Solidago canadensis L. Solidago flexicaulis L.

Sonchus asper (L.) Hill ssp. asper Taraxacum officinale G. Weber

Tilia americana L.

Trientalis borealis Raf. Ssp. borealis

Trifolium pratense L.

Trillium grandifolium (Michx.) Salisb.

Tussilago farfara L.
Ulmus americana L.
Veronica chamaedrys L.
Veronica officinalis L.
Viburnum acerifolium L.

Vicia cracca L.

Viola affinis J. Le Conte Vitus riparia Michx.

Zanthoxylum americanum Miller

Nightshade, Bittersweet Goldenrod, Canada Zigzag Goldenrod

Sow-Thistle, spiny-leaved

Dandelion

Basswood, American

Starflower Clover, Red

Trillium, White flowered

Coltsfoot
Elm, American
Speedwell, Bird's-Eye
Speedwell, Common
Viburnum, Maple-leaf
Vetch, Cow

Violet

Grape, Riverbank Prickly Ash

EMAN Data Sheets

	nunity Type								
ag #	Species name	Number of stems	Line (1, 2, 3, 4)	A Distance (m)	B Distance (m)	Canopy Width OR dbh (m)	Height (m)	Condition	Notes
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\neg							\vdash		\vdash
\neg					\vdash		-		$\overline{}$

Stand Name	Stand location (lat & long)	Quadrat Nº
Nested in quadrat NºQua	drat dimensions	ty type
Identification manual	Observer(s)	
Species name	Number of stems or clumps	Comments