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**CHANGES IN THE ABUNDANCE AND DISTRIBUTION
OF WOODY PLANTS RELATED TO DISPERSAL
MECHANISMS ALONG A FOREST COVER GRADIENT**

by

Thomas A. Contreras, M.A., M.Sc.

A thesis submitted to
The Faculty of Graduate Studies and Research
In partial fulfillment of
The requirements for the degree of

Doctor of Philosophy

Department of Biology
Carleton University
Ottawa, Ontario
January 11th, 2002

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Changes in the distributions of woody plants related to dispersal mechanisms along a
forest cover gradient.

Submitted by

Thomas A. Contreras, M.A., M.Sc.

In partial fulfillment of the requirements
For the degree of Doctor of Philosophy

Chair, Department of Biology

Thesis Supervisor

External Examiner

ABSTRACT

Seed dispersal direction and distance depend on the interaction between landscape structure and seed dispersal mechanism. I hypothesized that a reduction of forest cover in the landscape will affect the dispersal of animal-dispersed species differently than wind-dispersed species. Landscapes with less forest cover should have relatively lower densities of animal-dispersed plants (i.e., decreased landscape connectivity for animal dispersers) and relatively higher densities of wind-dispersed plants (i.e., fewer barriers to wind movement and increased connectivity) than landscapes with more forest cover.

In 1997 I sampled woody plant stem densities in 29 1-km² sample landscapes, along a gradient of decreasing forest cover. The mean stem density of animal-dispersed stems increased with decreasing forest cover in the landscape ($r^2 = 0.44$) with no change in the mean stem density of wind-dispersed species. Additional analyses using seed and stem densities in the landscape suggested that a reduction of forest cover in the landscape results in: i) a decreased dispersal of the seeds of both wind- and animal-dispersed forest-habitat species within forest habitats, ii) an increased dispersal of the seeds of wind- and animal-dispersed open-habitat species into open habitats, and iii) an increased dispersal of animal-dispersed open-habitat species into remaining forest habitat.

Based on these results, I predicted an increase in the emergence of seedlings in forest habitats following an ice storm in 1998. I also predicted a greater increase in the emergence of seedlings of open-habitat, animal-dispersed species in forest habitats since landscapes with less forest cover will have more of these kinds of seeds in remaining

forest patches. After resurveying the landscapes in 1998 and 1999 I found that the results supported my predictions.

My results suggest that landscape-scale forest patterns can affect vegetation composition within remaining forest patches. I speculate that the removal of forest from a landscape will increase the movement of animal-dispersed seeds from open habitats into remaining forest habitats in the landscape. Additional disturbances that damage or remove canopy crowns from forest patches would also result in the increased emergence of the seedlings of these species in remaining forest patches.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 POTENTIAL CONSEQUENCES OF HABITAT REMOVAL FOR PLANT SPECIES

Habitat loss is an inevitable consequence of increased human activity as certain landscape cover types, or elements, are modified to suit the needs of growing human populations (Meyer 1995). Removal or conversion of habitat often has dire consequences, not only for those organisms inhabiting areas where habitat removal has occurred, but also for those organisms left in remaining habitat. The removal of habitat from a landscape can reduce the number of individuals in a landscape more than would be predicted by the amount of habitat alone (Andrén 1994, Bender et al. 1998, Connor et al. 2000) since remaining individuals are often more vulnerable to local extinctions due to both demographic and environmental stochasticity (Andrén 1994, Fahrig and Merriam 1994, Harrison and Bruna 1999). This vulnerability is partly related to decreasing landscape connectivity, i.e., decreasing ability of animals to move through an increasingly hostile landscape (Fahrig and Merriam 1994).

Much of the primary literature examining the effects of habitat loss and changing landscape structure on populations has focused on animal species (see Fahrig and Merriam 1985 and 1994, Andrén 1994, Bender et al. 1998, Fahrig 1999, Harrison and

Bruna 1999, Mazerolle and Villard 1999, Trzcinski et al. 1999, Connor et al. 2000). There has been increased interest in the effects of habitat loss on plant dispersal with evidence from a number of modeling and empirical studies pointing to seed dispersal as an important mechanism in determining how plant species respond to habitat loss and changes in landscape structure (e.g., Primack and Miao 1992, Matlack 1994, Santos and Telleria 1994, Malanson 1996, Malanson and Armstrong 1996, Fröborg and Eriksson 1997, Grashof-Bokdam 1997, Guariguata and Pinard 1998, Foster et al. 1999, Sarlöv Herlin and Fry 2000, Pan et al. 2001).

Plants depend on the dissemination of their seeds in order to disperse distances greater than they could move by vegetative reproduction alone (Johnson et al. 1981, Howe and Smallwood 1982, Holt et al. 1995). This has implications not only for plant population dynamics, but it also influences how plant populations respond to natural and human-induced changes in their environment (Santos and Telleria 1994, Grashof-Bokdam 1997, Guariguata and Pinard 1998, Sarlöv Herlin and Fry 2000, Cadenasso and Pickett 2001). Seed dispersal mechanisms vary among plant species (Howe and Smallwood 1982) and impose limits on where seeds can be deposited (Howe and Smallwood 1982, McDonnell and Stiles 1983, Matlack 1989, Myster 1993, Portnoy and Willson 1993, Willson 1993, Masaki et al. 1994, Nathan and Muller-Landau 2000, Cadenasso and Pickett 2001). As a result, a plant species' distribution in a landscape may be linked to an interaction between that landscape's structure and the method of seed dispersal used by that plant species. The structure of the landscape may change in a way

that seed dispersal becomes either more difficult (decreased connectivity of the landscape) or less difficult (increased connectivity of the landscape).

In the eastern Ontario region, deciduous and mixed (deciduous/coniferous) forested areas are a dominant landscape feature (Chapman and Putnam 1984). Changes in the amount of forest in a landscape might affect the dispersal ability of seeds of different dispersal types across the landscape. For example, a reduction in the percent forest cover in a landscape might reduce the dispersal ability of animal-dispersed, forest plant species because forest animals may have reduced dispersal in landscapes where there is more nonforest habitat to traverse between forest patches. But for wind-dispersed species of forest habitats there may be a relative increase in dispersal distances since a reduction in forest cover may mean less wind attenuation and greater wind speeds through the landscape, even in remaining forest patches.

1.2 PLANT DISPERSAL MECHANISMS

1.2.1 ANIMAL-DISPERSED SEEDS

For woody plant species in the forests of the Ottawa, Ontario region, the acquisition and dispersal of seeds by animals occurs primarily through two methods: i) passive-internal dispersal (endozoochory) where seeds are produced within a fleshy fruit and are unintentionally ingested when the fruit is eaten (either passing through the animal's digestive tract or regurgitated by the animal after being separated from the fruit pulp) or ii) active-external dispersal (ectozoochory) where seeds are selected as food

items and then cached for a time before being consumed (Stiles 1992). In both instances, animals move the seeds away from the seed source (Stiles 1992, Willson 1992) and the distance and direction of dispersal will depend on seed retention time and movement of the animals (Stiles 1992).

While a discussion of the evolution of seed dispersal mechanisms of woody plant species is beyond the scope of this thesis, seed size and other characteristics related to seed germination and seedling establishment may be tied to the way in which seeds are dispersed by animals (Howe and Smallwood 1982, van der Pijl 1982, Stiles 1992, Steele et al. 1993, Steele et al. 1996, Hammond and Brown 1999, Nathan and Muller-Landau 2000, Vander Wall 2001, Jansen et al., in press). For endozoochorous species (e.g., *Rubus* L. (the Raspberries), and *Rhamnus* L. (the Buckthorns)), seeds must be small enough to pass through the digestive tracts of animals and they must possess tough seed coats that allow the seed to survive its journey through the digestive system (Stiles 1992). The trade-off is that tough seed coats must be weakened (scarified) in order for seeds to break dormancy (Stiles 1992). For many endozoochorous species this is accomplished through exposure of the seed to the chemical and physical processes that occur as seeds travel through the gut of the seed disperser as well as exposure to physical factors in the microhabitat in which the seed has been deposited (Schopmeyer 1974, Stiles 1992). However, even if deposited in a suboptimal microhabitat (e.g., low-light conditions), the seed coat allows the seed to remain dormant, resistant to dehydration and decomposition while in the litter or soil seed bank (Schopmeyer 1974, Pickett and McDonnell 1989,

Stiles 1992). For many of these species, seeds can survive for years, even decades (Bormann and Likens 1979, Peterson and Carson 1996).

For actively dispersed ectozoochorous species, larger seed sizes are possible since seeds do not have to pass through the gut of an animal-disperser. However there are also trade-offs associated with larger seed sizes. First, with larger amounts of stored food in each seed, seeds are more susceptible to predation by birds and mammals (Vander Wall 2001, Steele and Smallwood, in press). Second, larger seeds are more difficult to carry and therefore animals (Vander Wall 2001, Steele and Smallwood in press) must actively and purposely disperse seeds. As a result, distances may be shorter than those observed for the smaller, passively dispersed endozoochorous species (Grashof-Bokdam 1997, Vander Wall 2001).

1.2.2 WIND-DISPERSED SEEDS

For wind-dispersed species there are a variety of seed morphological types (van der Pijl 1982). For most species, seeds have structures that catch air currents. For species that belong to the genus *Populus* L., these structures are wisps of cotton-like threads attached to the seed. For others, like the Aceraceae (Maples), wing-like structures on seeds catch the wind and spin like helicopter blades (van der Pijl 1982). In both instances, the result is to increase the 'hang-time' of seeds as they fall from parent trees. This makes it easier to catch wind currents that may move them away from the parent and increases the probability that they will make it into microhabitats that are suitable for germination

(Burrows 1986, Matlack 1987). Dispersal distances are affected not only by the type of dispersal structure present but are also influenced by seed size, the height from which the seeds are released, and wind speeds (Matlack 1987, Johnson 1988, Greene and Johnson 1996).

In general, seeds dispersed by wind are at the mercy of prevailing winds so wind-dispersal is less 'directed' than the dispersal of animal-dispersed seeds. As a result, it's possible that the seeds are less likely to be dispersed into suitable germination sites than animal-dispersed species. However, many of these species are shade-tolerant, particularly species inhabiting forest habitats, so they have the ability to germinate within the canopy shadow of their parents, even when surrounded by high densities of competing siblings (Burns and Honkala 1990). These species can also remain suppressed in the understory as either seedlings or saplings until some disturbance opens up the canopy and allows greater light penetration to the forest floor (Canham 1985, Burns and Honkala 1990).

For shade intolerant, wind-dispersed species (particularly those with small seeds), secondary dispersal is an important mechanism and gives seeds a greater chance of reaching habitats conducive to germination, e.g., forest gaps and bare ground in open fields (Matlack 1989, Houle and Payette 1990, Greene and Johnson 1997). For species like those in the genus *Betula* L., seeds are small samaras that are initially dropped in the fall and winter. However, with snow and ice cover, the small seeds are blown along the snow and ice surfaces in the winter (Matlack 1989, Houle and Payette 1990, Greene and Johnson 1997). With no leaf cover, and many ground obstacles covered by snow and ice,

seeds can be blown great distances, in some instances hundreds of meters (Matlack 1989, Houle and Payette 1990, Greene and Johnson 1997).

1.3 THE INTERACTION BETWEEN SEED DISPERSAL MECHANISMS AND LANDSCAPE COMPOSITION

1.3.1 BACKGROUND

A reduction in the amount of forest cover in a landscape necessarily affects the distribution and abundance of plant species in that landscape (Gibson et al. 1988, Rudis 1995, Ferreira and Laurance 1997). With changes in landscape structure, we might predict changes in the distribution and abundance of remaining plants in the landscape due to either (i) changes in the dispersal ability of their seeds or (ii) changes in environmental factors affecting seed germination and seedling establishment (Bormann and Likens 1979, Gibson et al. 1988, Matlack 1993, Rudis 1995, Malanson and Armstrong 1996, Peterson and Carson 1996, Ferreira and Laurance 1997, Grashof-Bokdam 1997).

For sessile species such as plants, connectivity of the landscape is only relevant during seed dispersal. For animal-dispersed plants, connectivity is a matter of how changes in landscape structure might change the connectivity of the landscape for the animals responsible for seed dispersal. Where forest loss has reduced the connectivity of

the landscape for these animals, I hypothesize a reduction in the connectivity of the landscape for the plants whose seeds they disperse.

For wind-dispersed species, changes in landscape connectivity may be related to the elimination of barriers to wind movement. Following forest removal from a landscape, dispersal distances of the remaining wind-dispersed plant species might increase, since forests and woodlots are one of the primary barriers to wind movement (Johnson 1988, Matlack 1989). For example, it has been suggested that increased deforestation may increase the mean dispersal distance of both the seeds and pollen of species such as *Acer saccharum* Marsh. (Sugar Maple) or *Betula alleghaniensis* Britt. (Yellow Birch) (Foré et al. 1992, Houle and Payette 1990, Young and Merriam 1994). A reduction in the size of forest fragments may also increase dispersal of forest plant species with wind dispersed seeds, since smaller forest fragments would have less wind attenuation and, therefore, less resistance to seed movement within or between forest fragments (Howe and Smallwood 1982, Johnson 1988, Portnoy and Willson 1993, Greene and Johnson 1996). So while increased loss and fragmentation of forest will increase distances between forest fragments and decrease fragment sizes, there may be an increase in the mean dispersal distances of wind dispersed species and a greater probability of movement within or between remaining habitat (Howe and Smallwood 1982, Portnoy and Willson 1993).

Removal of forest from the landscape may also affect the response of remaining forest plant communities to natural disturbances (Bormann and Likens 1979, Gibson et

al. 1988, Rudis 1995). Disturbances can cause an increase in the abundance of species associated with earlier successional stages. Landscapes with lower forest cover may show an even greater increase in these species due to increased deposition of wind-dispersed species from nonforest habitats.

1.3.2 HYPOTHESES AND PREDICTIONS

Landscapes containing less forest should have higher densities of wind dispersed species and lower densities of animal dispersed species than landscapes containing more forest. Barriers to air movement will decrease as canopy trees are removed from the landscape, resulting in greater dispersal of windborne seeds and a higher recruitment rate of those species (Johnson 1988, Matlack 1989). Conversely, decreasing percent forest cover should reduce the effectiveness of animals as seed dispersers and the mean density of animal dispersed species within the landscape should also decrease.

It has also been suggested that there are correlations between seed dispersal mechanisms and other life history characteristics such as shade tolerance, seed size, and dormancy (Mladenoff 1990, Hammond and Brown 1995, Schupp 1995, Milberg et al. 1996, Metcalfe and Grubb 1997, Hyatt and Casper 2000). If so, relationships between the stem density of a dispersal type and changes in percent forest may be spurious. Species composition of the litter/soil seed bank may more accurately reflect the dispersal of seeds since the emergence of stems may depend on environmental factors in plots (Matlack 1993, Schupp 1995). I predicted that increased dispersal should translate into increased

disparity between the species pools of the soil seed bank and aboveground stems. I therefore predicted that for animal-dispersed species the similarity between the species composition of the soil seed bank and the species composition of aboveground stems at sampling sites within a landscape will increase with decreasing forest cover in the landscape. For wind-dispersed species I predicted a decrease in the similarity between seed bank and aboveground stem species pools with decreasing forest cover in the landscape since dispersal ability of these species should increase. Finally, if there is differential dispersal of animal and wind-dispersed species with changing forest cover in the landscape, this should be intensified by a large-scale disturbance that further reduces forest cover.

CHAPTER 2

CHANGES IN THE STEM DENSITY OF WOODY PLANTS WITH DIFFERENT SEED DISPERSAL MECHANISMS ALONG A FOREST COVER GRADIENT

2.1 CHAPTER SUMMARY

Seed dispersal allows plants to move greater distances than is possible by vegetative reproduction alone, and is an important consideration in the large-scale spatial dynamics of plant populations. Seed dispersal direction and distance depend on the interaction between landscape structure and seed dispersal mechanism. I hypothesized that landscapes with less forest cover should have lower densities of animal-dispersed plants (i.e., decreased landscape connectivity for animal dispersers) and higher densities of wind-dispersed plants (i.e., fewer barriers to wind movement) than landscapes with more forest cover. I sampled woody plant stem densities in 10 vegetation plots in each of 29 1-km² sample landscapes, along a gradient of decreasing forest cover. Plots were located in forest interior, forest edge, and old field/fencerow habitats.

I found an increase in the mean stem density of animal-dispersed stems with decreasing forest cover in the landscape ($r^2 = 0.44$), and no change in the mean stem density of wind-dispersed species. These relationships appear to be a reflection of i) increasing stem density of animal-dispersed species in forest edge habitat with decreasing landscape-scale forest cover and ii) no change in the stem density of wind-dispersed

species in any of the 3 habitat types surveyed. I speculate that reduced forest cover in the landscape causes an increase in dispersal of animal-dispersed woody species into forest edge habitats. I also speculate that, holding other factors constant, the changes in stem density I observed along the forest cover gradient may be seen over time in a single landscape when forest cover is removed.

2.2 INTRODUCTION

Empirical and modelling studies suggest the importance of seed dispersal in determining the distribution and abundance of plants in landscapes where habitat loss has occurred (e.g., Middleton and Merriam 1983, Gibson et al. 1988, Mladenoff et al. 1993, Lavorel et al. 1995, Matlack 1993 and 1994a, Malanson 1996, Grashof-Bokdam 1997, Sarlöv Herlin and Fry 2000). Since seed dispersal allows plants to move greater distances than is possible by vegetative reproduction alone (Johnson et al. 1981, Holt et al. 1995), it is an important consideration in the spatial dynamics of plant populations at large spatial scales (Matlack 1994a, Grashof-Bokdam 1997, Cain et al. 1998, Sarlöv Herlin and Fry 2000). Some studies have even suggested that the spatial arrangement of plant species and the community dynamics within remaining forest fragments are wholly dependent upon exogenous seed sources (Johnson et al. 1981, McClanahan 1986). How seed dispersal is affected by habitat loss and fragmentation depends on the spatial pattern and the structural complexity of the remaining vegetation (McDonnell and Stiles 1983, Houle and Payette 1990, Santos and Telleria 1994, Harvey 2000). Seed dispersal distance and

direction depend on the interaction between changes in the landscape and the seed dispersal mechanism (Masaki et al. 1994, Malanson and Armstrong 1996, Grashof-Bokdam 1997).

For animal-dispersed woody plant species in temperate forests, seed retention time is a function of animal physiology, morphology, and behavior (Stiles 1992). However, at a landscape scale, the dispersal distance of animal-dispersed seeds will also depend on the ability of animal seed dispersers to move through the landscape. Differences in the amount of appropriate habitat remaining in a landscape can affect the ability of animals to move from one habitat patch to another due to a possible reduction in the connectivity of the landscape for those dispersers (Taylor et al. 1993). This reduction in connectivity results from 3 factors related to habitat loss: i) fewer habitat patches in the landscape resulting in greater distances between patches; ii) fewer movement corridors between remaining habitat patches; and iii) the matrix between habitat patches is not conducive to movement of animals (Fahrig and Merriam 1985, Henein et al. 1998, Bennett 1999). A reduction in the movement of animal seed dispersers could result in a reduction in the abundance of animal-dispersed woody species in the landscape.

For wind-dispersed seeds the removal of vegetation can eliminate barriers to dispersal since vegetation can block air movement and reduce wind speeds (Johnson 1988, Matlack 1989) and a loss of forest cover greatly increases the potential distances that seeds can travel (see Matlack 1989, Houle and Payette 1990, Foré et al. 1992, Young

and Merriam 1994). A reduction in the size of forest fragments may increase dispersal of wind-dispersed seeds, since smaller forest fragments may have fewer barriers to air movement and, therefore, less resistance to seed movement within forest fragments (see Matlack 1989). Therefore, removal of forest could result in an increase in the dispersal distances of wind-dispersed species and a greater probability of movement within or between remaining forest in a landscape (Howe and Smallwood 1982, Portnoy and Willson 1993). This increase in movement would increase the abundance of wind-dispersed stems throughout the landscape.

The purpose of this study was to determine whether the amount of forest cover in a landscape affects the densities of animal and wind-dispersed woody plant species. I predicted that along a gradient of decreasing percent forest cover, the mean stem density of species with animal-dispersed seeds in the landscape would decrease, due to decreased landscape connectivity for animal seed vectors (Grashof-Bokdam 1997, Sarlöv Herlin and Fry 2000). Conversely, the mean stem density of wind-dispersed species in the landscape should increase as the percentage of forest cover decreases, since a decrease in forest cover will mean fewer barriers to wind movement (Houle and Payette 1990) and increased dispersal throughout the landscape.

2.3 METHODS

2.3.1 STUDY SITES

Stem counts were conducted from June 1997 to August 1997 in 29 non-overlapping 1-km² agricultural landscapes in the Ottawa, Ontario region (Fig. 2.1). The locations of the 29 landscapes were spread out over approximately 290,000 hectares. The use of 1-km² landscapes was based on the potential seed dispersal distances of forest tree and shrub species included in this study, as modelled by Ribbens et al. (1994) and revealed in a literature survey by H. Damman (pers. comm.; later published in Cain et al. 1998). I surveyed only those landscapes where deciduous forest was the dominant forest cover type. Dominant forest canopy and subcanopy species in the sample landscapes included *Acer rubrum* L. (Red Maple), Sugar Maple, *Fraxinus americana* L. (White Ash), *Fraxinus pennsylvanica* Marsh. (Green Ash), *Ostrya virginiana* (Mill.) K. Koch (American Hophornbeam), *Populus tremuloides* Michx. (Quaking Aspen), *Tilia americana* L. (American Basswood), and *Thuja occidentalis* L. (Eastern White-cedar) (see Table 2.1).

The 1-km² landscapes were chosen to represent a wide range of percent forest cover. Landscape boundaries were assigned using a 1-km UTM grid (Universal Transverse Mercator, North American Datum 1927) and the percentage of forest cover in each landscape was then estimated using unclassified Russian MK-4 satellite images (7.5 m x 7.5 m ground pixel size; 3 spectral bands: green, red, near infra-red; courtesy of Parks Canada; photos taken 21 May, 1991; see King et al. 1999) and digital 1:50,000 topographic

maps (National Topographic Data Base, Geomatics Canada). The ArcView (ArcView 3.2, ESRI, Redlands, CA) and MapInfo (MapInfo Corp., Troy, NY) Geographical Information System (GIS) software programs were used to estimate forest cover using both the topographic maps and the satellite imagery. For the purposes of this study, forest cover was identified as areas represented by vegetation polygons on the digital topographic maps. I estimated the amount of forest cover in the landscape using the vegetation polygons from the 1:50,000 topographic maps. These estimates were then corrected using the unclassified satellite image to remove areas not characterized by continuous overstory (e.g., fencerows, ditch margins, and old fields containing a few mature shrubs and trees). During site visits, landscapes were also ground-truthed to further assess whether my initial determinations of areas with continuous overstory in the landscape were reasonable. My estimates of forest cover for the twenty-nine landscapes ranged from 7% to 93% (Table 2.1). Qualitative comparisons of available air photos and topographic maps of the landscapes show that, for most of the landscapes used in this study, there has been relatively little change in forest boundaries over the past 25-30 years and that the boundaries of vegetation polygons from the topographic maps closely match existing forest boundaries.

2.3.2 MEAN STEM DENSITY

Within each landscape, stem counts were conducted in 10 vegetation-sampling plots, randomly placed in forest edge, forest interior, and old field/fencerow habitats in the landscape. Forest edge was defined as forest < 50 m from nonforest (see Matlack

1993, 1994b). I did not sample wetlands or any area that had been subject to human-related disturbance within at least two years prior to the stem counts. During the random placement of plots, those plots initially located in disturbed areas were relocated to the nearest undisturbed location.

I used a nested sampling plot design; two 1-m² quadrats for counting seedlings were placed within a 6.25-m x 12.5-m plot for counting and identifying stems <10 cm diameter at breast height (dbh) (but > 1 m in height), which was in turn nested within a 12.5-m x 25-m plot for counting stems $\geq$ 10 cm dbh (see Fig. 2.2: plots modified from a strip transect design described in Levenson (1981)). Narrow rectangular plots were used because many nonforest plots were located in, or along, narrow linear features, e.g., fencerows, ditches, and narrow riparian zones.

Using seed morphology and seed dispersal classifications from a number of sources (Schopmeyer 1974, Barnes and Wagner 1981, Soper and Heimberger 1982, Preston 1989, Burns and Honkala 1990, Cain et al. 1998, Sutherland et al. 2000), each species was assigned to one of two dispersal categories: animal-dispersed species or wind-dispersed species. The wind-dispersed category included both wind- and gravity-dispersed species, i.e., species that lack structures for wind-dispersal but are not animal-dispersed. All classifications were unambiguous except for *Tilia americana* L. *Tilia* is primarily gravity-dispersed, although there is evidence of secondary dispersal by animals (Burns and Honkala 1990). I classified it as a wind-dispersed species.

The mean stem density per plot of each dispersal type in a landscape was estimated by summing all stems of a particular dispersal type that were counted in a sampling plot (includes stems in all three size classes), and dividing by 10 (the number of sampling plots in the landscape). Mean stem densities were also calculated for each of the 3 habitat types (forest edge, forest interior, and old field/fencerow), where the stem total for a habitat type in a landscape was divided by the number of plots of that habitat type in that landscape. The combination of size/age classes into a single density measure may be problematic. The abundance of large stems may more closely reflect the effects of environmental factors on growth and mortality, while seedling abundance may be a better reflection of dispersal events (see Section 3.5). I felt that for the purposes of this study, differences in the mean stem density (for all size/age classes) and percent forest cover relationship between the two dispersal types would suggest some effect of dispersal. If seed dispersal mechanism was not an important factor in the response of woody plant species to changes in percent forest cover, then I would not expect to see a differential response.

Simple linear regression analyses were used to test for significant relationships between the mean stem density of the two dispersal types and percent forest cover. Simple linear regression models were also used to determine whether the relationships between the mean densities of animal- and wind-dispersed species and percent forest cover differed among habitat types. In instances where the assumptions of the analysis of variance were not met, Spearman's rank correlation was used instead of linear regression.

2.3.3 OTHER SPECIES CHARACTERISTICS

I was also concerned with the possibility of spurious relationships between seed dispersal mechanism and the amount of landscape forest cover. Other life history characteristics of a species may be associated with a particular mode of seed dispersal (Sutherland et al. 2000). If these associated characteristics are related to seed germination, seedling establishment, and the vegetative regeneration of a species, then I may find spurious results with regard to the relationship between seed dispersal mechanism and the amount of forest cover in a landscape. In an attempt to compensate for this problem, I decided to examine whether or not there were associations between the dispersal mode of the species in the sample landscapes and other life history characteristics that might affect stem distributions within a landscape.

First, species were assigned to one of three general habitat categories (HABITAT): forest, open field, and forest/open (Barnes and Wagner 1981, Soper and Heimberger 1982, Preston 1989, Burns and Honkala 1990, Sutherland et al. 2000). Species included in the forest/open category are those species found in both forest and open field habitats and therefore appear to have a wider range of habitat requirements. It should be noted that the habitat characteristic is an amalgamation of a number of species life history characteristics related to reproduction/regeneration, resource requirements, and growth. Some individual life history characteristics are, in some instances, inconsistent across all members of a habitat category. For example, *Betula papyrifera* Marsh. (Paper Birch) is found primarily in forest habitat and was classified as such.

However, it is also a forest gap specialist and its seeds do not germinate in shaded conditions unlike many other species in the forest category. Therefore, I felt it would be appropriate to include two other life history characteristics that may influence the regeneration and stem abundance of species in the study region: shade tolerance and the most common method of stem regeneration for a species.

I assigned each species to one of three shade tolerance classes: shade tolerant (shade), moderately shade tolerant (modshade), and shade intolerant (no shade) (Barnes and Wagner 1981, Soper and Heimberger 1982, Preston 1989, Burns and Honkala 1990, Sutherland et al. 2000). I defined regeneration as an increase in the number of stems through both sexual and asexual reproduction. This definition is appropriate since I measured stem density, and did not distinguish between genets (stems produced through seed germination and seedling establishment) and ramets (stems produced by cloning). Species were classified by their primary method of regeneration, (i) production of genets through seeds (seed), (ii) production of ramets through vegetative growth (root sprouting and sprouting from stems and branches (clonal) (Sutherland et al. 2000), or (iii) production of both genets and ramets, i.e., both types of reproduction contribute significantly to stem regeneration (seed/clonal) (Sutherland et al. 2000). Since many plant species utilize both forms of regeneration under certain conditions or at various times during their life cycle, this categorization is not absolute. but indicates the main mode of regeneration for each species.

G-tests of independence were conducted to determine if there were associations between the mode of seed dispersal and habitat, shade tolerance and mode of reproduction, for species in the sampled landscapes. Again, any such relationships would indicate that relationships between the density of stems of a particular dispersal type and percent forest cover could be spurious. *A posteriori* tests were used to determine which classes (columns or rows in the contingency table) were responsible for a lack of independence between variables. The class with the largest total chi-square value (sum of cell chi-square values across a single row or column) was removed from the contingency table and then *G* was recalculated. If *G* was no longer significant, then it was assumed that the class removed from the table was responsible for the lack of independence between the variables.

2.3.4 CANOPY COVER AND EDGE STRUCTURE

In addition to species attributes, there are plot attributes that might cause spurious relationships. Overhead canopy cover may influence seed germination and seedling establishment since changes in the amount of canopy cover may mean changes in light availability. If the degree of canopy cover in the plots changes with forest cover in the landscape, and if dispersal mechanism is related to canopy cover, there is the possibility of a spurious relationship between landscape forest cover and dispersal mechanism.

I used a "sight tube" to evaluate the amount of canopy cover at each plot (James and Shugart 1970). The sight tube was a 30-cm x 5-cm plastic tube with wire crosshairs

fastened at one end of the tube. Starting at the center of each plot, the observer took two steps north, held the tube directly above my head with the long axis of the tube perpendicular to the ground, and then looked through the tube. If any vegetation (e.g., branches, stems, and leaves) was sighted where the crosshairs intersected, then the observation was scored as a 'hit'. If no vegetation was sighted, then the observation was scored as a 'miss'. This was repeated nine more times along the north transect. I repeated this procedure for each of the other three cardinal directions (West, East, and South) giving a total of 40 observations for each plot. The canopy cover index for a plot was the total number of 'hits' per plot. I then calculated mean canopy cover indices for each habitat type in each landscape, and tested for correlations between the mean cover index for each habitat type, and percent forest cover.

A second plot attribute that may be related to forest amount in the landscape is the structural complexity (stem density and width) of forest edges. Loss and fragmentation of mature forest may increase the density of subcanopy stems within the remaining forest, due to greater lateral penetration of light into forest patches at the edge (Levenson 1981, Matlack 1994b). Therefore, there could be a negative correlation between percent forest cover in the landscape and the structural complexity of vegetation in forest edge plots. Two studies have shown that the numbers of animal-dispersed plant species in forest edges are often associated with edge structure (Kupfer and Runkle 1996, Sarlöv Herlin and Fry 2000). For example, Sarlöv Herlin and Fry (2000) found that animal-dispersed species were more commonly associated with edges that were wide (≥ 10 m) and had

relatively high shrub and sapling densities. Therefore, if I found a relationship between edge complexity and forest cover in the sampled landscapes, this could result in a spurious relationship between forest cover and dispersal mechanism.

I assigned the forest-nonforest interface closest to each forest edge plot one of three values based on its structural complexity (modified after Matlack (1993) and Sarlov Herlin and Fry (2000)). Edges that were not clearly defined (abutted old fields) with a high density of shrub and sapling cover had the greatest structural complexity and were assigned an index value of 3. Distinct edges with a closed side canopy were assigned an index value of 2. Finally, those forest edges that were distinct but with no side canopy were assigned an index value of 1. For each landscape I then calculated a mean structural complexity index for forest edge plots. I then tested for a correlation between percent forest cover and the mean structural complexity index across landscapes.

2.4 RESULTS

In all sampling plots combined I counted and identified 19,895 stems from 87 woody species (Table A.1). For all habitats combined, the relationship between the mean stem density for entire 1-km² landscapes and percent forest cover was not as predicted (Fig. 2.3). The mean stem density of animal-dispersed stems increased with decreasing percent forest cover in the landscape ($r^2 = 0.44$). There was no significant relationship between the density of wind-dispersed stems and percent forest cover in the landscape (Fig. 2.3). In separate analyses of the 3 habitat types, there was a significant increase in

mean stem density of animal-dispersed species in forest edge habitat with decreasing forest cover in the landscape (Fig. 2.4). For forest interior and old field/fencerow habitats there were no significant changes in stem density with decreasing percent forest cover for either dispersal type (Figs. 2.5 and 2.6).

There was a significant lack of independence between the seed dispersal mechanism for a species and two of the other three life history characteristics used in the study (Table 2.2). First, for species in the study landscapes, there appears to be a lack of independence between seed dispersal mechanism and the habitat it is commonly associated with (Table 2.2). Based on an *a posteriori* test, I conclude that the lack of independence is due primarily to the forest/open (habitat generalist) category. More animal-dispersed species than expected are considered to be forest/open species while fewer wind-dispersed species than expected are species commonly found in both forest and open field habitats. Second, based on a *G* test using dispersal type and shade tolerance, and the subsequent *a posteriori* test, I concluded that more animal-dispersed species than expected were moderately shade tolerant with fewer wind-dispersed species than expected being moderately shade tolerant (Table 2.2). There was no association between seed dispersal mechanism and whether a species primary method of regeneration is sexual or asexual.

I observed no significant correlations between the mean canopy cover index and percent forest cover for forest edge or old field/fencerow habitats (Fig. 2.7). For forest interior habitat there was a significant negative correlation, i.e., canopy cover in forest

interior plots increased with decreasing amount of forest in the landscape (Fig. 2.7). For all forest edge plots the mean edge structural complexity index was 1.87 ± 0.52 ($\bar{x} \pm 1$ SD). There was no significant relationship between the mean forest edge structural complexity index for each landscape and percent forest cover (Fig. 2.8).

2.5 DISCUSSION

Along a gradient of decreasing forest cover, I found an increase in the mean density of animal-dispersed stems and no change in the mean stem density of wind-dispersed species (Fig. 2.3-2.6), at the scale of 1-km² landscapes. These results appear to be a reflection of 1) increasing stem density of animal-dispersed species in forest edge habitat with decreasing percent forest cover (Fig. 2.3) and 2) no change in the stem density of wind-dispersed species in any of the 3 habitat types surveyed (Figs. 2.3-2.6). Even though the direction of the relationship for animal-dispersed species was opposite to my prediction, it provides support for the idea that landscape-scale processes can affect densities of woody plants at the local plot scale. In the statistical model, 44 percent of the total variation in mean stem density of animal-dispersed species can be explained by changes in the percent forest cover in the sampled landscapes. Considering the diversity of species represented in this broad dispersal category (Table A.1) and the large number of environmental factors and life history traits related to the successful establishment of seedlings, this result seems ecologically significant. I would have expected a relatively low amount of variance in mean stem densities to be explained by seed dispersal alone.

Are differences in seed dispersal mechanisms (wind vs. animal) the primary factor responsible for the explained variance in the statistical models or is the relationship due to other factor(s) related to both seed dispersal mode and forest cover? In the analyses of such possible factors, I found that animal-dispersed species in the study region tend to be species that are found in both forest and open habitats (generalist species). They also tend to be moderately shade tolerant (Table 2.2). It seems unlikely that stem densities in forest edges for such generalist species would be related to forest cover. Therefore, it is unlikely that these factors produced a spurious relationship between dispersal mode and forest cover in forest edges. Neither animal nor wind-dispersed species in the study landscapes had a greater propensity for asexual reproduction over the other dispersal group (Table 2.2), suggesting that regeneration mode was also not a factor. I also observed no significant relationships between percent forest cover and either canopy cover in edge plots or edge structural complexity (Figs. 2.7 and 2.8), indicating that these factors cannot explain the result for animal-dispersed stems.

The analyses of these other factors suggest that the correlation is not spurious. A review of the effects of habitat loss on species diversity (Andrn 1994), found an increase in the diversity and relative abundance of edge and habitat generalist species in landscapes where habitat loss and fragmentation has occurred. In agricultural landscapes, McAllister (1996) also found an increase in the number of forest edge and generalist bird species in the landscape as agricultural intensity increased (with a corresponding decrease in forest cover). While an increase in the number of these species does not necessarily

mean a greater number of individuals, one might assume a greater proportion of individuals in the landscape moving between nonforest and forest edge (Wegner and Merriam 1979). McDonnell and Stiles (1983) also suggest that avian seed dispersers foraging in nonforest habitats seek out forest edge habitat because the vegetation structure provides perching sites. Seeds are then deposited in this habitat by these dispersers, resulting in a greater movement of seeds from nonforest to forest edge habitat (Peterson and Carson 1996, Sarlöv Herlin and Fry 2000). Therefore, I speculate that an increase in the stem density of animal-dispersed stems with decreasing forest cover in the landscape is due to an increase in the movement of seed dispersers into forest edge habitat from nonforest habitat, corresponding with an increase in nonforest habitat in a landscape. This speculation is evaluated further in Chapter 3.

Few studies have looked at plant distribution and density in relation to landscape composition and structure at a large spatial scale and across a variety of woodlot and stand sizes (Grashof-Bokdam 1997). Fewer still have included non-forest habitat (Fritz and Merriam 1993, Sarlöv Herlin and Fry 2000). Even using a very coarse division of all woody plants into only two types, I found that I was able to explain 44 percent of the variation in animal-dispersed woody plant density in forest edges, using only the amount of forest cover in the landscape (Fig. 2.5). This suggests that some important factor(s) affecting dispersal operate at a landscape scale, i.e., at a scale larger than the stand or woodlot (see Cain et al. 1998, Grashof-Bokdam 1997). For animal-dispersed species, dispersers can move beyond stand/habitat boundaries (Myster and Pickett 1993).

Disturbances influencing seed dispersal can also operate at spatial scales larger than the mean dispersal distances of many plant species (Santos and Telleria 1994, Martinez del Rio *et al.* 1996). A landscape perspective is therefore necessary to understand how dispersal affects the distribution and abundance of woody plant species at local scales.

Of course, there are processes besides dispersal that affect plant abundance and diversity (Matlack 1993, Myster 1993, Myster and Pickett 1993, Ribbens *et al.* 1994, Bazzaz 1996, Brockway 1998). However, the results suggest that seed dispersal through the landscape, at least for animal-dispersed species, is an important factor in determining the abundance and distribution of these species. I also speculate that, holding other factors constant, the changes in stem density I observed in the landscapes along the forest cover gradient would be seen over time in a single landscape as forest cover is removed. With the loss of forest in a landscape I predict an increase in the stem density of animal-dispersed species in forest edge.

Table 2.1: Summary information for each of the 29 1-km² landscapes sampled during the summer of 1997 (June-August). Landscape numbers correspond with numbers in Figure 1. Determination of the three most abundant species in each landscape is based on stem counts for the ten vegetation plots in each landscape.

LANDSCAPE	% FOREST COVER	NUMBER OF PLOTS			3 most abundant species
		FOREST EDGE	FOREST INTERIOR	OLD FIELD- FENCEROW	
1	14	5	4	1	<i>Acer saccharum</i> / <i>Acer rubrum</i> / <i>Fraxinus pennsylvanica</i>
2	32	7	0	3	<i>Thuja occidentalis</i> / <i>Abies balsamea</i> / <i>Fraxinus pennsylvanica</i>
3	17	6	0	4	<i>Fraxinus americana</i> / <i>Tilia americana</i> / <i>Ostrya virginiana</i>
4	34	4	6	0	<i>Acer saccharum</i> / <i>Ostrya virginiana</i> / <i>Thuja occidentalis</i>
5	36	4	4	2	<i>Acer saccharum</i> / <i>Fraxinus americana</i> / <i>Thuja occidentalis</i>
6	40	3	6	1	<i>Ostrya virginiana</i> / <i>Acer saccharum</i> / <i>Tilia americana</i>
7	22	4	3	3	<i>Fraxinus pennsylvanica</i> / <i>Rhamnus cathartica</i> / <i>Quercus alba</i>
8	67	3	6	1	<i>Abies balsamea</i> / <i>Ostrya virginiana</i> / <i>Acer rubrum</i>
9	31	2	3	5	<i>Ostrya virginiana</i> / <i>Acer saccharum</i> / <i>Tilia americana</i>
10	23	1	7	2	<i>Acer saccharum</i> / <i>Ostrya virginiana</i> / <i>Tilia americana</i>
11	86	4	6	0	<i>Acer saccharum</i> / <i>Pinus strobus</i> / <i>Populus grandifolia</i>
12	22	3	1	6	<i>Fraxinus pennsylvanica</i> / <i>Acer rubrum</i> / <i>Acer saccharinum</i>
13	11	2	1	7	<i>Fraxinus americana</i> / <i>Fraxinus pennsylvanica</i> / <i>Acer saccharinum</i>
14	21	2	6	2	<i>Acer saccharum</i> / <i>Fraxinus pennsylvanica</i> / <i>Populus tremuloides</i>
15	13	2	3	5	<i>Acer saccharinum</i> / <i>Fraxinus pennsylvanica</i> / <i>Acer rubrum</i>
16	12	1	2	7	<i>Fraxinus pennsylvanica</i> / <i>Populus tremuloides</i> / <i>Zanthoxylum americana</i>
17	25	5	0	5	<i>Acer saccharum</i> / <i>Fagus grandifolia</i> / <i>Ostrya virginiana</i>
18	41	6	1	3	<i>Acer saccharum</i> / <i>Fraxinus americana</i> / <i>Ostrya virginiana</i>
19	7	4	0	6	<i>Acer saccharum</i> / <i>Tilia americana</i> / <i>Ostrya virginiana</i>
20	8	3	0	7	<i>Fraxinus pennsylvanica</i> / <i>Ulmus americana</i> / <i>Tilia americana</i>
21	8	3	0	7	<i>Fraxinus pennsylvanica</i> / <i>Ulmus americana</i> / <i>Picea glauca</i>
22	59	3	5	2	<i>Acer saccharum</i> / <i>Fagus grandifolia</i> / <i>Fraxinus pennsylvanica</i>
23	46	1	5	4	<i>Fraxinus pennsylvanica</i> / <i>Populus tremuloides</i> / <i>Acer rubrum</i>
24	13	2	0	8	<i>Acer rubrum</i> / <i>Ulmus americana</i> / <i>Populus tremuloides</i>
25	76	3	5	2	<i>Acer saccharum</i> / <i>Thuja occidentalis</i> / <i>Fraxinus pennsylvanica</i>
26	80	3	6	1	<i>Ostrya virginiana</i> / <i>Thuja occidentalis</i> / <i>Acer saccharum</i>
27	71	2	8	0	<i>Quercus rubra</i> / <i>Pinus strobus</i> / <i>Acer saccharum</i>
28	60	7	0	3	<i>Acer saccharum</i> / <i>Ostrya virginiana</i> / <i>Fagus grandifolia</i>
29	95	5	4	1	<i>Thuja occidentalis</i> / <i>Ostrya virginiana</i> / <i>Acer saccharum</i>
Total plots		100	92	98	

Table 2.2: Tests of independence (G tests) between seed dispersal mechanism and three other characteristics: habitat type (HABITAT), Shade tolerance (SHADE), and primary method of reproduction (REGENERATION). Number of species is the total number of woody species encountered in the study region (all sample landscapes). Numbers in parentheses are the expected values. *A posteriori* tests were conducted by removing the category with the greatest G value and then rerunning the G test. Resulting G values associated with an $\alpha > 0.05$ meant that the removed category was primarily responsible for the association between the life history characteristic and seed dispersal type.

<u>Characteristic</u>	<u>Number of species</u>		<i>G</i>	<i>p</i>	<u>a posteriori</u>	
	Animal-dispersed	Wind-dispersed			Class removed	<i>p</i>
HABITAT						
forest	17 (22)	24 (19)	7.094	0.029	forest/open	0.200
open field	16 (15)	12 (13)				
forest/open	14 (10)	4 (8)				
SHADE						
shade	9 (11)	12 (10)	11.444	0.003	modshade	0.656
modshade	27 (20)	9 (16)				
no shade	11 (16)	19 (14)				
REGENERATION						
seed	9 (10)	10 (9)	0.468	0.791		
clonal	7 (7)	5 (5)				
seed/clonal	31 (30)	25 (26)				

Figure 2.1: Location of 1-km² landscapes used in the study (A) and an example of a single 1-km² landscape (B). In both Figure 2.1A and Figure 2.1B, dark gray polygons (areas) represent forest cover, light gray polygons represent water (lakes, ponds, rivers, and ditches), solid black polygons represent urban areas, and black squares (outlines) represent the boundaries of the 1-km² landscapes. In Figure 2.1B, the solid black circles show the locations of the 10 sampling plots (see Fig. 2.2) within landscape 17. In Figure 2.1A the numbers correspond to landscape descriptions in Table 2.1.

Figure 2.2: Nested design of vegetation sampling plots. The 12.5 x 25.0 m plot was used to count and identify stems ≥ 10 cm in diameter (white); the 6.25 x 12.5 m plot was used to count stems < 10 cm in diameter but > 1 m in height (gray); the 1.0m quadrats were used to count woody seedlings, i.e., stems < 1 m in height (black).

Figure 2.3. Mean number of stems per plot (DENSITY; see section 2.3.2) for all habitats combined vs. percent forest cover in the landscape. ○ = wind-dispersed DENSITY; — — = relationship between wind-dispersed DENSITY and percent forest cover [$\text{Log}_{10}(\text{DENSITY}) = 0.0016(\text{PERFOR}) + 1.5412$; $r^2 = 0.0659$; $df = 1, 27$; $p = 0.1786$]. ■ = Animal-dispersed DENSITY; — = relationship between animal-dispersed DENSITY and percent forest cover [$\text{Log}_{10}(\text{DENSITY}) = -0.009(\text{PERFOR}) + 1.6239$; $r^2 = 0.4415$; $df = 1, 27$; $p < 0.0001$].

Figure 2.4: Mean number of stems per plot (DENSITY; see section 2.3.2) for forest edge habitat only vs. percent forest cover in the landscape. A. Relationship between wind-dispersed DENSITY in forest edge and percent forest cover [DENSITY = $-0.2537(\text{PERFOR}) + 63.368$; $r^2 = 0.1026$; $df = 1, 27$; $p = 0.0903$]. B. Relationship between animal-dispersed DENSITY in forest edge and percent forest cover [$\text{Log}_{10}(\text{DENSITY}) = -0.0104(\text{percent forest}) + 1.5059$; $r^2 = 0.2372$; $df = 1, 27$; $p = 0.0074$]. Only the relationship for animal-dispersed stems is significant at $\alpha = 0.05$.

A. Wind-dispersed

B. Animal-dispersed

Figure 2.5: Mean number of stems per plot (DENSITY; see section 2.3.2) for forest interior habitat only vs. percent forest cover in the landscape. A. Relationship between mean wind-dispersed stem density in forest interior and percent forest cover [DENSITY = $-0.0446(\text{percent forest}) + 57.161$; $r^2 = 0.0029$; $df = 1, 19$; $p = 0.8165$]. B. Relationship between mean animal-dispersed stem density in forest interior and percent forest cover [$\text{Log}_{10}(\text{DENSITY} + 1) = -0.0042(\text{percent forest}) + 1.2295$; $r^2 = 0.0546$; $df = 1, 19$; $p = 0.3081$]. Neither relationship is significant at $\alpha = 0.05$.

A. Wind-dispersed

B. Animal-dispersed

Figure 2.6: Mean number of stems per plot (DENSITY; see section 2.3.2) for old field/fencerow habitats only vs. percent forest cover in the landscape. A. Relationship between mean wind-dispersed stem density in old field/fencerow habitats and percent forest cover [Spearman's $r = 0.07391$; $N = 26$; $p = 0.7197$]. B. Relationship between mean animal-dispersed stem density in old field/fencerow habitats and percent forest cover [$\text{Log}_{10}(\text{DENSITY} + 1) = -0.0044(\text{PERFOR}) + 1.483$; $r^2 = 0.035$; $df = 1, 24$; $p = 0.3603$]. Neither relationship is significant at $\alpha = 0.05$.

A. Wind-dispersed

B. Animal-dispersed

Figure 2.7: Correlations between the mean canopy cover index per plot (MEAN COVER INDEX; see section 2.3.4) and percent forest cover (PERFOR) for each of the 3 habitats: A. Forest interior; B. Forest edge; C. Old field/fencerow. Only the forest interior correlation was significant at $\alpha = 0.05$.

A. Forest interior

B. Forest edge

C. Old field/fencerow

Figure 2.8: Correlation between mean edge structural complexity per plot (MEAN EDGE COMPLEXITY; see section 2.3.4) and percent forest cover. The relationship was not significant at $\alpha = 0.05$.

CHAPTER 3

THE INFLUENCE OF HABITAT ON THE DIFFERENTIAL DISPERSAL OF ANIMAL- AND WIND- DISPERSED WOODY PLANT SPECIES ALONG A FOREST COVER GRADIENT

3.1 CHAPTER SUMMARY

A reduction of forest cover in the landscape can enhance or hinder the movement of seeds across the landscape (i.e., a change in connectivity of the landscape) and affect the ability of woody plant species to colonize existing or newly formed habitat. Changes in landscape connectivity are likely to be different for wind- and animal-dispersed species and will differ depending on the cover type in which the seeds originate and the destination habitat. Therefore, I predicted that the effect of percent forest cover on mean stem and mean seed densities in the landscape should depend on dispersal type. In other words, I predicted a significant interaction between dispersal type (DISPERSAL) and percent forest cover in the landscape (PERFOR). I also hypothesized that the effect of percent forest cover, as well as the effect of the interaction term (DISPERSAL*PERFOR) would depend on the habitat in which the seed originated and the habitat in which it was deposited (i.e., changes in the differential dispersal of animal v. wind-dispersed species with different habitats). Using stem and seed counts from 290 sampling plots in 29 1-km² landscapes, I constructed general linear models for each of

twelve combinations of seed source habitat and destination habitat (Forest-Forest, Forest-Open, Open-Forest, and Open-Open) and plant age categories (seeds, stems, and all stems and seeds combined).

In addition to both seed and stem information from each of the landscapes, I also examined the influence of potentially confounding environmental factors using a similarity index that compares the species pools of seeds and aboveground stems at a site (Jaccard's similarity index). Additional general linear models were run for each of the four habitat categories with the similarity index for each landscape as a response variable in the model.

The results of the general linear models suggest that differential dispersal is only a consideration for open-habitat species being dispersed into forest habitats, with the dispersal of animal-dispersed open-habitat species increasing into forest habitats as percent forest cover in the landscape decreases. I hypothesize that while the dispersal of both animal and wind-dispersed open-habitat species increases with decreasing percent forest cover in the landscape, thick lateral side canopies make the penetration of wind-dispersed seeds into forest habitats difficult.

I speculate that with a removal of forest from the landscape, there should be an increase in the deposition of animal-dispersed seeds from open-habitats into remaining forest patches. I also speculated that because these species are primarily shade intolerant and can remain dormant in the seed bank for long periods of time, additional disturbance

in remaining forest habitat would mean an increase in the seedling establishment of these species.

3.2 INTRODUCTION

Changes in landscape structure can have consequences for the dispersal and movement of organisms within landscapes (Fahrig and Merriam 1985, Taylor et al. 1993, Andrn 1994, Grashof-Bokdam 1997, Bennett 1999). A reduction or complete removal of one or more landscape elements can reduce or hinder the movement of seeds across the landscape (i.e., a reduced connectivity of the landscape) and adversely affect the ability of plant species to colonize existing or newly formed habitat (Malanson and Armstrong 1996, Grashof-Bokdam 1997, Cadenasso and Pickett 2001).

Changes in landscape connectivity are also likely to be different for plant species with different dispersal mechanisms. In the previous study (Chapter 2, see section 2.5), I observed an increase in the mean density of animal-dispersed woody stems in landscapes along a gradient of decreasing forest cover (Fig. 2.3). Therefore, I rejected the initial hypothesis that with decreasing forest cover in the landscape the connectivity of animal-dispersed species will decrease (see section 2.2) and I hypothesized that with decreasing forest cover in the landscape there will be an increase in the connectivity of the landscape for animal-dispersed species. The relationship observed in Chapter 2 accounted for 44% of the variation in the mean stem density of animal-dispersed species, suggesting that dispersal may play a significant role in the distribution of these species at a landscape

scale (Fig. 2.3). Further statistical analyses suggested that this relationship was due to an increase in the movement of animal-dispersed seeds of open-habitat (nonforest) plant species in landscapes with reduced forest cover (see sections 2.4 and 2.5). For wind-dispersed species I had initially hypothesized that a reduction in forest cover would mean fewer barriers to wind movement and increased dispersal of seeds through the landscape. I found no significant relationship (at $\alpha = 0.05$) between the mean stem density of wind-dispersed species in the landscape and percent forest cover (section 2.4 and Fig. 2.3).

The results from Chapter 2, particularly those for animal-dispersed species, suggest that the relationship between the density of animal-dispersed species and percent forest cover in the landscape may depend on the habitat under consideration (forest, edge, or open habitats) and the habitat association of the plant species (forest- or open-habitat species). In landscapes with less forest, the seeds of animal-dispersed forest species are less likely to move greater distances through the landscape and are less likely to be deposited in forest habitats because of decreased connectivity of the landscape for forest-dwelling animal seed dispersers. Therefore, I expect decreased dispersal of forest-habitat animal-dispersed species into forest habitat with decreasing forest cover in the landscape. However, I do not expect changes in the seed dispersal of animal-dispersed forest-habitat species into open habitats since animal seed dispersers of forest habitats may be reluctant to move into, or through, nonforested areas of the landscape (Fahrig and Merriam 1985, Henein et al. 1998). Finally, the deposition of animal-dispersed seeds of open-habitat species into both forest edge and open habitats should increase with decreasing percent

forest cover in the landscape (sections 2.4 and 2.5). In contrast, for wind-dispersed forest species, decreasing forest cover in the landscape should increase dispersal (due to an increase the number of wind barriers) into all habitats in the landscape. See Table 3.1 for a summary of the predictions.

As indicated in Chapter 2, aboveground stems are the combined result of dispersal, germination, and stem establishment. However, the hypotheses above relating landscape-scale forest cover to plant density hinge on dispersal. The potential population density of all life history stages (seeds and all aboveground stems) may better reflect dispersal. In this chapter I use the combined density of aboveground stems and seeds in the seed bank as the response variable.

Another way to test for effects of landscape structure on dispersal is to compare the similarity in species pools between the aboveground stems and the seed bank. If seeds are dispersed widely through the landscape, the species pool in the seed bank at a site will be less similar to the aboveground species pool than when dispersal is limited. See Table 3.1 for specific predictions.

3.3 METHODS

3.3.1 STUDY SITES AND SAMPLING

I conducted stem counts and soil/litter sampling from June 1997 to August 1997 in 290 vegetation sampling plots in 29 1-km² agricultural landscapes in the Ottawa, Ontario region (see Section 2.3.1 for a full description of study landscapes). I assigned

landscape boundaries using a 1-km UTM grid (Universal Transverse Mercator, North American Datum 1927) and I estimated the percentage of forest cover in each landscape using Russian MK-4 satellite images (courtesy of Parks Canada) and topographic maps. I placed sampling plots randomly within landscapes in forest interior, forest edge, fencerow and old field habitats (see section 2.3.2 and Fig. 2.1). For this study I combined forest interior and edge categories into a single forest category and open-habitat plots consisted of old field and fencerow habitats.

To estimate seed density, I combined counts of seeds and seedlings, based on the following rationale. Environmental factors and other life history characteristics of a species influence whether its seeds remain in the seed bank for long periods of time or germinate quickly (Schopmeyer 1974, Mladenoff 1990, Peterson and Carson 1996, Ricard and Messier 1996, Hyatt and Casper 2000). This means that a combination of seeds and seedlings are needed to adequately represent all dispersed seeds. For example, the seeds of *Acer saccharum* Marsh. (Sugar Maple, a wind-dispersed species) can germinate even in the reduced light conditions found under full forest canopy (Canham 1985). With a germination rate of greater than 90%, this species forms a 'seedling bank' as opposed to a seed bank since seedlings can remain suppressed under forest canopy for long periods of time (Burns and Honkala 1990). Simply counting the number of Sugar Maple seeds present in the litter or soil would significantly underestimate the number of Sugar Maple seeds that had been deposited in a plot. Admittedly, I still may have underestimated both seed abundance and the number of species present in the seed

species pool for each of the sampling plots. But given the limitations of a study of this type (e.g., the large sampling effort required to use seed trapping at a landscape scale), this method does provide a better estimate of the abundance and species composition of seeds deposited in a plot than only sampling soil and litter.

I used seedling emergence from litter and soil samples taken at each vegetation sampling plot to estimate the species diversity and abundance of viable seeds in the litter and soil (the following methods have been modified from methods used or reviewed by Thompson and Grime 1979, Pratt et al. 1984, Scheiner 1988, Mladenoff 1990, Warr et al. 1993). Soil and litter samples were taken from 15 random locations in each of the 290 6.25-m x 12.5-m plots using a 4.6-cm diameter x 10-cm hand held soil corer, for a total of 4,350 samples (approximately 2.5 liters of soil/litter per plot) (see Fig. 2.2). The 10-cm core length also included the leaf litter layer. For each plot, I combined seeds from the 15 soil cores into a single sample.

I placed individual soil samples on aluminum trays and left them to dry at room temperature for 3-5 days. Once dry, the samples were put through a coarse mesh sieve (160-mm mesh) to remove sticks, leaves, and rocks. Larger seeds (e.g., acorns, hickory nuts, and large maple samara) were taken from the sieve and put back in the soil sample. I then placed the samples in shallow divided plastic trays (50.8-cm x 25.4-cm x 5.0-cm) with each section of the tray containing the soil from a sampling plot. I put approximately 2.5-3.0 cm of vermiculite in the bottom of each section of the tray and then the soil samples were placed on top of the vermiculite. The trays were then placed in the

greenhouses at Carleton University. Samples were watered daily. A 15-16 hour photoperiod was maintained throughout the study using natural and artificial lighting. I rotated trays bi-weekly to avoid potential effects of non-uniform lighting in the greenhouses. I also placed two trays of sterilized soil in each greenhouse (controls) to monitor seed contamination from sources other than the soil samples. As expected there were no woody seedlings found in the control trays.

As seeds germinated, I counted and identified seedlings to species, then removed the seedlings from the trays. Small seedlings were pulled from the soil (soil on the roots was washed back into the tray). However, I cut larger seedlings with scissors at the base of the stem and placed toothpicks at the stem base to mark the location of each cut stem. In this way, root or stem sprouts were identified and not included in the seedling counts. In instances where I was unable to identify seedlings, the seedlings were carefully transplanted to separate pots and allowed to grow until secondary leaves and other identifiable characteristics appeared. In some instances, identification to species was not possible, in which case I identified the seedling to genus.

Once all the seedlings in a tray had been removed, I waited approximately two weeks to see if any additional seedlings emerged. If no seedlings emerged during that time period, the soil was mixed and I repeated the process. I continued until no seedlings emerged during the two-week period following the mixing of a sample. This took approximately 3-4 months per sample.

Some species require a cold period before seeds will germinate (stratification) (Schopmeyer 1974, Burns and Honkala 1990). Therefore, following the initial 3-4 months in the greenhouse, I removed the soil samples from the greenhouse, dried them at room temperature, and placed them in cold storage (at 4°C) for approximately 4 months. I then repotted the samples and placed them in the greenhouse during the summer/fall of 1998, using the same procedure described above. This allowed the germination of seeds that may have been deposited in the spring and early summer of 1997 and required cold stratification before germinating.

In the sample landscapes, I identified stems to species or genus and counted them in each of the vegetation-sampling plots (10 plots per landscape). Larger stems (> 10 cm) were counted in 12.5-m x 25-m plots surrounding the 6.25-m x 12.5-m plots. Stems <10 cm diameter at breast height (dbh) but > 1 m in height were counted in the same 6.25-m x 12.5-m plots from which the soil samples were taken. Seedlings were counted in 2 1-m quadrats nested within each 6.25-m x 12.5-m plot (see Fig. 2.2 for a diagram of the sampling plot).

3.3.2 ANALYSES

For each sampling plot, I assigned all observed stems and seeds to one of two classes: *seeds* (consisting of both seeds in the litter/soil seed bank and seedlings (stems < 1-m in height)), and *stems* (stems > 1-m in height). I then assigned each woody plant species to one of two dispersal categories: animal-dispersed or wind-dispersed

(DISPERSAL) (see Section 2.3.2) (Schopmeyer 1974, Barnes and Wagner 1981, Soper and Heimberger 1982, Preston 1989, Burns and Honkala 1990, Cain et al. 1998, Sutherland et al. 2000). I also assigned each species to one of two general habitat categories (HABITAT): forest or open habitat (open habitat refers to any nonforest habitat, including both old fields and fencerows) (Barnes and Wagner 1981, Soper and Heimberger 1982, Preston 1989, Burns and Honkala 1990; see section 2.3.3).

Given the nested design of the vegetation sampling plots (Fig. 2.2), to calculate seed and stem densities of each dispersal and habitat type in a landscape, I adjusted the number of seeds and stems to a constant area for each plot. Therefore, the number of seeds observed in the fifteen soil cores (a sampling area of 0.025-m^2 per plot), the number of seedlings observed in the two 1-m quadrats per plot, and the number of stems $< 10\text{-cm}$ dbh but greater than 1-m in height (a sampling area of 78.125-m^2 per plot), were adjusted so that the number of seeds and stems would be the amount expected in a $12.5 \times 25\text{-m}$ plot area (given the number of seeds and stems observed in the smaller plots). I estimated mean seed (seeds and seedlings) and aboveground stem densities for each landscape by summing the adjusted number of seeds and stems of a dispersal type from all vegetation sampling plots of a particular habitat type in that landscape, and dividing by the number of sampling plots of that habitat type in the landscape. I calculated seed and stem densities for forest-habitat species in forest habitat, forest-habitat species in open habitat, open-habitat species in forest habitats, and open-habitat species in open habitats.

I used seed density, stem density, and the density of seeds and stems combined as response variables in general linear models that included the categorical variable for dispersal type (DISPERSAL), as well as the percent forest cover for each landscape (PERFOR). I used four sets of models since there were specific predictions with regard to each dispersal/habitat type. For some species/habitat types I predicted a differential response of animal and wind-dispersed species (see Table 3.1); therefore, I also included the interaction term DISPERSAL*PERFOR. The statistical significance of predictor variables in each of the models was evaluated using Type III sums of squares (SAS 1990).

To test my predictions concerning changes in the similarity between the species composition of the seed species pool (which includes seeds and seedlings, see above) vs. the stem species pool, I used the Jaccard's similarity coefficient (S_j),

$$S_j = \frac{a}{a + b + c} \quad [\text{Eq. 3.1}]$$

where a = number of species co-occurrences in the two species pools, b = number of species in the seed pool but not the stem pool, and c = number of species in the stem pool but not the seed pool (Clifford and Stephenson 1975, Krebs 1999). For each of the 29 landscapes, I calculated the Jaccard's similarity coefficient for each dispersal and habitat type.

I used general linear models with S_j (Jaccard's similarity coefficient) as the response variable and DISPERSAL and PERFOR as predictor variables. Again, I expected differences in the relationship between the similarity index and percent forest cover for the two dispersal types (Table 3.1). Therefore, I included the interaction term DISPERSAL*PERFOR in the models. I also included total species richness (S = number of species for all seeds and stems in the landscape sorted by habitat type) as a covariate in the models to control for any variance in S_j that might be accounted for by differences in species richness between landscapes. I predicted that with increasing species richness in a landscape, S_j values may decrease since the probability of matches between the seed and stem pools should decrease with increasing number of species present.

For all general linear models, if assumptions of analysis of variance were violated, the response variable used in that model was transformed and the analysis was re-run using the transformed response variable. For all but one of the remaining models either Log_{10} or arcsine transformations of the response variables were necessary to effectively reduce heterogeneity of the residual variances.

3.4 RESULTS

I observed 23 species of seeds, 43 species of seedlings, and 86 species of mature stems (Table A.2). *Rubus ideaus* L. (Common Red Raspberry), an animal-dispersed, open-habitat species, accounted for 72% of all seeds (excluding seedlings) recovered

from the litter and soil (Table A.2). Thirteen percent of the seeds recovered were from *Betula alleghaniensis* Britt. (Yellow Birch), a wind-dispersed, forest species (Table A.2).

Eighty-three percent of all seedlings observed in the study plots were wind-dispersed forest species and 93% of all seedlings observed were forest-habitat species (Table A.2). For mature stems, Common Red Raspberry, Sugar Maple, and *Fraxinus pennsylvanica* Marsh. (Green Ash) were the three most abundant stems observed in the study region (Table A.2). Of the five most abundant species of seeds (seeds and seedlings combined) and stems by habitat (Table 3.2), Sugar Maple was the most abundant species as both seeds and stems in forest, while Common Red Raspberry was the most abundant species in both species pools in open habitats. However, while Common Red Raspberry seeds were abundant in forest habitat, Common Red Raspberry stems were not abundant in forest habitat (Table 3.2). While Sugar Maple seeds were relatively abundant in open habitat, Sugar Maple stems were not abundant in open habitat (Table 3.2).

For forest-habitat species in forest habitats, the mean density of stems in the landscape increased with decreasing percent forest cover, while the mean density of seeds in the landscape decreased with decreasing percent forest cover in the landscape (Table 3.4 and Fig. 3.1). The mean density of all forest-habitat stems and seeds in open habitats increased with decreasing percent forest cover in the landscape (Tables 3.4 and Fig. 3.2). For open-habitat species in open habitats, mean stem density, mean seed density and the combined mean density of both stems and seeds all increased with decreasing forest cover in the landscape (Table 3.3 and Fig. 3.3).

Only one of the general linear models had a statistically significant interaction between dispersal type (wind v. animal) and percent forest cover in the landscape (DISPERSAL*PERFOR) (Tables 3.3 and 3.4). For open-habitat species in forest habitats, the mean stem densities of animal-dispersed species increased with decreasing percent forest cover in the landscape while there was a slight decrease in the mean density of wind-dispersed stems with decreasing percent forest cover (Table 3.4 and Fig. 3.4).

Neither PERFOR nor DISPERSAL*PERFOR were statistically significant predictors of the similarity between the stem and seed species pools for any of the species/habitat types (at $\alpha = 0.05$) (see Table 3.3). For forest-habitat species in forest habitat there was a greater mean similarity between the stem and seed species pools of wind-dispersed species than animal-dispersed species (Fig. 3.5). For open-habitat species in open habitats, the general linear model was marginally non-significant ($p = 0.051$) (Table 3.3) with the variable DISPERSAL having $p = 0.019$. For open-habitat species in open habitats, animal-dispersed species have a greater mean similarity index than wind-dispersed species (see Fig. 3.5).

3.5 DISCUSSION

While the variance explained by significant models was relatively large (range of r^2 values: 0.222 – 0.849; $\bar{x} \pm 1$ SE: 0.390 $\pm$ 0.062), few of the predicted relationships were significant (Table 3.3). A set of power analyses were run for each of the models using methods described in Sokal and Rohlf (1995) and Zar (1999) (see Table 3.5). For

the analyses, power was defined as the probability that a statistical test, in this case the F-test used in a general linear model, would correctly reject a null hypothesis when it was false (see Zar 1999). Power values ($1 - \beta$) for the predictor variables used in the analyses were relatively low (range of $1 - \beta$: 0.050 – 1.000; $\bar{x} \pm 1$ SE: 0.380 $\pm$ 0.051). Non-significant relationships consistently had lower power values than significant relationships. The low power values may indicate insufficient sample sizes, i.e., 29 landscapes was too few. Low sample sizes are a problem for many landscape-scale studies where there is a trade-off between the number of landscapes sampled and the ability to adequately sample each landscape (i.e., intensity of sampling effort (number of sample plots) within landscapes) (Brennan et al. in press). For this chapter, as well as Chapter 2, sampling effort within landscapes was an important consideration since the questions addressed by both this chapter and Chapter 2 required sampling in different habitat types across each landscape. Therefore, a study design with fewer sampling points in each landscape, so that more landscapes could have been sampled, would not have been adequate. Since the lack of power is problematic for interpretation of the non-significant relationships, I limit my interpretation of the analyses only to significant relationships.

Overall mean seed density of forest-habitat species in forest habitat decreased with decreasing forest cover in the landscape (Fig. 3.1). For animal-dispersed forest species this is consistent with my prediction (Table 3.1). However, for wind-dispersed forest species I had predicted an increase in the mean seed density with decreasing forest cover

in the landscape due to a decrease in the number of barriers to wind movement of wind (canopy trees) (Table 3.1).

For forest-habitat species, I observed changes in both mean stem and seed densities regardless of dispersal types (Table 3.3 and 3.4). Mean stem densities of forest-habitat species in forest habitats decreased with increasing forest cover in the landscape (Table 3.4 and Fig. 3.1). At first glance, this suggests decreased dispersal of forest species with increasing forest cover in the landscape. However, coupled with an increase in the mean density of seeds of these species in forest habitat (Table 3.4 and Fig. 3.1), the decrease in mean stem density suggests a 'thinning' of stems following seed germination and seedling establishment, i.e., a reduction in stem density due to competition with mature stems for resources, particularly light (Bazzaz 1996, Foré et al. 1997, Kupfer and Kirsch 1998). It is possible that forest patches in agricultural landscapes with a higher percentage of forest cover contain more mature trees and these patches have experienced less human-related disturbance (e.g., commercial and non-commercial wood-cutting) than forest patches in landscapes with less overall forest cover. While larger, more mature trees may have greater mean seed production than smaller, less mature stems, increased competition for resources may mean greater mortality for seedlings and intermediate age classes (Bazzaz 1996, Foré et al. 1997). *Post hoc* analyses did provide some support for this hypothesis. There was a significant positive correlation between the mean dbh of forest stems in a landscape and percent forest cover ($r = 0.518$, $p = 0.004$). There was also a significant negative correlation between the mean density of stems in forest plots

and percent forest cover in the landscape ($r = -0.533$, $p = 0.003$). In landscapes with more forest cover, forest habitats had larger trees at lower densities.

Mean stem densities of forest-habitat species in open habitats increased with decreasing forest cover in the landscape (Table 3.4 and Fig. 3.2). This is consistent with my hypothesis that in landscapes with reduced forest cover, there should be more generalist animals (Wegner and Merriam 1979, Andrén 1994, McAllister 1996; see section 2.5) acting as seed dispersers, moving seeds from forest habitat into adjoining nonforest habitats. This is also consistent with my hypothesis for wind-dispersed species: a decrease in forest cover in the landscape may increase wind speeds in these landscapes and increase the movement of wind-dispersed seeds from forest habitats into nonforest.

In forest habitats the mean stem density of open-habitat animal-dispersed species increased with decreasing forest cover with little or no decrease in the mean stem density of wind-dispersed species (Table 3.4 and Fig. 3.4). This result supports the hypothesis of increased dispersal of open-habitat animal-dispersed species into forest habitat with decreasing forest cover in the landscape which I proposed based on the results from Chapter 2 (see section 2.5). However, I did not observe the predicted increase in stem or seed densities of open-habitat wind-dispersed species with decreasing forest cover (Fig. 3.4). Cadenasso and Pickett (2001) suggest that the seeds of wind-dispersed open-habitat species are less likely to penetrate forest edges than animal-dispersed open-habitat species. Penetration of forest edges may become even more difficult when forest edges are dense (thick lateral canopy with many smaller shrub and subcanopy stems)

(Cadenasso and Pickett 2001). The mean edge structural complexity index for the sample landscapes suggests that forest edges in the landscapes were clearly defined with a dense side canopy (see section 2.3.4). I speculate that although dispersal ability may have increased for wind-dispersed open-habitat species in landscapes with low forest cover, there may have been little penetration of these seeds into forest habitats.

As predicted, the mean stem and seed densities of open-habitat species in open habitats increased with decreasing forest cover in the landscape (Table 3.4 and Fig. 3.3). Therefore, a decrease in the amount of forest cover in the landscape may increase the dispersal ability and connectivity of the landscape for seed dispersing animals of open habitats. For wind-dispersed species, the results support the hypothesis that a more open landscape with fewer barriers to wind movement (fewer canopy trees) increases the dispersal of wind-dispersed open-habitat species. Many of the wind-dispersed open-habitat species (e.g., *Populus*, *Salix*, and *Spiraea* spp.) are small-seeded species (see Soper and Heimberger (1982) and Burns and Honkala (1990)) whose seeds may have greater dispersal distances than some of the much larger wind-dispersed forest species (Sugar Maple for example) (Table A.1). Therefore, increased wind movement in the landscape may mean greater dispersal for these species. Unlike forest patches, open habitats do not have edge boundaries that act as barriers to seed movement.

Overall, mean S_j values were significantly higher for wind-dispersed species than animal-dispersed species across all landscapes (Fig. 3.5). I observed one significant overall model (forest-habitat species in forest habitats) and one marginally non-

significant overall model (open-habitat species in open habitats) with the Jaccard's similarity index (S_j) as a response variable (at $\alpha < 0.05$) (Table 3.3). Both models suggested differences in the mean similarity indices between wind- and animal-dispersed species. For forest-habitat species in forest habitats, there was greater mean similarity for wind-dispersed species than for animal-dispersed species (Fig. 3.5). For open-habitat species in open habitats, the mean similarity index was greater for animal-dispersed species than for wind-dispersed species. Under my original assumption of increasing similarity with decreasing dispersal ability, these results suggest that, in general, wind-dispersed species have lower dispersal ability than animal-dispersed species in forest habitat. However, for open-habitat species in open habitats, the results suggest that animal-dispersed species have lower dispersal ability than wind-dispersed species (Fig. 3.5). While open-habitat species of both dispersal types have increased dispersal in open habitats with decreasing forest cover in the landscape (Fig. 3.3), these results do suggest that in general, wind-dispersed species have greater dispersal ability than animal-dispersed species in open habitats.

Given the differences between the dispersal and habitat types observed, I speculate that removal of forest from a landscape would cause indirect changes in plant density and species composition. A reduction of forest cover in the landscape would increase the connectivity of the landscape for both wind- and animal-dispersed open-habitat species, although unlike animal-dispersed species, wind-dispersed species will be restricted primarily to open habitats due to their limited ability to penetrate more mature

forest edges. With a reduction in landscape forest cover, the increased deposition of the seeds of animal-dispersed, open-habitat species into forest habitats may mean a shift in the species composition of woody plant species in remaining forest patches, i.e., increased density and species richness of animal-dispersed species of open habitats. But many of these species are shade intolerant and their presence may be more pronounced in forest edges or small forest patches where there may be greater light penetration into patch interiors (see Kupfer and Runkle 1996). Therefore, in landscapes where forest cover has been removed, smaller forest patches may have increased colonization by shade intolerant, animal-dispersed species from nonforest habitat.

The implications of the study results are important in agricultural landscapes where the amount and configuration of nonforest cover types in the landscape are maintained by constant disturbance (e.g., agricultural fields and pastures, suburban development) and remaining forest patches in the landscape are often subjected to intense management and resource extraction (e.g., thinning of stems through commercial and fire-wood cutting). Based on the results of this study, these forest patches will be under constant invasion by animal-dispersed nonforest species. Therefore, I hypothesize that with a reduction in landscape forest cover there will be an increase in the deposition of open-habitat, animal-dispersed seeds into remaining forest habitat. In addition, further disturbance of remaining forest habitat may increase the emergence of the seedlings of these open-habitat, animal-dispersed in the disturbed forest habitats.

3.6 CONCLUSIONS

My results suggest that along a forest cover gradient there are accompanying changes in the connectivity of the landscape for seeds of both wind- and animal-dispersed species. For animal-dispersed species, seed dispersal across the landscape increases as forest cover in the landscape decreases. This is due primarily to an increase in the dispersal ability of open-habitat species. I observed increases in seed and stem densities for these species in both forest and open habitats with decreasing forest cover in the landscape. For wind-dispersed species the removal of barriers (canopy trees) to air movement in the landscape means greater dispersal of seeds in nonforest habitats. However, forest patches with dense edges may resist invasion by wind-dispersed open-habitat species. For forest species, increasing forest cover increases the connectivity of the landscape regardless of dispersal type. I also speculate that these changes in dispersal ability would occur as forest cover is removed from a single landscape.

This study is one of the first to look at how a landscape-scale gradient (percent forest cover) affects both the abundance and distribution of plants, using the landscape as the unit of observation. I have shown that there are effects at this scale, and that these effects are likely associated with changes in landscape connectivity. Similar multi-landscape studies have been conducted for animals (e.g., Wegner and Merriam 1979, Fahrig and Merriam 1985, Pither and Taylor 1998, Delin and Andrén 1999, Hokit et al. 1999, McIntyre and Wiens 1999, Naugle et al. 1999, Azevedo et al. 2000), but many empirical plant studies have focussed on effects of patch or stand structure on dispersal

(e.g., McDonnell and Stiles 1983, Houle and Payette 1990, Debussche and Isenmann 1994, Masaki 1994, Valido and Nogales 1994, Laman 1996, Burke and Nol 1998, Herrera 1998, Böhning-Gaese 1999, Ferguson and Drake 1999, Cadenasso and Pickett 2001; see also a review by Clark et al. 1999) and few have investigated the possible effects of landscape structure on plant dispersal (see Middleton and Merriam 1983, Matlack 1994a, Santos and Telleria 1994, Grashof-Bokdam 1997, Sarlöv Herlin and Fry 2000). My results indicate that there are landscape-scale effects, suggesting that further research at this scale would be fruitful for understanding the effects of human activities on abundance and distribution of plants.

Table 3.1: Predictions of the effect of increasing forest cover in the landscape. All predictions are made on the assumption that dispersal is the underlying mechanism (i.e., ignoring other possible mechanisms). DENSITY = predicted responses (relationships with predictor variables) for mean densities of seeds and stems combined; S_j = predicted responses (relationships with predictor variables) for the Jaccard's similarity index (similarity between aboveground stem and seed species pools). Predicted relationships: 0 = not significant at $\alpha = 0.05$; + = positive relationship; - = negative relationship. Predictor variables: PERFOR = percent forest cover in the landscape; DISPERSAL*PERFOR = interaction term, dispersal type * percent forest cover.

SPECIES-HABITAT/ PREDICTOR VARIABLE	RESPONSE VARIABLES	
	DENSITY	S_j
<u>Forest-Forest</u> PERFOR	0	0
DISPERSAL*PERFOR	Animal: + Wind: -	Animal: - Wind: +
<u>Forest-Open</u> PERFOR	-	+
DISPERSAL*PERFOR	Animal: 0 Wind: -	Animal: 0 Wind: +
<u>Open-Forest</u> PERFOR	-	+
DISPERSAL*PERFOR	0	0
<u>Open-Open</u> PERFOR	-	+
DISPERSAL*PERFOR	0	0

Table 3.2: Raw and relative abundance of the five most abundant species of seeds (seeds and seedlings combined) and stems in forest and open habitats.

SPECIES	Seeds			Stems		
	DISPERSAL.	Raw Total	Percent	SPECIES	DISPERSAL.	Raw Total
<u>FOREST HABITAT</u>						
<i>Acer saccharum</i> Marsh.	wind	2496	46.6	<i>Acer saccharum</i> Marsh.	wind	1961
<i>Rubus idaeus</i> L.	animal	790	14.7	<i>Fraxinus pennsylvanica</i> Marsh.	wind	840
<i>Fraxinus pennsylvanica</i> Marsh.	wind	331	6.2	<i>Ostrya virginiana</i> (Mill.) K. Koch	wind	703
<i>Acer rubrum</i> L.	wind	245	4.6	<i>Zanthoxylum americanum</i> Mill.	wind	687
<i>Ostrya virginiana</i> (Mill.) K. Koch	wind	202	3.8	<i>Rubus idaeus</i> L.	animal	546
<u>OPEN HABITAT</u>						
<i>Rubus idaeus</i> L.	animal	245	42.0	<i>Rubus idaeus</i> L.	animal	1528
<i>Acer saccharum</i> Marsh.	wind	120	20.5	<i>Vitis riparia</i> Michx.	animal	477
<i>Vitis riparia</i> Michx.	animal	38	6.5	<i>Rubus occidentalis</i> L.	animal	359
<i>Ostrya virginiana</i> (Mill.) K. Koch	wind	30	5.1	<i>Parthenocissus vitacea</i> (Knerr.) Hitchc.	animal	341
<i>Fraxinus pennsylvanica</i> Marsh.	wind	22	3.8	<i>Spiraea alba</i> Du Roi	wind	320
						6.1

Table 3.3: Summary of results for general linear models for each of the four response variables (ALL = density of stems and seeds combined for each landscape, STEMS = density of stems for each landscape, SEEDS = density of seeds (seeds and seedlings) for each landscape, and S_j = Jaccard's similarity index for each landscape). F and p-values for individual variables in each model are based on Type III sums of squares. For the models: Log₁₀ = response variable was Log₁₀-transformed, Arcsin = response variable was Arcsine-transformed.

SPECIES- HABITAT/ PREDICTOR VARIABLE	RESPONSE VARIABLES															
	ALL				STEMS				SEEDS				S_j			
	r^2	F	df	p	r^2	F	df	p	r^2	F	df	p	r^2	F	df	p
Forest-Forest																
Overall Model	0.427	13.41	3, 54	<0.0001	Log ₁₀	17.55	3, 54	<0.0001	Log ₁₀	6.13	3, 54	0.001	Log ₁₀	10.60	4, 51	<0.0001
DISPERSAL		18.28	1, 54	<0.0001		13.31	1, 54	0.001		2.42	1, 54	0.126		20.06	1, 51	<0.0001
PERFOR		0.82	1, 54	0.369		9.25	1, 54	0.004		4.94	1, 54	0.030		0.47	1, 51	0.498
DISPERSAL*PERFOR		0.75	1, 54	0.390		0.02	1, 54	0.878		0.40	1, 54	0.529		0.53	1, 51	0.469
S_j														0.12	1, 51	0.727
Forest-Open																
Overall Model	Log ₁₀	4.57	3, 48	0.006	Log ₁₀	9.89	3, 48	<0.0001	Log ₁₀	1.81	3, 48	0.158		1.89	4, 41	0.131
DISPERSAL	0.222	0.11	1, 48	0.737		0.000	1, 48	0.999		0.000	1, 48	0.988		0.004	1, 41	0.951
PERFOR		6.35	1, 48	0.015		29.60	1, 48	<0.0001		0.002	1, 48	0.961		5.20	1, 41	0.028
DISPERSAL*PERFOR		3.43	1, 48	0.070		0.01	1, 48	0.921		1.90	1, 48	0.174		0.51	1, 41	0.480
S_j														0.03	1, 41	0.860
Open-Forest																
Overall Model	Log ₁₀	105.30	3, 54	<0.0001	Log ₁₀	8.08	3, 54	0.00016	Log ₁₀	101.15	3, 54	<0.0001	Arcsin	0.55	4, 42	0.698
DISPERSAL	0.845	111.89	1, 54	<0.0001		17.12	1, 54	<0.0001		109.73	1, 54	<0.0001		0.09	1, 42	0.765
PERFOR		0.02	1, 54	0.888		1.98	1, 54	0.165		0.01	1, 54	0.920		0.24	1, 42	0.626
DISPERSAL*PERFOR		0.84	1, 54	0.363		4.37	1, 54	0.041		0.37	1, 54	0.546		0.31	1, 42	0.578
S_j														1.57	1, 42	0.217
Open-Open																
Overall Model	Log ₁₀	21.30	3, 48	<0.0001	Log ₁₀	6.01	3, 48	0.001	Log ₁₀	25.56	3, 48	<0.0001	Log ₁₀	2.63	4, 36	0.051
DISPERSAL	0.571	18.36	1, 48	<0.0001		2.41	1, 48	0.127		32.22	1, 48	<0.0001		5.99	1, 36	0.019
PERFOR		10.92	1, 48	0.002		4.19	1, 48	0.046		15.83	1, 48	<0.0001		0.58	1, 36	0.452
DISPERSAL*PERFOR		0.0003	1, 48	0.984		0.52	1, 48	0.472		2.11	1, 48	0.153		1.21	1, 36	0.278
S_j														0.14	1, 36	0.713

Table 3.4: Predicted responses (see Table 3.1) and summary of results (regression coefficients) for predictor variables in each of the general linear models. Response variables: ALL = mean densities of seeds and stems combined; STEMS = mean densities of stems only; SEEDS = mean densities of seeds (seeds and seedlings); S_j = Jaccard's similarity index for seeds v. stems. Predictor variables: PERFOR = Percent forest cover in the landscape; DISPERSAL*PERFOR = interaction term, dispersal type * percent forest cover. Relationship: + = significantly positive; - = significantly negative. Significance of predictor variable: * $p < 0.05$, *** $p < 0.001$.

SPECIES-HABITAT/ PREDICTOR VARIABLE	Predicted Responses		Regression Coefficients For Model Predictor Variables			
	DENSITY	S_j	ALL	STEMS	SEEDS	S_j
<u>Forest-Forest</u> PERFOR	0	0	-5.2305	-0.0063*	0.0122*	-0.0001
DISPERSAL*PERFOR	Animal: + Wind: -	Animal: - Wind: +	Animal: -0.2324 Wind: -10.229	Animal: -0.0066 Wind: -0.0060	Animal: 0.0087 Wind: 0.0157	Animal: 0.0005 Wind: -0.0003
<u>Forest-Open</u> PERFOR	-	+	-0.0146*	-0.0196***	-0.0004	0.0023*
DISPERSAL*PERFOR	Animal: 0 Wind: -	Animal: 0 Wind: +	Animal: -0.0253 Wind: -0.0039	Animal: -0.020 Wind: -0.0193	Animal: -0.0112 Wind: 0.0105	Animal: 0.0015 Wind: 0.0028
<u>Open-Forest</u> PERFOR	-	+	0.0005	-0.0043	-0.0004	-0.0008
DISPERSAL*PERFOR	0	0	Animal: -0.0026 Wind: 0.0036	Animal: -0.0107* Wind: 0.0021	Animal: -0.0025 Wind: 0.0018	Animal: -0.0021 Wind: 0.0008
<u>Open-Open</u> PERFOR	-	+	-0.0171***	-0.0085*	-0.0230***	-0.0005
DISPERSAL*PERFOR	0	0	Animal: -0.0172 Wind: -0.0170	Animal: -0.0055 Wind: -0.0115	Animal: -0.0314 Wind: -0.0146	Animal: -0.0011 Wind: 0.0002

Table 3.5: Results of power analyses (Power = $1 - \beta$) for each of the general linear models in Table 3.3. A single asterisk (*) denotes where predictor variables in a model were found to be significant in the general linear model (at $\alpha = 0.05$). A double asterisk (**) denotes a significant predictor variable but the overall model was not significant.

SPECIES-HABITAT/ PREDICTOR VARIABLE	POWER ($1 - \beta$)			
	ALL	STEMS	SEEDS	S_j
<u>Forest-Forest</u>				
DISPERSAL	0.994*	0.964*	0.316	1.000*
PERFOR	0.138	0.864*	0.581*	0.100
DISPERSAL*PERFOR	0.130	0.053	0.093	0.110
S				0.050
<u>Forest-Open</u>				
DISPERSAL	0.062	0.050	0.050	0.300
PERFOR	0.697*	1.000*	0.050	0.590**
DISPERSAL*PERFOR	0.427	0.051	0.257	0.100
S				0.040
<u>Open-Forest</u>				
DISPERSAL	1.000*	0.991*	1.000*	0.050
PERFOR	0.052	0.267	0.051	0.070
DISPERSAL*PERFOR	0.140	0.527*	0.090	0.080
S				0.230
<u>Open-Open</u>				
DISPERSAL	0.994*	0.314	1.000*	0.650**
PERFOR	0.918*	0.506*	0.985*	0.110
DISPERSAL*PERFOR	0.050	0.106	0.281	0.190
S				0.060

Figure 3.1: Plots of Log_{10} -transformed mean density per sampling plot (see section 3.3.2) of forest-habitat species in forest habitat for stems (A) and seeds (B) v. percent forest cover in the landscape (see Tables 3.3 and 3.4 for statistical information from the general linear model).

A. Stem density of forest-habitat species in forest habitat

B. Seed density of forest-habitat species in forest habitat

Figure 3.2: Plots of Log_{10} -transformed mean density per sampling plot (see section 3.3.2) of forest-habitat species in open habitats for all stems and seeds combined (A) and stems (B) v. percent forest cover in the landscape (see Tables 3.3 and 3.4 for statistical information for the general linear model).

A. Density of all stems/seeds combined (forest-habitat species in open habitats)

B. Stem density of forest-habitat species in open habitats

Figure 3.3: Plots of Log_{10} -transformed mean density per sampling plot (see section 3.3.2) of open-habitat species in open habitats for all stems and seeds combined (A), stems (B), and seeds (seeds and seedlings combined (C) v. percent forest cover in the landscape (see Tables 3.3 and 3.4 for statistical information for the general linear model).

A. Density of all stems and seeds combined (open-habitat species in open habitats)

B. Stem density of open-habitat species in open habitats

C. Seed density of open-habitat species in open habitats

Figure 3.4: Plots of Log_{10} -transformed mean stem density per sampling plot (see section 3.3.2) of open-habitat species in forest habitat v. percent forest cover in the landscape (see Tables 3.3 and 3.4 for statistical information for the general linear model). Wind-dispersed, open-habitat species ($\circ$, — —) and animal-dispersed, open-habitat species ($\blacksquare$, —).

Figure 3.5: Mean Jaccard's similarity index (S_j) for wind- and animal-dispersed forest-habitat species in A. Forest-habitat species in forest habitats and B. Open-habitat species in open habitats. Error bars represent 95% confidence intervals.

A. Forest-habitat species in forest habitats

B. Open-habitat species in open habitats

CHAPTER 4

EFFECTS OF A LARGE DISTURBANCE ON THE SPECIES COMPOSITION AND DENSITY OF WOODY SEEDLINGS WITH DIFFERENT DISPERSAL MECHANISMS

4.1 CHAPTER SUMMARY

Results from the previous two chapters suggest that the seed dispersal ability of woody plant species across landscapes depends on i) whether seeds are dispersed by animals or wind and ii) the amount of forest cover in the landscape (landscape structure). As the percentage of forest cover in the landscape decreases the results suggest that the movement of animal-dispersed seeds from nonforest habitat (old fields and fencerows) into forest habitat increases. I suggest that this is due to the increased numbers and movement of animal seed dispersers (those associated with nonforest habitats) into forest habitats as landscape forest cover decreases. For wind-dispersed woody plant species, the results suggest an increase in the dispersal ability of open-habitat, wind-dispersed species with decreasing forest cover in the landscape. But unlike animal-dispersed species, the dispersal of open-habitat, wind-dispersed species into forest habitats does not appear to increase with decreasing forest cover in the landscape. The dense side canopies of forest patches in my sample landscapes likely act as barriers to the movement of these seeds into forest habitat.

In January 1998, the winter following the field sampling for Chapters 2 and 3, a large ice storm struck the Ottawa region. I predicted that the loss of tree canopy associated with ice storm damage would accentuate the effects of decreasing forest cover in the landscape. Landscapes with less forest cover should have more seeds of animal-dispersed species in the soil and litter of forest plots, which would germinate and become established as seedlings due to increased light availability following the storm. In contrast, the results of Chapters 2 and 3 suggested that seeds of wind-dispersed species are confined to their respective habitats (open habitat or forest), although dispersal within open habitat increases with decreasing forest cover in the landscape. I predicted no change in the relationship between seedling emergence and percent forest cover for wind-dispersed species following a disturbance of the canopy because i) input of wind-dispersed seeds in forest habitats is from forest species and open-habitat, wind-dispersed species are restricted to open habitats and ii) wind-dispersed forest species are generally shade tolerant and seeds will germinate irrespective of light availability.

In 1998 and 1999 I resampled the vegetation plots described in Chapters 2 and 3. As predicted, for animal-dispersed species the slope of the relationship between mean seedling density and percent forest cover in the landscape was significantly more negative (increasing negative slope) in the two years following the ice storm. There was no change in the observed relationship between seedling emergence and percent forest cover in the landscape for wind-dispersed species following the ice storm. My results suggest that the relationship between dispersal ability and percent forest cover in the

landscape can influence the response of woody plant species to additional disturbance. Therefore, human-induced changes to landscape structure can have consequences for the composition and structure of forest plant communities following natural disturbances.

4.2 INTRODUCTION

4.2.1 DISTURBANCE AND SEED DISPERSAL

Natural and human-induced disturbances have been shown to drive many changes in forest plant communities (Bormann and Likens 1979, Pickett and White 1985, Bazzaz 1996). The spatial extent and severity of a disturbance determines the degree of change in species composition as well as changes in population age structure and the distribution of individuals (White 1979, Abrams and Scott 1989, Everham and Brokaw 1996, Kupfer and Runkle 1996, Leak and Smith 1996, Elliott et al. 1997, Pontauiller et al. 1997). For example, forest disturbances give seedlings and saplings of some forest canopy species a chance to become established by opening up the canopy and increasing the amount of light available to developing seedlings and saplings (Canham 1985, Orwig and Abrams 1995, Kupfer and Runkle 1996, Foré et al. 1997, Goebel and Hix 1997, Emborg 1998, Van Pelt and Franklin 1999). In mature and old growth plant communities, disturbances can reset successional clocks and give species associated with earlier successional stages an opportunity to become re-established, if even for a relatively short period of time (Bormann and Likens 1979, Bazzaz 1996, Kupfer and Runkle 1996, Goebel and Hix 1997).

Disturbances affecting large areas may create more opportunities for the establishment of seedlings than disturbances with a smaller spatial extent (Everham and Brokaw 1996). Following severe disturbances, sources of potential recruits from within the existing community may die (Turner et al. 1998), reducing competition and increasing opportunities for the germination of seeds from the soil seed bank or the germination of seeds that have dispersed into the site following the disturbance (Bormann and Likens 1979, Turner et al. 1998).

The results from the previous two chapters suggest that the seed dispersal of woody plant species across landscapes depends on i) the dispersal mechanism and ii) the landscape structure (amount of forest in the landscape). In landscapes with little forest cover, animal-dispersed seeds from open habitats (old fields and fencerows) are readily dispersed into forest habitats (see sections 2.5 and 3.5). As the percentage of forest cover in the landscape decreases, the movement of animal-dispersed seeds from open habitats into forest habitat increases (see section 3.5 and Table 3.4). This relationship is probably due to an increase in the connectivity of the landscape for animal seed dispersers associated with nonforest and forest edge habitats as landscape forest cover decreases (see sections 2.5 and 3.5).

For wind-dispersed woody plant species, there is an increase in the dispersal ability of open-habitat wind-dispersed species with decreasing forest cover in the landscape (see Table 3.3 and Fig. 3.3). But unlike animal-dispersed species, the dispersal of open-habitat wind-dispersed species into forest habitats does not increase with

decreasing forest cover in the landscape (see Table 3.3 and Fig. 3.4). I hypothesized that this was due to the dense lateral canopies of forest edges in the sample landscapes and an inability of wind-dispersed seeds of open habitats to penetrate the dense forest edges (see section 3.5).

In 1998 a large ice storm struck the Ottawa, Ontario region. I predicted that the relationships observed in the previous two chapters would be accentuated by canopy damage caused by the storm. The ice storm should cause an increase in the openness of the forest canopy which would create conditions conducive to seed germination, particularly for those species that are shade intolerant, e.g., most species of open habitats (see Tables A.1 and A.2). Therefore, with decreasing forest cover in the landscape and the accompanying influx of the seeds of open-habitat, animal-dispersed species into remaining forest habitats in the landscape, I predicted that the increased light availability would increase seedling establishment for these species.

4.2.2 THE ICE STORM OF 1998

In January of 1998, eastern Ontario, southern Quebec, and most of the northeastern United States were hit by an unusually large ice storm. The spatial extent of the storm was unlike anything experienced in the region in recent history, with nearly 10-million ha of woodlands in eastern Ontario and southern Quebec affected (Kerry et al. 1999, Ontario Ministry of Natural Resources 1998, Irland 1998). This storm was also one of the most severe ice storms in recent North American history (Environment Canada

1998, Irland 1998, Kerry et al. 1999). In the Ottawa, Ontario region more than 85-mm of freezing rain, ice pellets, and snow were deposited from 5 January to 10 January, 1998 (Environment Canada 1998). For comparison, previous large ice storms (1942, 1961, and 1986) in the Ottawa region only deposited between 30 and 40 mm of freezing rain per event (Shilts 1998).

Immediately following the storm, observations from helicopter flights over the affected areas in eastern Ontario by the Ontario Ministry of Natural Resources suggested a patchy distribution of storm-related damage to hardwood canopy trees (Ontario Ministry of Natural Resources 1998). Patches of severe damage, where crown loss for all canopy trees exceeded 75%, were interspersed among areas of light to medium damage (where 25 to 75% of canopy trees had 0 to 75% crown loss) (Ontario Ministry of Natural Resources 1998). Observations in all 192 forest plots described in Chapters 2 and 3 indicated that canopy crowns were not entirely lost and crown loss in the study region was extremely variable, with a mean crown loss for canopy trees of $31.87 \pm 40.31\%$ ($\bar{x} \pm 1$ SD) (Charbonneau et al. in review). On these plots, no storm-related mortality of canopy trees was observed in 1998, 1999, 2000, or 2001 (T. Contreras, J. Holland, and L. Fahrig, unpublished data). Charbonneau et al. (in review) have shown that the degree of crown damage exhibited by a canopy stem depended on inherent species characteristics (i.e., wood strength and crown architecture) and stem size. This may help explain the patchy nature of canopy damage where the amount of ice deposited across a forest patch

was relatively constant: susceptible stems were damaged while stems with greater wood strength and smaller sizes suffered little or no damage.

4.2.3 PREDICTIONS

The goal of this study was to determine if there was an influence of percent forest cover in the landscape on the emergence of woody seedlings (i.e., changes in seedling density and species richness) following the ice storm of 1998. The ice storm did not create immediate changes in the availability of nutrients since coarse woody debris from the storm will take decades to decompose and there was little soil disturbance in sampling plots (T. Contreras, J. Holland, and L. Fahrig, unpublished data). Therefore, any changes in woody plant species composition and woody seedling densities would have come about primarily through increased light availability and other associated microclimatic factors due to an opening up of the forest canopy by the storm.

I predicted increased germination of animal-dispersed, open-habitat species in forest habitat with decreasing forest cover in the landscape. Storm-related canopy damage will increase light availability in forest plots, and forest plots in landscapes with low forest cover have more open-habitat animal-dispersed seeds than those in landscapes with high forest cover (Chapter 3). This should result in more of these seedlings emerging following the storm in the forest plots of landscapes with low amounts of forest cover. In those landscapes with high forest cover I would expect fewer seedlings of these species emerging following the ice storm. Therefore, I predict that for open-habitat, animal-

dispersed species, the strength of the relationship between seedling emergence (e.g., mean seedling density and mean species richness) in forest plots and percent forest cover in the landscape should increase in the years following the storm, i.e., the relationship will become even more negative.

Based on the results from Chapter 3, there appears to be little dispersal of wind-dispersed species between open habitats and forest (see section 3.5). In addition, most wind-dispersed forest species in our study plots are shade tolerant (see Tables A.1 and A.2) and increased light availability following the storm should not have a large effect on seed germination for these species (Burns and Honkala 1990). Therefore, for wind-dispersed species, I predicted no change in the relationship between mean species richness and mean seedling density with changing forest cover in the landscape following the ice storm of 1998.

4.3 METHODS

4.3.1 STUDY SITES AND SEEDLING SAMPLING

Stem counts were conducted from June to August in 1997, 1998, and 1999 in forest plots in each of the 29 1-km² agricultural landscapes used in the previous 2 studies (192 forest plots total) (Fig. 2.1; see Section 2.3.1 for a description of the sample landscapes). Percent forest cover in each of the 29 landscapes (PERFOR) was estimated using digital topographic maps and unclassified Russian MK-4 satellite data (see section 2.3.1).

For each plot I used two 1-m² quadrats for counting seedlings (see Fig. 2.2 for plot design). In each plot, stems were identified to species or genus. While I had previously classified seedlings as any woody stem < 1 meter in height (see section 2.3.2), for this set of analyses my goal was to look at pre- v. post storm changes in seedling emergence. Therefore, I used only those seedlings that had germinated during, or just prior to, each sampling period. Newly germinated seedlings were identified by the presence of cotyledons.

Species richness for each sampling plot (S) was the number of species in the two 1-m² quadrats per sampling plot. Mean seedling density for a plot (DENSITY) was the total number of seedlings for both 1-m² quadrats divided by two (the number of quadrats per sampling plot) (see Fig. 2.2). Although woody seedlings and sprouts were, in some instances, difficult to identify to species, all were identified to genus. Using information from Schopmeyer (1974), Barnes and Wagner (1981), Soper and Heimberger (1982), Preston (1989), Burns and Honkala (1990), Cain et al. (1998), and Sutherland et al. (2000), each seedling was assigned to one of two dispersal categories (DISPERSAL): animal-dispersed species or wind-dispersed species (see Section 2.3.2).

4.3.2 VARIABLE DESCRIPTIONS AND STATISTICAL ANALYSES

I used two sets of general linear models, one set for each of the two dispersal types, i.e., wind- and animal-dispersed species. In each set there were two general linear models: i) a model with seedling species richness in each sampling plot as the response

variable and ii) a model with mean seedling density in each sampling plot as the response variable. In all four models I included YEAR (the sampling year, 1997, 1998, and 1999), as well as PERFOR (the percentage of forest cover in the landscape). The test of the predictions outlined in section 4.2.3 are a test of pre- and post-storm changes in the relationship between the response variables (seedling species richness and mean seedling density) and percent forest cover in the landscape. Therefore, I also included the interaction term YEAR*PERFOR in each of the models. A significant interaction term in the model would suggest a change in the relationship between the seedling emergence variables (richness and density) and percent forest cover in the landscape following the ice storm of 1998. The significance of predictor variables in the model was based on F tests using Type III Sums of Squares, with $\alpha = 0.05$ (SAS 1990). In situations where assumptions of the F test were not met, response variables were transformed and the models were recalculated using the transformed response variables. In situations where class variables were significant, pairwise comparisons were used to determine significant differences between classes. In all cases, categorical variables included more than 2 classes so Scheffé tests were used to control for an increase in the probability of Type I error rates associated with multiple comparisons (Zar 1999).

Variables associated with seedling emergence

To control for the influence of factors unrelated to the ice storm on both seedling species richness and mean seedling density, I also included a number of other variables in

the models that are often associated with seedling emergence (Burns and Honkala 1990, Bazzaz 1996, Kupfer and Runkle 1996, Palik et al. 2000). These factors are related to physical conditions within plots and plot locations in the study region (e.g., possible gradients in forest and soil types). In 1998 the location of each sampling plot (using the Universal Transverse Mercator projection, North American Datum 1927) was estimated using a handheld Global Positioning System (GPS) (Lowrance Electronics, Inc., Tulsa, OK).

The extent of the study region was approximately 290,000 ha and included 5 different physiographic regions (from west to east: Smiths Falls Limestone Plain (S), Ottawa Valley Clay Plains (O), North Gower Drumlin Field (N), Winchester Clay Plain (W), and Russell/Prescott Sand Plains (R) (see Chapman and Putnam (1984) for a full description of each region). Locations within each physiographic region not only have similar geomorphology, but also similar soil and forest types as well as similar land use practices and patterns of use (e.g., agricultural practices and human population densities). Using the plot position data, I attempted to control for differences between sampling plots related to different forest and soil types across the study region by assigning each plot to a specific physiographic region and including that information in each of the models (PHYSREG). In addition, the soil moisture of each sampling plot (PLOTMOIST) was broadly classified in 1997 using a nominal scale of 1 to 5 with 1 representing dry, well-drained soil and 5 representing wet and poorly-drained soil with evidence of standing water occurring at some point during or just prior to the growing season. This variable

was also included in the models. Soil moisture and the presence of standing water during, or prior to, the growing season would affect seedling emergence and soil moisture may be an indicator of soil type at the plot scale (e.g., heavy clay soils would result in poor drainage while sandy or rocky soils might mean good drainage and no standing water).

The distance of each sampling location from forest edge, as well as the orientation of each edge (direction forest edge faces), may also affect the likelihood of seedling germination and the growth of root sprouts (Matlack 1993, Matlack 1994b, Kupfer and Runkle 1996, Kupfer et al. 1997). Both factors influence light penetration and microclimatic factors such as relative humidity, temperature, and wind speeds (Matlack 1993, Matlack 1994b). Using plot position data, digital topographic maps, and unclassified Russian MK-4 satellite data (see Section 2.3.1), I estimated the distance of each sampling plot from forest edge (EDGEDIST) and determined the orientation (azimuth) of the forest edge nearest each plot (EDGEOR). For each plot the edge orientation azimuth was sine-transformed so that all bearings between 0° and 180° had positive values (with $90^{\circ} = 1$ and both 0° and 180° equal to 0) and all bearings between 180° and 360° had negative values (with $270^{\circ} = -1$) (see Zar 1999). The sine-transformation of azimuth data allowed me to use values in the statistical models which give an indication of directionality, i.e., positive values suggest an easterly direction while negative values suggest a westerly direction (see Zar 1999).

I also included slope (SLOPE) and slope aspect (SLOPEASP) for each plot in the models. Slope and slope aspect may also influence microclimatic conditions. For

example, in the study region, sites on southwest-facing slopes would be more exposed to prevailing winds and, as a result, experience lower relative humidity and greater wind speeds than sites on more east-facing slopes. Using a clinometer, slope estimates were made by sighting down slope from an edge of the sampling plot perpendicular to the direction of the slope and farthest from the base of the slope. From the same position I then sighted down slope with a compass to determine the slope aspect (azimuth). As with EDGEOR, all slope aspect data were sine-transformed.

In each model I included the Julian date when each plot was sampled (DAY). I assumed that because plots were not sampled simultaneously during each sampling year, plots sampled later in the summer might have more seedlings present (Bazzaz 1996). It is also possible that for some species, herbivory may reduce the number of seedlings present in plots sampled later in the growing season, particularly for those sites closest to nonforest habitats (Ostfeld et al. 1997, Cadenasso and Pickett 2000).

4.4 RESULTS

Over the 3-year period there were 3,798 seedlings from 50 species of woody plants observed in the 192 forest plots (Table 4.1). Twenty-nine of the 50 species were not observed in the summer of 1997 (the summer preceding the ice storm) and there was an overall increase in species richness from 1997 to 1999 for all species combined (Fig. 4.1). This increase was predominantly due to a steady increase in animal-dispersed species richness over the 3-year period (Table 4.1 and Fig. 4.1).

Sixty-seven percent of all seedlings observed were wind-dispersed (see Table 4.1 and Fig. 4.2). The total numbers of animal-dispersed seedlings increased over the 3-year period while for wind-dispersed species there was a drop in the number of stems in 1998 with a subsequent increase in 1999 (Table 4.1 and Fig. 4.2).

For species richness, there was no significant interaction between YEAR and PERFOR for either animal or wind-dispersed species (Table 4.2) although YEAR was a significant predictor of species richness for both dispersal types (Table 4.2). For animal-dispersed species mean species richness increased significantly following the ice storm with species richness increasing significantly each year (Scheffé tests: all comparisons were statistically significant, $p < 0.01$) (Fig. 4.3). For wind-dispersed species there was no significant change in mean species richness from 1997 to 1998 (Scheffé test: $p > 0.05$), although mean species richness for wind-dispersed species in 1999 was significantly greater than 1998 (Scheffé test: $p < 0.01$) (Fig. 4.3). Percent forest cover in the landscape (PERFOR) was a significant predictor of the species richness of wind-dispersed species (see Table 4.3) although the decrease in species richness with decreasing percent forest cover in the landscape was very small (Fig. 4.4).

Due to a lack of homogeneity of residual variance, seedling densities were Log_{10} -transformed. The variable YEAR was a significant predictor of mean seedling density for both dispersal types (Table 4.2, Fig. 4.5). There was a significant interaction between YEAR and PERFOR for animal-dispersed species and, as predicted, the relationship between mean seedling density and percent forest cover in the landscape became more

negative in the 2 years following the ice storm (absolute value of the slope of the best-fit lines increased for both years following the ice storm) (Fig. 4.6). As predicted there was no significant interaction between YEAR and PERFOR for wind-dispersed species (Table 4.3).

4.5 DISCUSSION

There were significant changes in the mean species richness and mean seedling density of woody seedlings following the ice storm of 1998 (Tables 4.2 and 4.3). For animal-dispersed species, both species richness and mean seedling densities increased following the ice storm (Figs. 4.3 and 4.5). As predicted for the mean seedling density of animal-dispersed species, there was a significant interaction between pre- and post-storm sampling years (YEAR) and percent forest cover in the landscape (PERFOR) with the slope of the relationship between mean seedling density and percent forest cover in the landscape becoming more negative (increasing negative slope) in the two years following the ice storm (Table 4.3 and Fig. 4.6). Landscapes with less forest cover had more animal-dispersed open-habitat individuals in the seed/seedling pool than landscapes with more forest cover (Chapter 3). Landscapes with less forest cover therefore had more seeds available to germinate and become seedlings as ice storm damage opened up the canopy. While the species richness of animal-dispersed species increased post-storm (1998 and 1999, see Fig. 4.3), there was no significant relationship between species richness and percent forest cover in the landscape (PERFOR) and no significant

interaction between YEAR and PERFOR (Table 4.2). Assuming adequate power for the analysis, one possible explanation for the lack of a significant change in the relationship is that the species pool for animal-dispersed species was relatively consistent across all sample landscapes. The primary source of animal-dispersed seeds in forest habitats was open-habitat species with relatively few seeds from forest and canopy tree species found in forest plots (see section 3.5). While an increase in light penetration due to damage from the ice storm would increase the number of seeds germinating, the seeds may have been drawn from a relatively small species pool (see Tables 4.1 and A.2).

As with animal-dispersed species, I observed significant changes in both species richness and the mean seedling densities of wind-dispersed species following the ice storm of 1998 (Tables 4.2 and 4.3). As predicted, however, there were no significant interactions between sampling year and percent forest cover in the landscape for either richness or density (Table 4.2 and 4.3) although the species richness of wind-dispersed seedlings decreased significantly with decreasing forest cover in the landscape (Table 4.2 and Fig. 4.4). Forest-habitat species are the primary source of most wind-dispersed seeds in forest habitats (Chapter 3). Therefore, an increase in species richness of wind-dispersed species may have been due to an increase in the number of wind-dispersed forest species as the amount of forest in the landscape increased.

The results from the 1997-1999 data suggest that animal-dispersed species are better able to take advantage of even the moderate loss of canopy caused by the ice storm, particularly in landscapes where forest cover had been reduced. More open-

habitat, animal-dispersed species were dispersed into forest habitats in landscapes with reduced forest cover (Table 3.2 and Fig. 3.4). Many of these species are shade intolerant (Tables A.1 and A.2) and are unable to germinate in forest habitat, although many have tough seed coats that allow them to remain dormant in the litter and soil seed banks (Table A.2) (see Peterson and Carson 1996). Following a disturbance that opens the canopy, these seeds are able to germinate and take advantage of the increased light availability. Seeds produced in 1998 that required a cold period before germinating, would have been a significant component of the seedlings that appeared in 1999. It is interesting to note that of the 26 animal-dispersed seedling species encountered in forest plots from 1997-1999, only 6 species were seen in 1997 (Table 4.1). In comparison, 15 of the 24 wind-dispersed seedling species encountered in forest plots during the study were observed in 1997 (Table 4.1). It has been shown that many animal dispersed species are capable of quickly colonizing disturbed areas (Bormann and Likens 1979). Unlike other studies (Bormann and Likens 1979, Grashof-Bokdam 1997, Sarlöv Herlin and Fry, 2000), however, this study has also shown that for animal-dispersed species, differences in landscape structure (amount of forest cover in the landscape) can have a significant effect on colonization rates.

It has been demonstrated that the colonization of recently cleared forest by animal-dispersed species occurs relatively quickly because seeds of these species are present in the soil seed bank (Bormann and Likens 1979). Barring any other large-scale disturbance, these early-colonizing animal-dispersed species will be displaced by more

shade tolerant forest species over time (Bormann and Likens 1979, Grime 1979, Bazzaz 1996, Kupfer and Runkle 1996). But considering the results of this study in the context of constant anthropogenic disturbances in agricultural landscapes, it is clear that forest patches in agricultural landscapes with reduced forest cover will be under constant invasion by these species.

It remains to be seen how persistent the observed changes will be. With moderate damage, canopy closure may occur relatively quickly. This could result in an increased mortality rate for new seedlings and sprouts of open-habitat, animal-dispersed species in subsequent years. Based on the results of this study, however, canopy disturbances in landscapes where forest has been removed will mean increased colonization by animal-dispersed species in the forest patches of agricultural landscapes.

Table 4.1: Seedlings observed in forest plots during the study (summers 1997-1999). Habit refers to the dominant growth form of the species (from Soper and Heimberger (1982) and Preston (1989)).

	Habit	Seedling Totals		
Species		1997	1998	1999
<u>Animal-dispersed</u>				
<i>Amelanchier</i> Medik.	Shrub	0	0	5
<i>Amelanchier laevis</i> Weig.	Shrub	0	0	2
<i>Aronia melanocarpa</i> (Michx.) Ell.	Shrub	0	0	7
<i>Carya cordiformis</i> (Wang.) K. Koch	Tree	10	2	1
<i>Cornus alternifolia</i> L. fil.	Shrub	0	11	3
<i>Cornus stolonifera</i> Michx.	Shrub	0	11	1
<i>Fagus grandifolia</i> Erhr.	Tree	2	9	5
<i>Malus</i> Mill.	Tree	0	0	1
<i>Parthenocissus vitacea</i> (Knerr.) Hitchc.	Vine	0	107	261
<i>Prunus serotina</i> Erhr.	Tree	0	2	1
<i>Prunus virginiana</i> L. fil.	Tree	0	0	15
<i>Quercus alba</i> L.	Tree	0	1	1
<i>Quercus macrocarpa</i> Michx.	Tree	1	0	0
<i>Rhamnus cathartica</i> L.	Shrub	0	112	96
<i>Rhamnus frangula</i> L.	Shrub	0	0	2
<i>Rhus radicans</i> L.	Vine	0	0	122
<i>Ribes cyanosbati</i> L.	Shrub	0	1	12
<i>Ribes lacustre</i> (Pers.) Poir.	Shrub	0	0	2
<i>Rubus idaeus</i> L.	Shrub	11	61	84
<i>Rubus occidentalis</i> L.	Shrub	6	0	0
<i>Rubus pubescens</i> Raf.	Shrub	0	25	176
<i>Thuja occidentalis</i> L.	Vine	0	0	1
<i>Vaccinium myrtilloides</i> Michx.	Shrub	0	14	0
<i>Viburnum lentago</i> L.	Shrub	0	1	0
<i>Vitis riparia</i> Michx.	Vine	26	10	12
<i>Zanthoxylum americanum</i> Mill.	Tree	0	4	13

Table 4.1: continued

	Habit	Seedling Totals		
Species		1997	1998	1999
<u>Wind-dispersed (cont.)</u>				
<i>Abies balsamea</i> (L.) Mill.	Tree	0	1	3
<i>Acer negundo</i> L.	Tree	3	0	98
<i>Acer nigrum</i> Michx.	Tree	0	1	0
<i>Acer rubrum</i> L.	Tree	104	15	19
<i>Acer saccharinum</i> L.	Tree	112	2	1
<i>Acer saccharum</i> Marsh.	Tree	996	53	106
<i>Acer spicatum</i> Lam.	Tree	0	2	0
<i>Betula alleghaniensis</i> Britt.	Tree	2	1	0
<i>Betula papyrifera</i> Marsh.	Tree	43	1	0
<i>Carpinus caroliniana</i> Walt.	Tree	6	23	8
<i>Fraxinus americana</i> L.	Tree	26	7	2
<i>Fraxinus nigra</i> Marsh.	Tree	2	3	12
<i>Fraxinus pennsylvanica</i> Marsh.	Tree	179	30	245
<i>Ostrya virginiana</i> (Mill.) K. Koch	Tree	38	70	209
<i>Pinus strobus</i> L.	Tree	1	2	5
<i>Pinus sylvestris</i> L.	Tree	4	0	0
<i>Populus</i> L.	Tree	0	6	1
<i>Populus balsamifera</i> L.	Tree	0	0	8
<i>Populus grandidentata</i> Michx.	Tree	1	0	0
<i>Populus tremuloides</i> Michx.	Tree	0	20	15
<i>Salix alba</i> L.	Shrub	0	0	3
<i>Tilia americana</i> L.	Tree	12	14	8
<i>Ulmus</i> L.	Tree	0	1	0
<i>Ulmus americana</i> L.	Tree	4	13	7
Number of animal-dispersed species		6	15	22
Number of wind-dispersed species		16	19	18
Total species		22	34	40
Total of animal-dispersed seedlings		56	371	823
Total of wind-dispersed seedlings		1533	265	750
Total seedlings		1589	636	1573

Table 4.2: General linear models for animal and wind-dispersed species with the species richness of seedling at each sampling site as the response variable. F values for variables are calculated using Type III sums of squares (see Zar 1999). For significant qualitative predictor variables I have included a comparison between classes and for significant quantitative predictor variables I have provided the coefficient. See section 4.3.2 for a full description of the predictor variables and for class abbreviations.

Model	Variable	F	df	p	Comparisons-Coefficients
Animal-dispersed¹					
	YEAR	9.661	2	<0.0001	1998, 1999 > 1997
	PERFOR	1.173	1	0.279	
	YEAR*PERFOR	0.200	2	0.819	
	PLOTMOIST	0.433	4	0.785	
	PHYSREG	2.768	4	0.027	R > N, S
	EDGEDIST	0.375	1	0.540	
	EDGEOR	1.259	1	0.262	
	SLOPE	2.447	1	0.118	
	SLOPEASP	2.933	1	0.087	
	DAY	8.036	1	0.005	0.0025
Wind-dispersed²					
	YEAR	4.829	2	0.008	1999 > 1998
	PERFOR	10.291	1	0.001	0.0018
	YEAR*PERFOR	1.724	2	0.179	
	PLOTMOIST	2.961	4	0.019	3 > 1, 2
	PHYSREG	2.640	4	0.033	N, W > S
	EDGEDIST	0.898	1	0.344	
	EDGEOR	0.145	1	0.704	
	SLOPE	4.309	1	0.038	-0.0141
	SLOPEASP	0.011	1	0.918	
	DAY	3.878	1	0.049	0.0014

¹Overall model: $R^2 = 0.152$; $F = 5.537$; $df = 18, 557$; $p < 0.000001$

²Overall model: $R^2 = 0.097$; $F = 3.322$; $df = 18, 557$; $p = 0.000005$

Table 4.3: General linear models for animal and wind-dispersed species with Log_{10} -transformed mean seedling density for each sampling site as the response variable. F values for variables are calculated using Type III sums of squares (see Zar 1999). For significant qualitative predictor variables I have included a comparison between classes and for significant quantitative predictor variables I have provided the coefficient. See section 4.3.2 for a full description of the predictor variables and for class abbreviations.

Model	Variable	F	df	p	Comparisons-Coefficients
Animal-dispersed¹					
	YEAR	16.839	2	<0.0001	1999, 1998 > 1997
	PERFOR	2.887	1	0.090	
	YEAR*PERFOR	3.441	2	0.033	1997: -0.00000005 1998: -0.0009 1999: -0.0029
	PLOTMOIST	1.306	4	0.267	
	PHYSREG	2.454	4	0.045	R > S
	EDGEDIST	0.129	1	0.720	
	EDGEOR	1.373	1	0.242	
	SLOPE	0.520	1	0.471	
	SLOPEASP	1.356	1	0.245	
	DAY	2.061	1	0.152	
Wind-dispersed²					
	YEAR	13.466	2	<0.0001	1997 > 1999 > 1998
	PERFOR	0.062	1	0.804	
	YEAR*PERFOR	2.022	2	0.133	
	PLOTMOIST	2.566	4	0.037	3 > 2, 1
	PHYSREG	0.301	4	0.877	
	EDGEDIST	0.492	1	0.483	
	EDGEOR	0.021	1	0.885	
	SLOPE	4.814	1	0.029	-0.006
	SLOPEASP	0.961	1	0.327	
	DAY	1.952	1	0.163	

¹Overall model: $R^2 = 0.148$; $F = 5.338$; $df = 18, 557$; $p < 0.000001$

²Overall model: $R^2 = 0.123$; $F = 4.325$; $df = 18, 557$; $p < 0.000001$

Figure 4.1: Seedling species richness for 1997-1999. Total refers to species richness for both animal and wind-dispersed species combined.

Figure 4.2: Number of seedlings observed from 1997-1999. Total refers to the total number of seeds for both wind- and animal-dispersed seedlings combined.

Figure 4.3: Mean seedling species richness per plot (S) for animal and wind-dispersed species across the three sampling years: 1997 (pre-storm), 1998, and 1999. Error bars represent 95% confidence intervals. Significantly different mean S values within a dispersal class are represented by different letters (significant differences between mean S values based on Scheffé tests where $\alpha = 0.05$).

Figure 4.4: Relationship between the species richness of wind-dispersed seedlings per plot (S) and percent forest cover in the landscape (PERFOR).

Figure 4.5: Mean seedling density per plot for animal- and wind-dispersed species across the three sampling years: 1997 (pre-storm), 1998, and 1999 (post-storm). Error bars represent 95% confidence intervals. Significantly different mean seedling densities within a dispersal class are represented by different letters (significant differences between mean seedling densities based on Scheffé tests where $\alpha = 0.05$).

Figure 4.6: Mean Log_{10} -transformed seedling densities per plot of animal-disperse species v. percent forest cover in the landscape for each of the three sampling years: 1997 (pre-storm) = $\circ$, —; 1998 (post-storm) = $\square$, —; and 1999 (post-storm) = Δ , - -.

CHAPTER 5

GENERAL CONCLUSIONS

5.1 DO CHANGES IN LANDSCAPE STRUCTURE INFLUENCE THE ABUNDANCE AND DISTRIBUTION OF WOODY PLANTS IN REMAINING HABITATS?

A number of studies have shown that changes in landscape structure (e.g., changes in habitat amount, configuration of remaining habitat, and/or mean habitat patch size within landscapes) affect the abundance and distribution of animals (see Fahrig and Merriam 1985 and 1994, Andrén 1994, Bender et al. 1998, Fahrig 1999, Harrison and Bruna 1999, Mazerolle and Villard 1999, Trzcinski et al. 1999, Connor et al. 2000, Langlois et al. 2001). In many instances, animals with different dispersal abilities (e.g., differences in vagility) are affected differently by identical structural changes in landscapes (Andrén 1994, Bender et al. 1998). Based on the results presented in this thesis, I conclude that, like animals, changes in landscape structure will have an effect on the abundance and distribution of woody plants remaining in the landscape beyond what would be predicted strictly by changes in habitat amount (i.e., loss of forest and the resulting increase in the amount of nonforest habitat). My results suggest that changes in the distribution and abundance of woody plant species within a landscape are due as

much to changes in a plant species' dispersal ability as they are to changes in environmental conditions associated with rates of seed germination and seedling establishment.

The seed density of open-habitat species in open habitats increases with decreasing forest cover in the landscape. For animal-dispersed open-habitat species, reduced forest cover may increase the connectivity of the landscape for animal seed dispersers, assuming forest habitat is a barrier to movement. For wind-dispersed open-habitat species there is less forest cover to interfere with the movement of air currents in the landscape and seeds are moved greater distances.

While mean stem densities of animal-dispersed, open-habitat species increased in forest habitats with decreasing forest cover in the landscape, the mean seed densities of wind-dispersed, open-habitat species did not (Fig. 3.4). This suggests that the dispersal ability of wind-dispersed species did not change in the same way as animal-dispersed species. Forest edge vegetation may act as a barrier to the movement of open-habitat wind-dispersed species into forest.

Additional disturbance in remaining forest patches (e.g., partial removal of canopy stem crowns) affected the emergence of seedlings and produced differences in the distribution of wind v. animal-dispersed seedlings along a forest cover gradient. In landscapes where there was reduced forest cover, the increased input of animal-dispersed seeds into forest patches likely resulted in a greater number of seeds present and a greater

number of seedlings germinating following the disturbance than in the forest patches of landscape with more forest cover.

5.2 IMPLICATIONS AND FUTURE DIRECTIONS

I was unable to control for factors associated with the seed and seedling mortality. Seed predation and seedling herbivory are important factors in determining the density of both seeds and stems in various habitats, particularly along forest edges (Ostfeld et al. 1997). There is also some evidence to suggest that the population dynamics of seed predators and seedling herbivores (mostly small mammal species) depends on changes in landscape structure (Santos and Telleria 1994). It is possible that if changes in small mammal densities are correlated with forest cover amount in the landscape then changes in seed, seedling, and even mature stem densities, could be a result of the relationship between seed and stem mortality and percent forest cover in the landscape.

To my knowledge, this is the first empirical study to examine changes in both plant species richness and the stem/seed density of plant species with different dispersal mechanisms along a gradient of landscape structure (amount of forest cover) across multiple landscapes. Other studies have extrapolated from the patch-scale to make inferences about effects of landscape structure (e.g., Matlack 1994a, Burke and Nol 1998) and some have studied a single large landscape (e.g., Elliott et al. 1997, Sarlöv Herlin and Fry 2000). Those studies have generally found a decrease in the species diversity of habitat patches with increasing distances between habitat patches in the landscape (Sarlöv

Herlin and Fry 2000; see also Grashof-Bokdam 1997). They suggest that species with generally long-distance dispersal are less affected by increasing distances between habitat patches and the species richness for these species is generally greater in more isolated patches than the species richness of species with lower dispersal ability (Grashof-Bokdam 1997, see also Metzger 2000). My results also suggest the importance of dispersal mechanisms in determining changes in the distribution of plant species within landscapes.

My results are important when considering the possible consequences of forest removal in a single landscape. I speculate that a reduction in forest cover within a landscape results in increased deposition of animal-dispersed seeds of nonforest habitats into both forest and nonforest habitats. There would also be an increase in the dispersal of seeds of nonforest, wind-dispersed species, but seed deposition would be restricted primarily to nonforest habitats. There would also be a reduction in the dispersal of both wind- and animal-dispersed forest species within forest habitats. Reducing the amount of forest habitat in the landscape would increase the invasion of remaining forest habitat by animal-dispersed species of nonforest habitats and canopy cover in remaining forest patches may make the germination and seedling establishment of these species difficult (many are shade intolerant). But as shown in Chapter 4, an opening up of the forest canopy by a disturbance will increase seedling emergence of these species. While changes in landscape forest cover might also have an effect on wind-dispersed forest species, their generally short dispersal distances means that seed placement is usually

within the stand or forest patch in which they originated. Even for those species with long distance secondary dispersal (e.g., *Betula alleghaniensis* Britt.), their germination requirements are quite strict (high light and bare substrate; see Burns and Honkala 1990, Sutherland et al. 2000) and they are unable to persist for long periods of time in the litter and soil (Mladenoff 1990, Peterson and Carson 1996). Also, less directed dispersal by prevailing winds means a relatively lower probability of reaching suitable microhabitats when compared to the more directed dispersal of animal-dispersed seeds with comparable seed dispersal distances (Schupp 1993, Cadenasso and Pickett 2001).

Given the nature of human-induced forest loss in agricultural and urban landscapes (Levenson 1981, Middleton and Merriam 1983, Hinsley et al. 1998, de Blois et al. 2001), there is constant perturbation of areas where forest cover has been removed (e.g., agricultural fields, pastures, housing developments, and urban areas). For landscapes with reduced forest cover, I expect a continual invasion of seeds of animal-dispersed species of open habitats into remaining forest patches and invasion of these species would increase with the removal of additional forest from the landscape. How this might affect the recruitment of forest species still needs to be investigated although the potential for increased recruitment of animal-dispersed, open-habitat species in forest does seem reasonable. In addition, many animal-dispersed open-habitat species have seeds that are capable of remaining dormant in the soil seed bank for long periods of time. Additional research will be needed to determine to what degree changes in stem

distributions for animal-dispersed species in landscapes are attributable to the deposition of their seeds in response to changes in landscape structure.

APPENDIX A

SPECIES LISTS

The following tables are species lists of observed stems, seedlings and seeds. Table A.1 lists stems observed in 1997 and the number of stems refers to both seedlings and larger stems. The number of observed stems are organized by species and by habitat (forest interior, forest edge, and old field/fencerow). Table A.2 lists a breakdown of species by size/age class: seeds, seedlings, and stems observed in 1997.

Table A.1: List of species found as stems in the study landscapes. Total refers to the total number of stems found and percent refers to the raw total number of stems for a species divided by the raw total number of stems for all species combined multiplied by 100. Refer to the section 2.3.3 for an explanation of dispersal, habitat, shade tolerance, and regeneration categories.

Species	Abundance						Life History Characteristics				
	All Habitats		Forest Edge		Forest Interior		Field/Fencerow Total Percent	Dispersal	Habitat	Shade Tolerance	Regeneration
	Total	Percent	Total	Percent	Total	Percent					
<i>Acer saccharum</i> Marsh.	4596	23.10	1947	25.57	2510	37.42	139	2.49	forest	shade	seed/clonal
<i>Rubus idaeus</i> L.	2149	10.80	462	6.07	93	1.39	1594	28.60	open	no shade	seed/clonal
<i>Fraxinus pennsylvanica</i> Marsh.	1407	7.07	656	8.61	515	7.68	236	4.23	forest	shade	seed/clonal
<i>Osirea virginiana</i> (Mill.) K. Koch	1016	5.11	433	5.69	463	6.90	120	2.15	forest	shade	seed/clonal
<i>Zanthoxylum americanum</i> Mill.	819	4.12	582	7.64	123	1.83	114	2.05	open	mod/shade	clonal
<i>Parthenocissus vitacea</i> (Kner) H. H. H.	660	3.32	207	2.72	108	1.61	345	6.19	forest/open	mod/shade	clonal
<i>Ilex verticillata</i> L.	655	3.29	175	2.30	443	6.61	37	0.66	forest	shade	seed/clonal
<i>Ulmus americana</i> L.	640	3.22	228	2.99	92	1.37	320	5.74	forest	mod/shade	seed/clonal
<i>Fraxinus americana</i> L.	596	3.00	236	3.10	214	3.19	146	2.62	forest	mod/shade	seed/clonal
<i>Rhamnus cathartica</i> L.	582	2.93	245	3.22	272	4.06	65	1.17	forest	shade	seed
<i>Urtica repens</i> Michx.	564	2.83	67	0.88	0	0.00	497	8.92	forest open	mod/shade	seed/clonal
<i>Ulmus americana</i> L.	526	2.64	380	4.99	119	1.77	27	0.48	forest	shade	clonal
<i>Rhus radicans</i> L.	472	2.37	183	2.40	210	3.13	79	1.42	forest/open	mod/shade	seed/clonal
<i>Fraxinus nigra</i> Marsh.	447	2.25	179	2.35	261	3.89	7	0.13	forest	mod/shade	seed/clonal
<i>Rubus occidentalis</i> L.	382	1.92	10	0.13	7	0.10	365	6.55	open	mod/shade	seed/clonal
<i>Spiraea alba</i> Du Roi	344	1.73	3	0.04	0	0.00	341	6.12	open	no shade	seed/clonal
<i>Acer saccharinum</i> L.	254	1.28	188	2.47	55	0.82	11	0.20	forest	no shade	seed/clonal
<i>Thuja occidentalis</i> L.	214	1.08	107	1.41	75	1.12	32	0.57	forest	shade	seed/clonal
<i>Populus tremuloides</i> Michx.	208	1.05	31	0.41	117	1.74	60	1.08	open	no shade	clonal
<i>Prunus serotina</i> Ehrh.	208	1.05	98	1.29	33	0.49	77	1.38	forest/open	no shade	seed/clonal
<i>Tsuga canadensis</i> (L.) Carr.	200	1.01	88	1.16	112	1.67	0	0.00	forest	shade	seed
<i>Fagus grandifolia</i> Ehrh.	188	0.94	97	1.27	91	1.36	0	0.00	forest	shade	seed/clonal
<i>Quercus rubra</i> L.	156	0.78	30	0.39	125	1.86	1	0.02	forest	mod/shade	seed/clonal
<i>Pinus strobus</i> L.	148	0.74	23	0.30	119	1.77	6	0.11	forest	mod/shade	seed
<i>Carya cordiformis</i> (Wang.) K. Koch	140	0.70	64	0.84	70	1.04	6	0.11	forest	shade	seed/clonal
<i>Populus balsamifera</i> L.	135	0.68	0	0.00	3	0.04	132	2.37	forest/open	no shade	clonal
<i>Cornus stolonifera</i> Michx.	117	0.59	0	0.00	3	0.04	114	2.05	open	no shade	seed/clonal

Table A.1: continued

Species	All Habitats				Abundance				Life History Characteristics				
	Total		Forest Edge		Forest Interior		Old Field/Fencerow		Dispersal	Habitat	Shade Tolerance	Regeneration	
	Percent	Total	Percent	Total	Percent	Total	Percent	Total					
<i>Abies balsamea</i> (L.) Mill.	99	0.50	39	0.51	54	0.81	6	0.11	wind	forest	shade	seed	
<i>Cornus rugosa</i> Lam.	99	0.50	14	0.18	15	0.22	70	1.26	animal	forest/open	modshade	seed/clonal	
<i>Acer negundo</i> L.	95	0.48	9	0.12	0	0.00	86	1.54	wind	open	no shade	seed/clonal	
<i>Betula papyrifera</i> Marsh.	93	0.47	48	0.63	45	0.67	0	0.00	wind	forest	no shade	seed/clonal	
<i>Juniperus communis</i> L.	93	0.47	19	0.25	0	0.00	74	1.33	animal	open	no shade	clonal	
<i>Quercus macrocarpa</i> Michx.	82	0.41	15	0.20	55	0.82	12	0.22	animal	forest	modshade	seed/clonal	
<i>Amus incana</i> (L.) Moench	79	0.40	8	0.11	3	0.04	68	1.22	wind	open	no shade	seed	
<i>Ribes</i> L.	79	0.40	49	0.64	10	0.15	20	0.36	animal	forest	modshade	seed	
<i>Viburnum lentago</i> L.	77	0.39	56	0.74	0	0.00	21	0.38	animal	forest/open	modshade	seed/clonal	
<i>Crataegus</i> L.	74	0.37	30	0.39	1	0.01	43	0.77	animal	open	no shade	seed	
<i>Rhamnus frangula</i> L.	70	0.35	69	0.91	0	0.00	1	0.02	animal	forest/open	no shade	seed	
<i>Salix discolor</i> Muhl.	66	0.33	0	0.00	0	0.00	66	1.18	wind	open	no shade	seed/clonal	
<i>Rubus</i> L.	65	0.33	65	0.85	0	0.00	0	0.00	animal	forest/open	modshade	seed/clonal	
<i>Carpinus caroliniana</i> Walt.	61	0.31	49	0.64	12	0.18	0	0.00	wind	forest	shade	seed	
<i>Ribes americanum</i> Mill.	61	0.31	18	0.24	23	0.34	20	0.36	animal	forest	modshade	seed/clonal	
<i>Populus grandidentata</i> Michx.	59	0.30	32	0.42	27	0.40	0	0.00	wind	open	no shade	clonal	
<i>Taxus canadensis</i> Marsh.	55	0.28	24	0.32	31	0.46	0	0.00	animal	forest	shade	clonal	
<i>Quercus alba</i> L.	53	0.27	25	0.33	18	0.27	10	0.18	animal	forest	modshade	seed/clonal	
<i>Betula alleghaniensis</i> Britt.	51	0.26	25	0.33	26	0.39	0	0.00	wind	forest	modshade	seed/clonal	
<i>Ulmus rubra</i> Muhl.	50	0.25	50	0.66	0	0.00	0	0.00	wind	forest	modshade	seed/clonal	
<i>Rubus pubescens</i> Raf.	49	0.25	49	0.64	0	0.00	0	0.00	animal	forest/open	modshade	seed/clonal	
<i>Salix bobbiana</i> Sarg.	43	0.22	0	0.00	0	0.00	43	0.77	wind	forest/open	modshade	seed/clonal	
<i>Cornus alternifolia</i> L. fil.	33	0.17	31	0.41	2	0.03	0	0.00	animal	forest/open	modshade	seed/clonal	
<i>Picea glauca</i> (Moench) Voss	33	0.17	30	0.39	0	0.00	3	0.05	wind	forest	shade	seed	
<i>Pinus sylvestris</i> L.	31	0.16	27	0.35	0	0.00	4	0.07	wind	forest	no shade	seed	
<i>Salix alba</i> L.	27	0.14	0	0.00	0	0.00	27	0.48	wind	forest/open	no shade	clonal	
<i>Vaccinium myrtilloides</i> Michx.	27	0.14	0	0.00	27	0.40	0	0.00	animal	open	modshade	seed/clonal	
<i>Rubus hispido</i> L.	26	0.13	0	0.00	15	0.22	11	0.20	animal	forest/open	modshade	seed/clonal	
<i>Hamamelis virginiana</i> L.	25	0.13	25	0.33	0	0.00	0	0.00	wind	forest	shade	seed	
<i>Acer pennsylvanicum</i> L.	24	0.12	3	0.04	21	0.31	0	0.00	wind	forest	shade	seed	

Table A.1: continued

Species	Abundance						Life History Characteristics				
	All Habitats		Forest Edge		Forest Interior		Dispersal	Habitat	Shade Tolerance	Regeneration	
	Total	Percent	Total	Percent	Total	Percent					
<i>Aronia melanocarpa</i> (Michx.) Ell.	24	0.12	0	0.00	24	0.36	0	0.00	forest	modshade	clonal
<i>Amelanchier</i> Medik.	23	0.12	3	0.04	17	0.25	3	0.05	forest	shade	seed/clonal
<i>Ribes lacustre</i> (Pers.) Poir.	23	0.12	20	0.26	0	0.00	3	0.05	forest/open	modshade	seed
<i>Lonicera canadensis</i> Bartt.	20	0.10	0	0.00	20	0.30	0	0.00	open	modshade	seed/clonal
<i>Acer spicatum</i> Lam.	16	0.08	8	0.11	8	0.12	0	0.00	forest	shade	seed/clonal
<i>Prunus pennsylvanica</i> L. fil.	16	0.08	2	0.03	0	0.00	14	0.25	open	no shade	seed/clonal
<i>Prunus virginiana</i> L. fil.	16	0.08	0	0.00	0	0.00	16	0.29	forest/open	modshade	clonal
<i>Viburnum acerifolium</i> L.	15	0.08	15	0.20	0	0.00	0	0.00	open	modshade	seed/clonal
<i>Malus</i> Mill.	14	0.07	1	0.01	1	0.01	12	0.22	open	modshade	seed/clonal
<i>Salix</i> L.	13	0.07	0	0.00	0	0.00	13	0.23	open	no shade	seed/clonal
<i>Pinus resinosa</i> Ait.	12	0.06	12	0.16	0	0.00	0	0.00	forest	modshade	seed
<i>Sambucus pubens</i> Michx.	12	0.06	10	0.13	1	0.01	1	0.02	open	shade	seed/clonal
<i>Symphoricarpus albus</i> (L.) Blake	10	0.05	0	0.00	0	0.00	10	0.18	open	no shade	seed/clonal
<i>Juglans cinerea</i> L.	9	0.05	6	0.08	2	0.03	1	0.02	forest	no shade	seed/clonal
<i>Rubus allegheniensis</i> Porter	8	0.04	0	0.00	3	0.04	5	0.09	open	no shade	seed/clonal
<i>Salix eriocephala</i> Michx.	8	0.04	0	0.00	0	0.00	8	0.14	open	no shade	seed/clonal
<i>Viburnum rafinesquianum</i> Schult.	8	0.04	0	0.00	0	0.00	8	0.14	forest	modshade	seed/clonal
<i>Salix petiolaris</i> J.E.Sm.	7	0.04	0	0.00	3	0.04	4	0.07	open	no shade	seed/clonal
<i>Rosa blanda</i> Ait.	6	0.03	0	0.00	6	0.09	0	0.00	open	no shade	seed/clonal
<i>Corylus cornuta</i> Marsh.	5	0.03	0	0.00	0	0.00	5	0.09	forest	no shade	seed/clonal
<i>Lonicera tatarica</i> L.	5	0.03	0	0.00	0	0.00	5	0.09	open	modshade	seed
<i>Dirca palustris</i> L.	4	0.02	2	0.03	2	0.03	0	0.00	forest	shade	seed
<i>Pinus banksiana</i> Lamb.	4	0.02	4	0.05	0	0.00	0	0.00	forest	no shade	seed
<i>Salix fragilis</i> L.	4	0.02	0	0.00	0	0.00	4	0.07	open	no shade	seed/clonal
<i>Populus deltoides</i> Bartt.	3	0.02	0	0.00	0	0.00	3	0.05	open	no shade	seed/clonal
<i>Acer nigrum</i> Michx.	2	0.01	2	0.03	0	0.00	0	0.00	forest	shade	seed/clonal
<i>Lonicera oblongifolia</i> (Goldie) Hook.	2	0.01	2	0.03	0	0.00	0	0.00	forest	modshade	seed/clonal
<i>Ribes cyanosbat</i> L.	2	0.01	0	0.00	2	0.03	0	0.00	forest	modshade	seed
<i>Salix humilis</i> Marsh.	1	0.01	0	0.00	0	0.00	1	0.02	forest/open	modshade	seed/clonal
<i>Spiraea tomentosa</i> L.	1	0.01	0	0.00	0	0.00	1	0.02	open	no shade	seed/clonal

Table A.2: List of species in each of the 3 size/age categories: seeds, seedlings, and stems used in Chapter 3. Total refers to the raw number of individuals observed and percent refers to the raw total number of individuals for a species in that size/age class divided by the raw total number of individuals for all species in that size/age class combined multiplied by 100. Refer to section 2.3.3 for an explanation of DISPERSAL, HABITAT, and SHADE. (?) = no available information for a variable).

Species	Total	Percent	DISPERSAL	HABITAT	SHADE
Seeds					
<i>Rubus idaeus</i> L.	960	72.07	animal	open	no shade
<i>Betula alleghaniensis</i> Britt.	170	12.76	wind	forest	modshade
<i>Sambucus pubens</i> Michx.	76	5.71	animal	open	shade
<i>Crataegus</i> L.	22	1.65	animal	open	no shade
<i>Vitis riparia</i> Michx.	22	1.65	animal	forest/open	modshade
<i>Diervilla lonicera</i> Mill.	20	1.50	animal	open	modshade
<i>Ostrya virginiana</i> (Mill.) K. Koch	12	0.90	wind	forest	shade
<i>Zanthoxylum americanum</i> Mill.	12	0.90	animal	open	modshade
<i>Rubus occidentalis</i> L.	11	0.83	animal	open	modshade
<i>Acer negundo</i> L.	4	0.30	wind	open	no shade
<i>Rhamnus cathartica</i> L.	4	0.30	animal	forest	shade
<i>Rubus odoratus</i> L.	4	0.30	animal	open	no shade
<i>Betula papyrifera</i> Marsh.	3	0.23	wind	forest	modshade
<i>Fraxinus americana</i> L.	2	0.15	wind	forest	modshade
<i>Fraxinus pennsylvanica</i> Marsh.	2	0.15	wind	forest	shade
<i>Acer rubrum</i> L.	1	0.08	wind	forest	shade
<i>Carya cordiformis</i> (Wang.) K. Koch	1	0.08	animal	forest	shade
<i>Cornus</i> L.	1	0.08	animal	?	?
<i>Pinus strobus</i> L.	1	0.08	wind	forest	modshade
<i>Populus tremuloides</i> Michx.	1	0.08	wind	open	no shade
<i>Rhus typhina</i> L.	1	0.08	wind	open	no shade
<i>Rosa blanda</i> Ait.	1	0.08	animal	open	no shade
<i>Ulmus americana</i> L.	1	0.08	wind	forest	modshade

Table A.2: continued

Species	Total	Percent	DISPERSAL	HABITAT	SHADE
Seedlings (stems < 1m in height)					
<i>Acer saccharum</i> Marsh.	2616	56.72	wind	forest	shade
<i>Fraxinus pennsylvanica</i> Marsh.	351	7.61	wind	forest	shade
<i>Acer rubrum</i> L.	250	5.42	wind	forest	shade
<i>Ostrya virginiana</i> (Mill.) K. Koch	220	4.77	wind	forest	shade
<i>Fraxinus nigra</i> Marsh.	149	3.23	wind	forest	modshade
<i>Fraxinus americana</i> L.	125	2.71	wind	forest	modshade
<i>Acer saccharinum</i> L.	114	2.47	wind	forest	no shade
<i>Rubus idaeus</i> L.	75	1.63	animal	open	no shade
<i>Rhamnus cathartica</i> L.	69	1.50	animal	forest	shade
<i>Tilia americana</i> L.	69	1.50	wind	forest	shade
<i>Carya cordiformis</i> (Wang.) K. Koch	68	1.47	animal	forest	shade
<i>Ulmus americana</i> L.	55	1.19	wind	forest	modshade
<i>Betula papyrifera</i> Marsh.	48	1.04	wind	forest	no shade
<i>Quercus macrocarpa</i> Michx.	37	0.80	animal	forest	modshade
<i>Tsuga canadensis</i> (L.) Carr.	32	0.69	wind	forest	shade
<i>Rhus radicans</i> L.	30	0.65	animal	forest/open	modshade
<i>Vaccinium myrtilloides</i> Michx.	27	0.59	animal	open	modshade
<i>Quercus rubra</i> L.	26	0.56	animal	forest	modshade
<i>Vitis riparia</i> Michx.	26	0.56	animal	forest/open	modshade
<i>Spiraea alba</i> Du Roi	24	0.52	wind	open	no shade
<i>Parthenocissus vitacea</i> (Knerr.) Hitchc.	21	0.46	animal	forest/open	modshade
<i>Zanthoxylum americanum</i> Mill.	20	0.43	animal	open	modshade
<i>Acer negundo</i> L.	19	0.41	wind	open	no shade
<i>Rhamnus frangula</i> L.	17	0.37	animal	forest/open	no shade
<i>Pinus sylvestris</i> L.	15	0.33	wind	forest	no shade
<i>Prunus serotina</i> Ehrh.	11	0.24	animal	forest/open	no shade
<i>Viburnum acerifolium</i> L.	11	0.24	animal	open	modshade
<i>Ribes americanum</i> Mill.	10	0.22	animal	forest	modshade
<i>Ribes</i> L.	10	0.22	animal	forest	modshade

Table A.2: continued

Species	Total	Percent	DISPERSAL	HABITAT	SHADE
Seedlings (cont.)					
<i>Pinus strobus</i> L.	8	0.17	wind	forest	modshade
<i>Ribes lacustre</i> (Pers.) Poir.	8	0.17	animal	forest/open	modshade
<i>Quercus alba</i> L.	7	0.15	animal	forest	modshade
<i>Acer pensylvanicum</i> L.	6	0.13	wind	forest	shade
<i>Carpinus caroliniana</i> Walt.	6	0.13	wind	forest	shade
<i>Rubus occidentalis</i> L.	6	0.13	animal	open	modshade
<i>Fagus grandifolia</i> Ehrh.	5	0.11	animal	forest	shade
<i>Amelanchier</i> Medik.	4	0.09	animal	forest	shade
<i>Betula alleghaniensis</i> Britt.	4	0.09	wind	forest	modshade
<i>Ulmus rubra</i> Muhl.	4	0.09	wind	forest	modshade
<i>Crataegus</i> L.	3	0.07	animal	open	no shade
<i>Populus grandidentata</i> Michx.	3	0.07	wind	open	no shade
<i>Thuja occidentalis</i> L.	2	0.04	wind	forest	shade
<i>Abies balsamea</i> (L.) Mill.	1	0.02	wind	forest	shade
Stems (stems > 1m in height)					
<i>Rubus idaeus</i> L.	2074	13.57	animal	open	no shade
<i>Acer saccharum</i> Marsh.	1980	12.96	wind	forest	shade
<i>Fraxinus pennsylvanica</i> Marsh.	1056	6.91	wind	forest	shade
<i>Zanthoxylum americanum</i> Mill.	799	5.23	animal	open	modshade
<i>Ostrya virginiana</i> (Mill.) K. Koch	796	5.21	wind	forest	shade
<i>Parthenocissus vitacea</i> (Kneerr.) Hitchc.	639	4.18	animal	forest/open	modshade
<i>Ulmus americana</i> L.	585	3.83	wind	forest	modshade
<i>Vitis riparia</i> Michx.	538	3.52	animal	forest/open	modshade
<i>Rhamnus cathartica</i> L.	513	3.36	animal	forest	shade
<i>Fraxinus americana</i> L.	471	3.08	wind	forest	modshade
<i>Tilia americana</i> L.	457	2.99	wind	forest	shade
<i>Rhus radicans</i> L.	442	2.89	animal	forest/open	modshi
<i>Acer rubrum</i> L.	405	2.65	wind	forest	shad

Table A.2: continued

Species	Total	Percent	DISPERSAL	HABITAT	SHADE
Stems (cont.)					
<i>Rubus occidentalis</i> L.	376	2.46	animal	open	modshade
<i>Spiraea alba</i> Du Roi	320	2.09	wind	open	no shade
<i>Fraxinus nigra</i> Marsh.	298	1.95	wind	forest	modshade
<i>Thuja occidentalis</i> L.	212	1.39	wind	forest	shade
<i>Populus tremuloides</i> Michx.	208	1.36	wind	open	no shade
<i>Prunus serotina</i> Ehrh.	197	1.29	animal	forest/open	no shade
<i>Fagus grandifolia</i> Ehrh.	183	1.20	animal	forest	shade
<i>Tsuga canadensis</i> (L.) Carr.	168	1.10	wind	forest	shade
<i>Acer saccharinum</i> L.	140	0.92	wind	forest	no shade
<i>Pinus strobus</i> L.	140	0.92	wind	forest	modshade
<i>Populus balsamifera</i> L.	135	0.88	wind	forest/open	no shade
<i>Quercus rubra</i> L.	130	0.85	animal	forest	modshade
<i>Cornus stolonifera</i> Michx.	117	0.77	animal	open	no shade
<i>Cornus rugosa</i> Lam.	99	0.65	animal	forest/open	modshade
<i>Abies balsamea</i> (L.) Mill.	98	0.64	wind	forest	shade
<i>Juniperus communis</i> L.	93	0.61	animal	open	no shade
<i>Alnus incana</i> (L.) Moench	79	0.52	wind	open	no shade
<i>Viburnum lentago</i> L.	77	0.50	animal	forest/open	modshade
<i>Acer negundo</i> L.	76	0.50	wind	open	no shade
<i>Carya cordiformis</i> (Wang.) K. Koch	72	0.47	animal	forest	shade
<i>Crataegus</i> L.	71	0.46	animal	open	no shade
<i>Ribes</i> L.	69	0.45	animal	forest	modshade
<i>Salix discolor</i> Muhl.	66	0.43	wind	open	no shade
<i>Rubus</i> L.	65	0.43	animal	forest/open	modshade
<i>Populus grandidentata</i> Michx.	56	0.37	wind	open	no shade
<i>Carpinus caroliniana</i> Walt.	55	0.36	wind	forest	shade
<i>Taxus canadensis</i> Marsh.	55	0.36	animal	forest	shade
<i>Rhamnus frangula</i> L.	53	0.35	animal	forest/open	no shade
<i>Ribes americanum</i> Mill.	51	0.33	animal	forest	modshad

Table A.2: continued

Species	Total	Percent	DISPERSAL	HABITAT	SHADE
Stems (cont.)					
<i>Rubus pubescens</i> Raf.	49	0.32	animal	forest/open	modshade
<i>Betula alleghaniensis</i> Britt.	47	0.31	wind	forest	modshade
<i>Quercus alba</i> L.	46	0.30	animal	forest	modshade
<i>Ulmus rubra</i> Muhl.	46	0.30	wind	forest	modshade
<i>Betula papyrifera</i> Marsh.	45	0.29	wind	forest	no shade
<i>Quercus macrocarpa</i> Michx.	45	0.29	animal	forest	modshade
<i>Salix hebbiana</i> Sarg.	43	0.28	wind	forest/open	modshade
<i>Cornus alternifolia</i> L. fil.	33	0.22	animal	forest/open	modshade
<i>Picea glauca</i> (Moench) Voss	33	0.22	wind	forest	shade
<i>Salix alba</i> L.	27	0.18	wind	forest/open	no shade
<i>Rubus hispida</i> L.	26	0.17	animal	forest/open	modshade
<i>Hamamelis virginiana</i> L.	25	0.16	wind	forest	shade
<i>Aronia melanocarpa</i> (Michx.) Ell.	24	0.16	animal	forest	modshade
<i>Lonicera canadensis</i> Bartr.	20	0.13	animal	open	modshade
<i>Amelanchier</i> Medik.	19	0.12	animal	forest	shade
<i>Acer pensylvanicum</i> L.	18	0.12	wind	forest	shade
<i>Acer spicatum</i> Lam.	16	0.10	wind	forest	shade
<i>Pinus sylvestris</i> L.	16	0.10	wind	forest	no shade
<i>Prunus pensylvanica</i> L. fil.	16	0.10	animal	open	no shade
<i>Prunus virginiana</i> L. fil.	16	0.10	animal	forest/open	modshade
<i>Ribes lacustre</i> (Pers.) Poir.	15	0.10	animal	forest/open	modshade
<i>Malus</i> Mill.	14	0.09	animal	open	modshade
<i>Salix</i> L.	13	0.09	wind	open	no shade
<i>Pinus resinosa</i> Ait.	12	0.08	wind	forest	modshade
<i>Sambucus pubens</i> Michx.	12	0.08	animal	open	shade
<i>Symphoricarpus albus</i> (L.) Blake	10	0.07	animal	open	no shade
<i>Juglans cinerea</i> L.	9	0.06	animal	forest	no shade
<i>Rubus allegheniensis</i> Porter	8	0.05	animal	open	no shade
<i>Salix eriocephala</i> Michx.	8	0.05	wind	open	no shade

Table A.2: continued

Species	Total	Percent	DISPERSAL	HABITAT	SHADE
Stems (cont.)					
<i>Viburnum rafinesquianum</i> Schult.	8	0.05	animal	forest	modshade
<i>Salix petiolaris</i> J.E.Sm.	7	0.05	wind	open	no shade
<i>Rosa blanda</i> Ait.	6	0.04	animal	open	no shade
<i>Corylus cornuta</i> Marsh.	5	0.03	animal	forest	no shade
<i>Lonicera tatarica</i> L.	5	0.03	animal	open	modshade
<i>Dirca palustris</i> L.	4	0.03	animal	forest	shade
<i>Pinus banksiana</i> Lamb.	4	0.03	wind	forest	no shade
<i>Salix fragilis</i> L.	4	0.03	wind	open	no shade
<i>Viburnum acerifolium</i> L.	4	0.03	animal	open	modshade
<i>Populus deltoides</i> Bartr.	3	0.02	wind	open	no shade
<i>Acer nigrum</i> Michx.	2	0.01	wind	forest	shade
<i>Lonicera oblongifolia</i> (Goldie) Hook.	2	0.01	animal	forest	modshade
<i>Ribes cyanosbatii</i> L.	2	0.01	animal	forest	modshade
<i>Salix humilis</i> Marsh.	1	0.01	wind	forest/open	modshade
<i>Spiraea tomentosa</i> L.	1	0.01	wind	open	no shade

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