

INFLUENCES OF PAST AGRICULTURE AND PRESENT ENVIRONMENT
ON PLANT DISTRIBUTIONS: POPULATION ECOLOGY
OF THREE FERN SPECIES IN CENTRAL NEW YORK FORESTS

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by

Kathryn McQuilkin Flinn

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Kathryn McQuilkin Flinn, Ph.D.

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The development of forests on abandoned agricultural lands provides an ideal context to examine the relative roles of disturbance history and environmental conditions in shaping plant communities. Herbaceous plants typical of uncleared forests may remain absent from forests regrowing after agriculture, either because dispersal limits their distributions, or because lasting environmental changes limit their ability to establish and persist. Here I investigate how these processes affect plant distributions across the post-agricultural landscape of central New York, focusing on three fern species.

First I review relevant literature on the recolonization of post-agricultural forests by herbaceous plants. Next, in 20 adjacent pairs of forests that were never cleared for agriculture and forests that established 85-100 years ago on plowed fields, I assess the influence of past agriculture on present environmental conditions, including tree community structure and composition, soil physical and chemical properties and light availability. Compared to soils of adjacent uncleared stands, post-agricultural forest soils were similar in physical properties and chemical properties associated with pH, but had less organic matter, carbon and phosphorus, and reduced spatial heterogeneity in pH and water content. I examine how individual species interact with post-agricultural habitats by comparing the demography of three fern species with contrasting distributions across forests of different history, *Dryopteris carthusiana*, *Dryopteris intermedia*, and *Polystichum acrostichoides*, using descriptive and experimental approaches to specify which life history stages limit colonization,

and which traits explain the species' distributions. Among the three species and between forests types, I compare the size and fecundity of adult plants; the deposition and storage of spores; the reproductive success and selfing ability of gametophytes; rates of germination and establishment in various microsites; and the distribution of juvenile plants across these microsites. As adult plants of all three species had similar or greater performance in post-agricultural forests, and spore availability far exceeded recruitment rates, the availability of suitable sites for establishment appeared to limit population growth and spread. In both field and laboratory experiments, the species' reproductive success and selfing ability matched their distributions, suggesting that selfing may facilitate colonization in these species, and their reproductive biology may determine their distributions.

BIOGRAPHICAL SKETCH

Kathryn McQuilkin Flinn was born on October 25, 1978 in Pittsburgh, Pennsylvania, to Charles Curtis and Diana Lytle Flinn. She grew up near the town of Indiana in rural western Pennsylvania, a historical hotbed of Scots-Irish Presbyterians, a mined-out coal region, and the self-proclaimed Christmas Tree Capital of the World.

Ms. Flinn's ecological education began in childhood, with much time spent outdoors. As practical biologists, a forester and a dietician, her parents cultivated their daughter's love of nature and science. Her father took her along wood-cutting, blackberry-picking, coon-hunting, fishing; and her mother cheerfully tolerated these uncivilized pursuits. They brought her and her brother Martin to spend weeks of each summer swimming in the lake on the Flinn farm near St. Louis, Missouri. They marked off her very own five-by-five-foot plot of the family's vast vegetable garden and set her to work. Ms. Flinn also showed an early interest in cryptogams, harboring an uncanny fascination with a grotto-like mossy spot in the woods at the edge of the backyard. She graduated from Indiana High School in 1996.

Ms. Flinn then went to the College of William and Mary in Williamsburg, Virginia, concentrating in both Biology and English. In the Biology department, she was most fortunate to meet Martha Case, Stewart Ware and Donna Marie Eggers Ware. With them, and with steadfast friend and crack naturalist Heather Sahli, she spent many pleasant days botanizing. Thus Ms. Flinn began to learn botany in the swamps and sandy oak woods of Virginia's Tidewater, as well as on numerous pilgrimages to the Blue Ridge. At the same time, S. Ware's stories about Catherine Keever's studies of old-field succession captured her fancy. Her honors thesis project, with advisor Martha Case, used herbarium specimens to document historical changes in the distribution and abundance of American ginseng.

Ms. Flinn spent the summer of 1999 at the University of Michigan Biological Station, in northernmost lower Michigan. There she worked with Allison Snow to investigate how pollinator preferences could influence the persistence of crop genes in wild plant populations. Chasing bees through wild radish patches, she gained her first experience of field ecology research.

By this time Ms. Flinn had decided to pursue her interest in understanding patterns of plant distribution and diversity, and particularly how they interact with human and natural disturbances. In 2000, she came to Cornell University to work with Peter Marks and to study the legacies of agriculture in the forests of Tompkins County, New York. During her graduate studies, Ms. Flinn also enjoyed field ecology courses at Archbold Biological Station in Florida and the Laboratory of Tree-Ring Research at the University of Arizona in Tuscon. In July 2006 she will begin postdoctoral research, studying the evolutionary ecology of sedges with Martin Lechowicz, Marcia Waterway and Graham Bell, at McGill University in Montréal, Québec.

As for man, his days are as grass:
as a flower of the field, so he flourisheth.
For the wind passeth over it, and it is gone;
and the place thereof shall know it no more.

Psalm 103

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Rob Hirsch, Catharine Hoffman, Scott Roche, Véronique Connolly, and Brian Tarpinian, as well as Peter, Sana and Mark.

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My work benefited from opportunities to travel, present research and interact with colleagues at the Harvard Forest in Petersham, Massachusetts, David Foster and Glenn Motzkin, and at the Laboratory for Forest, Nature and Landscape Research in Leuven, Belgium, especially Bea Bossuyt and Kris Verheyen. Dom Paolillo, Don Farrar, Tom Ranker and Jordan Metzgar provided crucial advice and encouragement about growing fern gametophytes.

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CHAPTER ONE
RECOVERY OF FOREST PLANT COMMUNITIES IN
POST-AGRICULTURAL LANDSCAPES

Abstract. As landscapes throughout Europe and eastern North America recover from past agricultural use, forests continue to reflect their agricultural history. For centuries after agriculture has ceased, plant communities on abandoned agricultural lands remain impoverished in herbaceous species characteristic of uncleared forests. To facilitate the recovery of biological diversity in these forests, and to anticipate the effects of future land-use decisions, we need to understand the process of recolonization. The unique interactions between forest herbs and agricultural history also allow us to explore some universal questions in ecology, such as how dispersal and environment limit species distributions.

INTRODUCTION

The profound impacts of human land use on biological diversity via habitat loss and fragmentation cause intense concern among ecologists and conservationists. Despite the abundance and importance of restored habitats, however, much less attention has focused on how communities respond as landscapes recover from human disturbance. Understanding the long-term consequences of past land-use decisions is critical, not only to inform resource managers about existing communities, but also to predict the effects of future disturbance and environmental change.

Today, many landscapes worldwide continue to bear the imprint of historical land-use patterns. Across much of Europe and eastern North America, for example, phases of forest clearance for agriculture were followed by agricultural abandonment and forest regrowth (Figure 1.1). In some regions, forests that developed on former

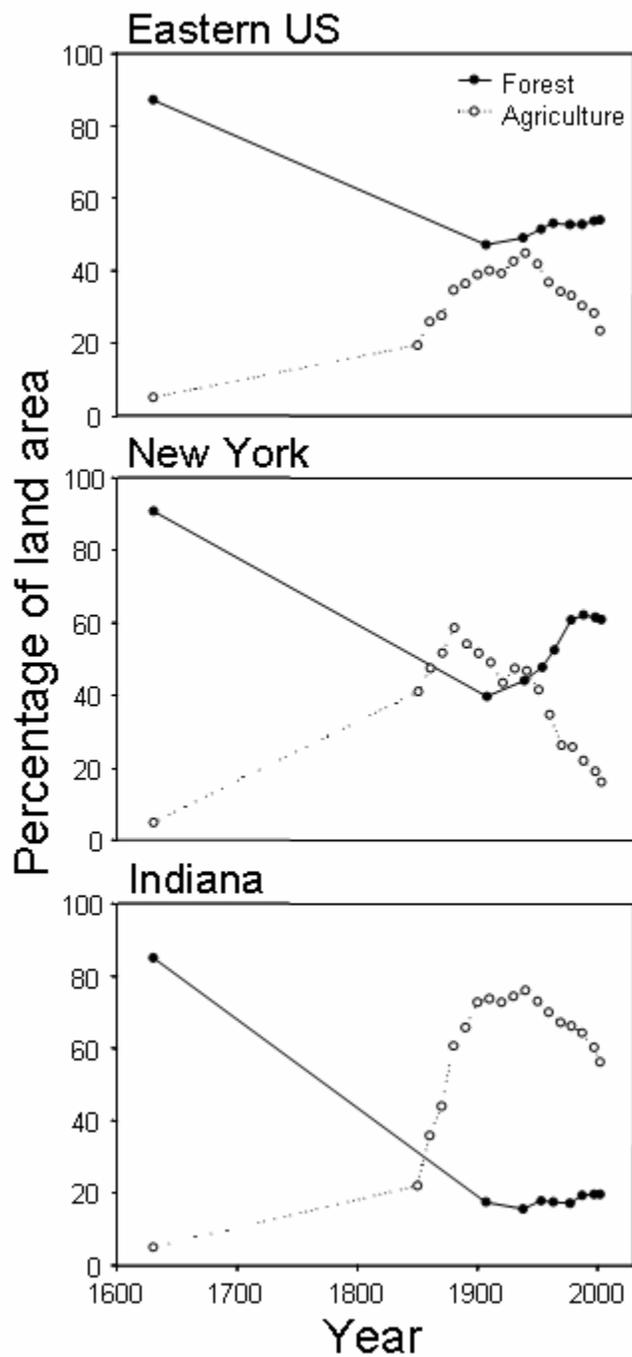


Figure 1.1. Changes over time in forest cover and agricultural land area in the eastern US (all states east of the Mississippi River) and the states of New York and Indiana. Land cover estimates for 1700 are approximate. From USDA Forest Inventory and Analysis and Agriculture Census data (Smith et al. 2004).

agricultural lands represent as much as 80% of current forest cover (Foster 1992, Grashof-Bokdam and Geertsema 1998). These habitats often differ in vegetation and soils from forests that were never cleared for agriculture, even 2000 years after reforestation (Dupouey et al. 2002). Such observations lead ecologists to ask whether post-agricultural forests will ever resemble their pre-disturbance condition. If so, how long will it take? Or, has human land use created novel communities that will persist unless active restoration intervenes?

At the same time, these patterns also raise basic ecological questions about controls on species distribution and abundance. Landscapes with a history of agriculture provide an ideal opportunity to assess the influence of past disturbance versus environmental conditions on current vegetation. In fact, it has become increasingly clear that many modern patterns and processes cannot be explained without taking into account the pervasive and persistent legacies of historical land use. Following the classic work of Rackham (1980) and Peterken (1981) in Britain, ecologists have shown a growing interest in investigating how past land use shapes current communities. While interactions between agricultural history and present-day forest communities have been examined across the neotropics and elsewhere, the past several decades have seen a spate of particularly active research (~100 papers in the past 20 years) focusing on herbaceous understory plants in north-temperate deciduous forests. Here we highlight the key insights that have emerged from this work and discuss new directions.

Reconstructing history

All studies of the implications of past land use rely on accurate reconstructions of history. Historical land-use maps and aerial photographs provide the most useful information for documenting forest cover changes over time. These sources can

distinguish remnants of ancient forest from recent, restored forests on former agricultural lands and establish the age of recent patches (Smith et al. 1993). More specific site histories, including whether a parcel of land was plowed or pastured, may be constructed through interviews with landowners and observations of field evidence such as stone walls, treefall pits and mounds, and open-grown trees (Marks and Gardescu 2001). These methods yield detailed, spatially explicit historical reconstructions that typically span 100-400 years and range from individual woodlots to whole counties. They thereby complement historical information from other approaches, such as palynology and dendrochronology, by providing a unique intermediate time scale and a high level of local detail.

Defining forest types

Forest patches in post-agricultural landscapes can be differentiated with two sets of terms (Rackham 1980, Peterken 1981). “Primary” forests were never cleared for agriculture, whereas “secondary” forests developed on former agricultural land. In most of Europe, where agricultural use and abandonment may predate the oldest land-use maps, identifying primary forests is difficult or impossible. Thus, woodlands are often functionally classified as “ancient”—forests that have existed continuously since the time of the earliest land-use maps, or “recent”—forests that originated after that time on land known to have been in agriculture. We use the terms “ancient” and “recent” forest in this paper.

In North America, ancient forests are generally also primary. In Europe, ancient forests may include both primary and ancient secondary forests. Primary forests are not necessarily old-growth. In fact, nearly all primary forests have been selectively cut, and many have been grazed by livestock. Clearing and agricultural activities in the surrounding landscape also affect habitats within existing primary forests.

Focusing on forest herbs

Agriculture alters entire plant communities, including tree and shrub species composition. After abandonment, old fields are initially colonized by herbaceous species that prefer open habitats. A dense thicket of shrubs and trees typically develops within 30-40 years, and a closed tree canopy in about 60-80 years. Dominant tree genera in both European and eastern North American temperate deciduous forests include beech (*Fagus*), maple (*Acer*), basswood (*Tilia*) and oak (*Quercus*), with a few conifers such as pine (*Pinus*). The identity and relative abundance of canopy species in post-agricultural forests often differ from communities undisturbed by agriculture (e.g. Motzkin et al. 1996). However, recolonization by forest herbs has been of particular interest as forests regrow, since herbaceous understory species represent the majority of plant diversity in temperate forests, and unlike many trees and shrubs, forest herb populations are not altered by planting and harvesting. Forest herbs also share life-history traits that may make them more sensitive to habitat loss and fragmentation, such as short-distance seed dispersal mechanisms, short seed dormancy, low seedling recruitment, and long pre-reproductive periods (Whigham 2004). Post-agricultural landscapes thus provide an opportunity to see how species evidently adapted to temporally stable, spatially continuous habitats respond to dynamic and fragmented landscapes.

Dispersal versus recruitment limitation

Having distinguished habitats with different histories and identified species of interest, ecologists can ask, how does vegetation vary with land-use history, and more interestingly, why? To what extent are species distributions determined by the availability of suitable habitat, and to what extent are they determined by chance, history and limited dispersal? These are fundamental questions in ecology, and to

address them in this context it is necessary to assess whether land-use history influences environmental conditions in current forests, as well as what roles land-use history and environmental conditions play in determining plant distribution, diversity and performance (Figure 1.2). Types of information collected to date include descriptions of forest environments and vegetation, including their relationships with plant life-history traits and landscape attributes; observational studies of plant performance; and experimental introductions.

ENVIRONMENTAL CHARACTERIZATIONS

Agriculture potentially affects vegetation both directly, by locally eliminating plants and propagules of forest species, and indirectly, by altering environmental conditions. To fully assess these impacts, it is important to know how ancient and recent forests differ in the environment they provide for understory plants. Soils recovering from agriculture generally have higher pH and nutrient concentrations and lower organic matter content than soils under continuous forest cover (Koerner et al. 1997). However, the magnitude and persistence of these differences show tremendous variation among regions. Recent forest soils may continue to reflect their agricultural history over 100 years after reforestation (Koerner et al. 1997, Verheyen et al. 1999, Dupouey et al. 2002). Alternatively, as an equal number of studies have found, they may become broadly similar to ancient forest soils within that time (Kalisz 1986, Compton and Boone 2000, Flinn et al. 2005). This regional variation can be difficult to predict because it depends on complex interactions among inherent soil fertility, the nature and duration of agricultural use, and time since abandonment. Thus, environmentally mediated effects of land use on vegetation may be quite important in some landscapes while nonexistent in others.

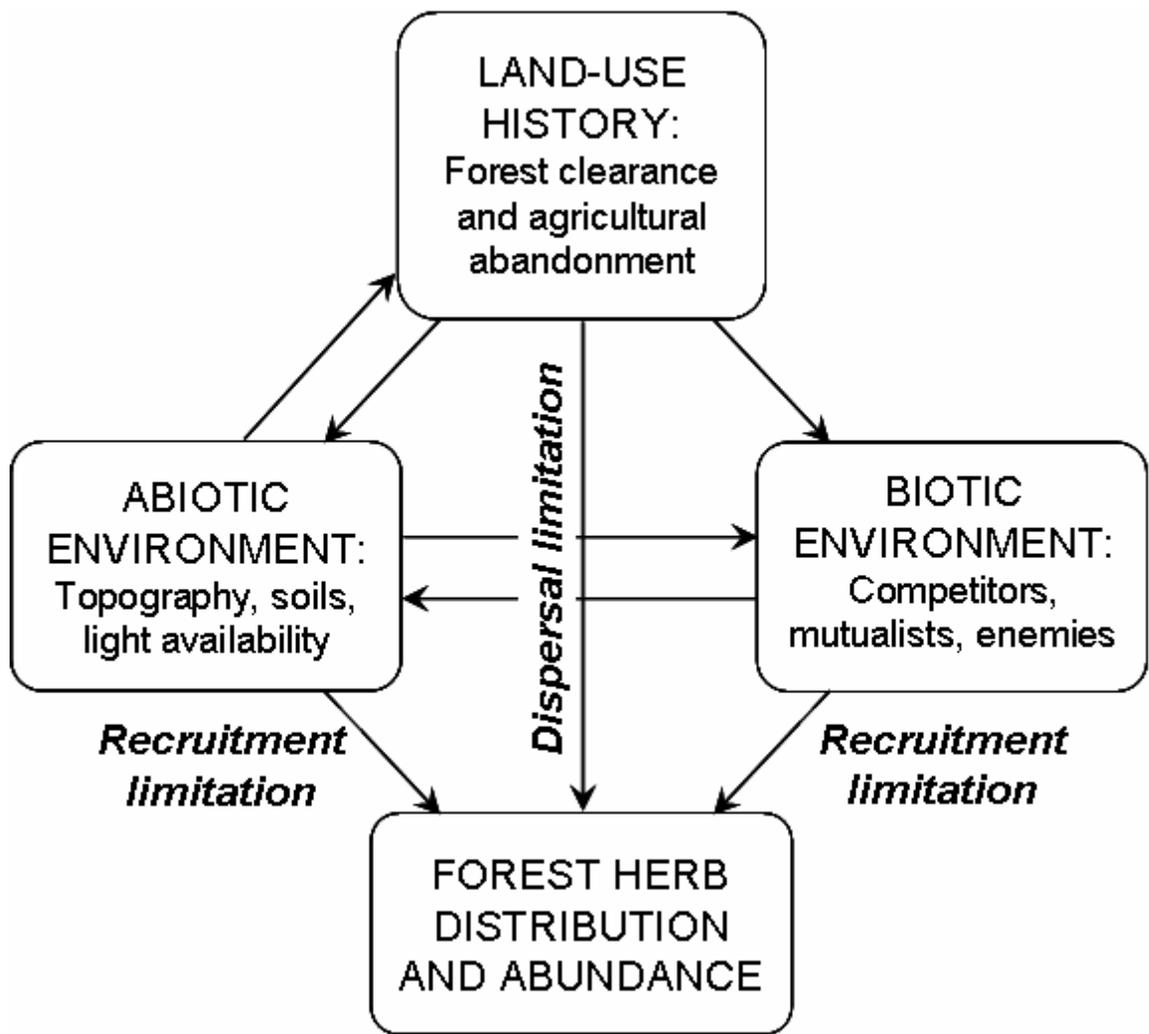


Figure 1.2. Conceptual diagram showing both direct and indirect effects of land-use history on forest herb distribution and abundance. Forest clearance destroys and fragments forest herb communities, and agricultural abandonment creates new, unoccupied habitats, producing dispersal limitation. Agriculture may also impose recruitment limitation on forest herb populations by altering biotic and abiotic environments.

A major caveat in interpreting environmental differences between ancient and recent forests, as well as their implications for plant communities, is that geographical patterns of land use and environmental variation are often confounded. Steeper slopes, poorer soils, and wetter areas are less likely to be cleared for agriculture and more likely to be abandoned (Foster 1992, Matlack 1997, Flinn et al. 2005). Differences in environment and vegetation among current forest types may result from initial conditions rather than agricultural land use itself. Particularly in regions with limited forest cover, investigators must rely on some overlap in environmental conditions between forest types and attempt to isolate the direct effects of land use statistically. One way to control for pre-existing environmental variation is to focus on regions where past land use varies across an area homogenous in topography and soils (Motzkin et al. 1996). Within more diverse landscapes, variation in prior conditions can be eliminated by selecting adjacent pairs of sites that share similar topography and soils, but that differ in history (Kalisz 1986, Singleton et al. 2001, Flinn et al. 2005).

VEGETATION COMPOSITION

Differences between the understory communities of ancient and recent forests have been thoroughly documented in regions throughout Europe (Peterken and Game 1984, Dzwonko and Loster 1989, Graae 2000, Wulf 2004) and the northeastern US (Matlack 1994, Motzkin et al. 1996, Singleton et al. 2001, Bellemare et al. 2002). One recent study also compared the vegetation of former coppice woodlands and meadows in Japan (Ito et al. 2004). From this body of work, the principal result is abundantly clear: land-use history has a consistently strong influence on plant diversity and distributions. The impact of past land use on vegetation patterns can equal or even override the effects of topography, soils, subsequent disturbance, and current

management (Motzkin et al. 1996). In many landscapes, variation in plant community composition largely reflects the former distribution of woodlots and agricultural fields (Glitzenstein et al. 1990, Foster 1992, Motzkin et al. 1996, Dupouey et al. 2002).

In fact, modern vegetation can be specifically associated with particular types of former agricultural use, such as croplands, pastures, or hay meadows, and species may respond quite differently to different forms of agriculture (Koerner et al. 1997, Grashof-Bokdam and Geertsema 1998, Stover and Marks 1998, Wulf 2004). Former pastures tend to be most similar to ancient forests in species richness and composition, in part because the lack of plowing allowed relict populations of forest plants to persist (Glitzenstein et al. 1990, Koerner et al. 1997, Wulf 2004). Specific agricultural practices have unique effects, and finer categories may be necessary to discern them (cf. Verheyen et al. 1999).

Comparing species richness

One way to compare the effects of land-use history across different regions is to examine the species richness of recent forests relative to ancient forests. Comparisons of species richness depend, in part, on how species pools are defined, and these definitions have not been consistent across studies. Some restrict surveys to species that grow exclusively in forests, whereas some include all species growing in forests, regardless of their habitat affinity. Old-field species that persist as forests develop may contribute to higher total diversity in recent forests. On a Massachusetts sand plain, for example, lands taken out of cultivation 30-50 years before had the highest species richness of any community type, due to a high frequency of weedy and early successional species (Motzkin et al. 1996). However, most studies focusing on “native woodland species” or “ancient forest species” have found reduced species richness in understory communities of recent forests compared to ancient forests

(Peterken and Game 1984, Dzwonko and Loster 1989, Matlack 1994, Bossuyt et al. 1999, Singleton et al. 2001, Vellend 2004; Figure 1.3).

This result is not universal; some recent forests are apparently old enough to have gained species numbers comparable to those found in ancient forests. In several studies, older recent forests (>70 years old) had similar forest herb species richness to ancient forests, and only younger recent forests had less richness (e.g. Bellemare et al. 2002). Another case where recent forests may show greater species richness than ancient forests is in regions with acidic, nutrient-poor soils and naturally species-poor communities. There, disturbance and nutrient enrichment from cultivation may facilitate colonization by a wider range of species (e.g. Koerner et al. 1997). In this respect, Graae (2000) provides an interesting contrast between two regions of Denmark, Hornsherred and Himmerland. Hornsherred has more nutrient-rich soils and more species-rich communities, and in this region ancient forests had greater species richness than recent forests. In Himmerland, with more sandy, acidic soils and generally lower species richness, ancient and recent forests had similar numbers of species. Nonetheless, the general reduction in diversity in recent versus ancient forests demonstrates that some forest herb distributions must be limited either by their ability to disperse to new habitats, their ability to establish and persist there, or both. Some species that are relatively common in ancient forests may remain almost entirely absent from recent forests, and the metapopulation persistence of these species may be threatened.

Relationships with life-history traits

Knowing which life-history traits characterize species that successfully occupy recent forests may suggest what processes control the recolonization of post-agricultural landscapes by forest herbs. Among traits, dispersal mechanisms have

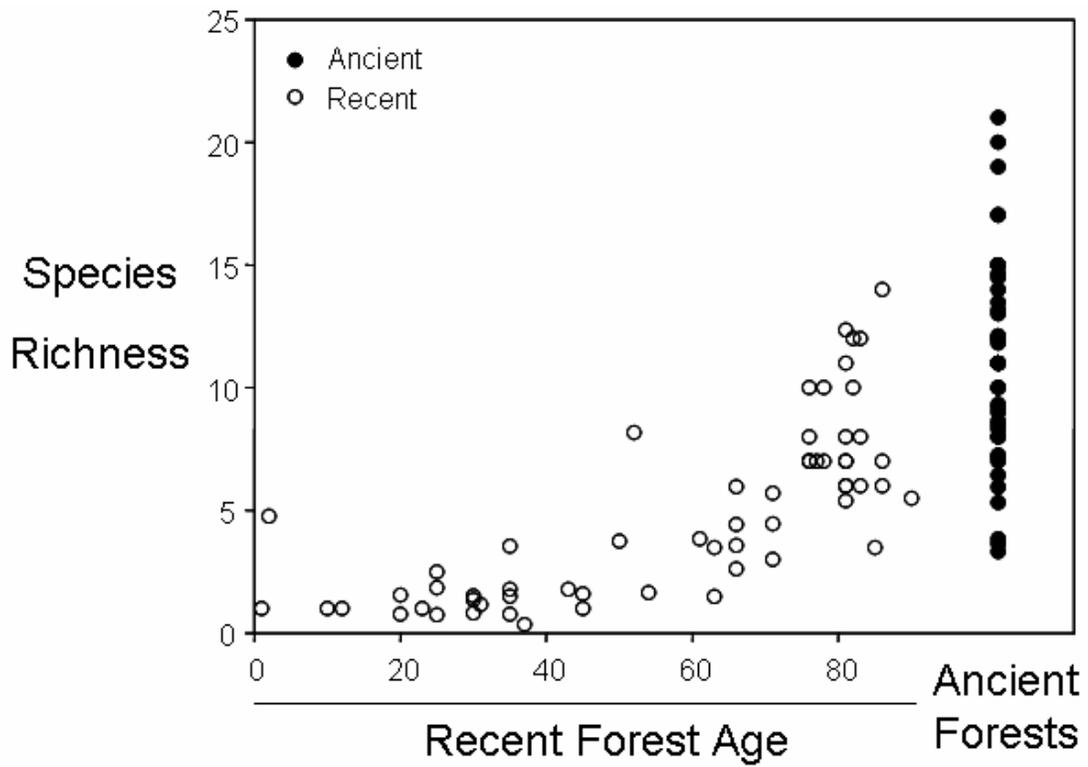


Figure 1.3. Species richness of recent forests (number of forest herb species per 180 m² area) increases through time (years since abandonment from agriculture), approaching the range spanned by ancient forests. From a synthesis of vegetation surveys in central New York (Flinn and Marks 2004).

received by far the most attention. If dispersal ability primarily limits species distributions, then better dispersers should be more abundant than other species in recent forests. A number of studies have found evidence to support this prediction. Species with adaptations for dispersal by vertebrates and wind tend to have considerably higher migration rates than species dispersed by ants and those that lack morphological adaptations for dispersal (Dzwonko and Loster 1992, Matlack 1994, Grashof-Bokdam and Geertsema 1998, Brunet and von Oheimb 1998). Nevertheless, many studies have failed to find associations between dispersal mode and colonization ability (Mabry et al. 2000, Singleton et al. 2001, Ito et al. 2004, Wulf 2004). Although an intuitively attractive approach, attempts to relate dispersal mode to colonization ability have not always been fruitful, in part because dispersal classes based on seed morphology may poorly represent realized dispersal distances (Vellend et al. 2003).

Relationships with time and distance

Predictions that diversity in recent forests should increase with age and decline with isolation also rest on the hypothesis that dispersal controls species distributions. Many studies have documented increases in understory species richness with recent forest age (Dzwonko and Loster 1992, Brunet and von Oheimb 1998, Grashof-Bokdam and Geertsema 1998, Bossuyt et al. 1999, Flinn and Marks 2004; Figure 1.3). Although recent forests gain measurable numbers of species over timescales of decades, both empirical observations and models indicate that full recovery will take several centuries at least (Vellend 2003).

Declines in diversity with distance from source habitats have been equally well-documented. Recent forests adjacent to ancient forests tend to have greater species richness than isolated recent forests (Peterken and Game 1984), and among isolated recent forests, those closer to ancient forests tend to have higher levels of diversity

(Dzwonko and Loster 1992, Matlack 1994, Flinn and Marks 2004). Within adjacent stands, species richness often declines with distance from the ancient forest boundary (Matlack 1994, Brunet and von Oheimb 1998, Bossuyt et al. 1999, Singleton et al. 2001). Several studies have examined patch occupancy patterns of individual species in greater detail. For example, Verheyen et al. (2003) created unusually fine-scale species distribution maps to analyze the influences of forest age, distance from species-specific colonization sources, and environmental variables on colonization patterns. They found the joint effects of time and distance were by far the most important factors explaining the distributions of most species. Taken together, the association of colonization success with recent forest age and isolation, and with species' dispersal-related traits, all point to dispersal as a major driver of post-agricultural forest colonization.

PERFORMANCE OBSERVATIONS

To test the hypothesis that depressed demographic performance in recent forests may also limit species distributions, a few studies have compared plant performance between ancient and recent forests. Contrary to predictions, performance in recent forests has often been similar or even enhanced in some species. In wintergreen (*Gaultheria procumbens*), a woody, clonal understory species largely restricted to ancient forests in central Massachusetts, various measures of vegetative and reproductive performance were either similar or higher in recent forests than in ancient forests (Donohue et al. 2000). Endels et al. (2004) also found generally better performance in recent forests, including higher densities of seedlings and juveniles, for three forest herbs in central Belgium. In contrast, white trillium (*Trillium grandiflorum*) plants of the same age were smaller and less likely to flower in recent than in ancient forests in central New York, at sites with high soil pH (Vellend 2005).

Clearly, individual species interact differently with the habitats created by past land use, and many of these interactions still need to be investigated.

EXPERIMENTAL INTRODUCTIONS

Several recent studies have experimentally introduced forest herb species into restored habitats. Successful seed sowings and adult transplants in unoccupied recent woods suggest that seed dispersal limits some species distributions (Petersen and Phillipp 2001, Heinken 2004), but they are difficult to interpret without comparisons to ancient forests and unsown control plots. Experimental populations in ancient and recent forests often perform equally well. For example, planted seeds and adults of four forest herb species showed no consistent differences between forest types in seed germination, seedling survival, or adult performance (Singleton 1998). Where differences between forest types have arisen, plants in recent forests have sometimes shown better survival and performance. In Verheyen and Hermy's (2004) experiment, two of four planted species had higher seedling survival and adult performance in recent than in ancient forest. Likewise, Graae et al. (2004) sowed seeds of eight species in both ancient and recent forests. Seed addition increased establishment of four species, and for three species, seedling establishment increased more dramatically in recent than in ancient forest. This result clearly indicates that, at least for these species, seed limitation was stronger in recent forest than in ancient, and conditions for seedling establishment in recent forest were favorable—possibly more favorable than in ancient forest. Still, these studies have been relatively short-term compared to the life spans of these species, and it remains an open question whether their results will hold over longer time scales.

NEW DIRECTIONS

Much progress has been made in elucidating the influence of past land use on present-day patterns of forest herb distribution and diversity. The arrival of seeds in recent forests appears to be a critical step limiting the colonization process, and at least for some species, environmental conditions that inhibit establishment or population growth may also slow colonization. Thus, simple seed introductions may go a long way toward restoring plant communities in recent forests, though overcoming environmental limitation may prove more complex. Results to date also point to some important directions for future research.

Population ecology

Patterns of post-agricultural colonization have been extensively documented, but the population-level processes underlying them remain poorly understood. Perhaps the first priority for future work should be detailed studies of individual species' ecology that can unambiguously identify these processes. In particular, the indirect methods applied so far tend to oversimplify the dichotomy between dispersal and recruitment limitation. The two are not mutually exclusive; in fact, many plant populations may be limited by a combination of seed and microsite availability (Eriksson and Ehrlén 1992). Though several studies have measured seed germination and establishment or adult plant performance, only Donohue et al. (2000) estimated demographic rates for different life stages with matrix population models. Such studies are essential for evaluating population viability in forests with different land-use histories, as well as for identifying the demographic transitions most critical to population establishment and growth. Since most forest herbs are long-lived perennials (Whigham 2004), demographic studies of at least 3-4 years are greatly needed.

A few studies have used molecular markers to document the impacts of land-use history on genetic variation (Jacquemyn et al. 2004, Vellend 2004). Where bottlenecks have reduced genetic diversity (Vellend 2004), forest herb populations in recent forests could suffer from inbreeding depression, which may further hinder colonization. Finer-scale genetic studies may yield important insights into the demographic history and mating patterns of recent populations.

Community interactions

While some studies have correlated plant performance with abiotic environmental conditions, the biotic environment has received little attention. Plant mutualists and enemies often play an important role in determining patterns of spread (Torchin and Mitchell 2004), but their role in this context is unclear. An exception is the study by Mitchell et al. (2002), which showed that a lack of seed-dispersing ants cannot explain limited forest herb colonization of recent forests in the southern Appalachians. In European recent forests, competition with a dense cover of nettle (*Urtica dioica*) may inhibit colonization by forest herbs (Endels et al. 2004, De Keersmaecker et al. 2004). However, in general we simply do not know how the presence or abundance of pollinators, herbivores, mycorrhizal fungi, pathogens, and other organisms influence forest herb colonization of post-agricultural forests.

The interaction between land-use history and herbivory may prove a particularly fruitful area for future research. Deer populations have grown considerably over the past 100 years in both Europe and eastern North America, in part because old fields and developing forests provide ideal habitat and abundant forage (Côté et al. 2004). Herbivory by deer can have severe detrimental effects on the growth and reproduction of forest herbs, reducing the abundance of preferred browse plants such as *Trillium* species (Russell et al. 2001). However, deer also disperse seeds of at least some forest

herbs (Vellend et al. 2003), so an evaluation of their net effect on plant communities must consider both herbivory and seed dispersal. In the context of forest herb recovery, one key unanswered question is whether deer have differential effects in ancient versus recent forests. If deer prefer post-agricultural habitats, herbivory might slow the recovery of forest herb populations.

Landscape-level approaches

The wealth of descriptive data on forest herb distributions has created excellent opportunities to observe vegetation changes directly, rather than infer them from chronosequences. Colonization and extinction, the processes that determine metapopulation dynamics and viability at the landscape scale, are usually difficult to study in long-lived plants. However, since initial surveys of some landscapes were conducted over 25 years ago (Peterken and Game 1984), resurveys could yield direct estimates of colonization and extinction rates. Harmer et al. (2001), for example, compared multiple surveys spanning 100 years of forest development on two abandoned arable fields. More systematic efforts across entire networks of sites could produce valuable information on landscape-scale metapopulation dynamics.

In the same way, the accumulation of similar studies from different regions generates great potential for comparison and synthesis across landscapes. Within regions, we may understand what drives variation among forest patches in species diversity and composition, but we know much less about how landscape-level differences in land-use history or environmental conditions may shape vegetation. For example, habitat destruction may cause delayed extinctions of long-lived plants, so that landscapes fragmented relatively recently may show elevated levels of patch occupancy for poor colonizers compared to landscapes fragmented earlier.

Comparative and synthetic research across landscapes can begin to address such issues.

Predictive models

Finally, predicting the influence of future land-use decisions on forest herb distributions and diversity will require the development of mathematical models. In fragmented habitats, the metapopulation framework provides a powerful tool for modeling landscape-scale dynamics. However, most metapopulation models treat habitat patch networks as static, whereas the most interesting feature of many landscapes is habitat turnover—the creation and destruction of forests through time. Recent progress has been made in constructing models applicable to dynamic, north-temperate landscapes (Matlack and Monde 2004, Verheyen et al. 2004), but parameterization of such models presents considerable challenges. Direct estimates of colonization and extinction rates from resurvey studies could be highly valuable in this regard. As forest clearance and agricultural abandonment continue worldwide, both models and empirical work will provide knowledge essential for understanding current plant communities, guiding conservation efforts, and informing land-use decisions.

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CHAPTER TWO

AGRICULTURAL LEGACIES IN FOREST ENVIRONMENTS: TREE COMMUNITIES, SOIL PROPERTIES AND LIGHT AVAILABILITY

Abstract. Temperate deciduous forests across much of Europe and eastern North America reflect legacies of past land use, particularly in the diversity and composition of plant communities. Intense disturbances such as clearing forests for agriculture may cause persistent environmental changes that continue to shape vegetation patterns as landscapes recover. We assessed the long-term consequences of agriculture for environmental conditions in central New York forests, including tree community structure and composition, soil physical and chemical properties and light availability. To isolate the effects of agriculture, we compared 20 adjacent pairs of forests that were never cleared for agriculture (primary forests) and forests that established 85-100 years ago on plowed fields (secondary forests).

Tree communities in primary and secondary forests had similar stem density, though secondary forests had 14% greater basal area. Species composition differed dramatically between the two forest types, with primary forests dominated by *Acer saccharum* and *Fagus grandifolia* and secondary forests by *Acer rubrum* and *Pinus strobus*. Primary and secondary forests showed no consistent differences in soil physical properties, or in the principal gradient of soil fertility associated with soil pH. Within stands, however, soil water content and pH were more variable in primary forests. Secondary forest soils had 15% less organic matter, 16% less total carbon and 29% less extractable phosphorus in the top 10 cm than adjacent primary stands, though the ranges of the forest types mostly overlapped. Understory light availability in primary and secondary forests was similar.

These results suggest that, within 100 years, post-agricultural stands have recovered conditions comparable to less-disturbed forests in many attributes, including tree size and number, soil physical properties, soil chemical properties associated with pH, and understory light availability. The principal legacies of agriculture that remain in these forests are the reduced levels of soil organic matter, carbon and phosphorus; the spatial homogenization of soil properties; and the altered species composition of the vegetation.

INTRODUCTION

Human land use has transformed temperate deciduous forests worldwide. Throughout Europe and eastern North America, converting forests to agricultural fields destroyed and fragmented extensive areas of continuous habitat, while later farmland abandonment created new forests on cleared lands (Rackham 1986, Williams 1989). Forests growing on former agricultural fields comprise over half of current forest cover in many regions (Vellend 2003). Though these widespread, common habitats hold great potential for the restoration of biological diversity in reforested landscapes, it is unclear how much post-agricultural forests will grow to resemble the communities they replaced and how long full recovery may take. Plant community composition, structure and function in these forests often remain distinct from forests not cleared for agriculture, even centuries after abandonment (Glitzenstein et al. 1990, Foster 1992, Motzkin et al. 1996, Koerner et al. 1997). In particular, post-agricultural forests consistently lack the diversity of herbaceous species characteristic of less-disturbed temperate deciduous forests (Peterken and Game 1984, Dzwonko and Loster 1989, Matlack 1994, Bossuyt et al. 1999, Singleton et al. 2001, Vellend 2004). Since herbs comprise the majority of plant species richness in temperate forests, their recovery is a primary concern.

Facilitating recolonization by native plants in landscapes recovering from agriculture requires an understanding of the processes that control species distributions across habitats of different history. Since successful colonization involves both the ability to disperse to new sites and the ability to establish and persist in new habitats, a key goal is to evaluate the relative roles of dispersal ability vs. environmental interactions. Most studies of post-agricultural colonization have focused on dispersal, which appears to limit the distributions of many herbaceous species (Ehrlén and Eriksson 2000; reviewed by Flinn and Vellend 2005). However, environmental conditions in post-agricultural forests may also differ, and much less is known about how habitat quality contributes to the colonization process.

A necessary first step is to assess the effects of historical agriculture on current forest environments. Soil changes following cultivation and during early stages of forest regrowth have received the most thorough study. In temperate regions, cultivation reduces soil carbon by an average of 30% (Post and Mann 1990, Johnson 1992, Davidson and Ackerman 1993, Murty et al. 2002). As forests develop on old fields, numerous studies have found that soil acidity increases and organic matter, carbon and nitrogen reaccumulate (Billings 1938, Thorne and Hamburg 1985, Richter et al. 1994, Hooker and Compton 2003). The immediate consequences of clearing and abandoning farmland are thus well-documented, but the magnitude and persistence of these changes have been surprisingly variable among regions. In northern France, for example, soil texture and chemistry remained altered from Roman agriculture 2000 years before (Dupouey et al. 2002), and other sites showed agricultural legacies in forest soils for at least a century (Koerner et al. 1997, Wilson et al. 1997, Compton et al. 1998, Verheyen et al. 1999). By contrast, some former agricultural fields have largely recovered the soil characteristics of forests never cleared for agriculture within 100 years (Kalisz 1986, Compton and Boone 2000, Dzwonko 2001, Graae et al.

2003). The strength of lasting effects depends on complex interactions between initial site conditions and the nature, duration and intensity of agricultural use. Studies focused solely on soil properties have thus found unpredictable results, while few have attempted to characterize other aspects of the environment such as light or moisture regimes (Dzwonko 2001, De Keersmaecker et al 2004).

Also often ignored are agricultural legacies in the spatial heterogeneity of environmental conditions. Besides altering mean levels of resource availability, cultivation likely changes the degree and spatial scale of variability. For example, much forest-floor heterogeneity is created when trees uproot to form pits and mounds; the resulting gradients in soil acidity, temperature, moisture, litter cover and humus depth influence small-scale species distributions (Beatty 1984). Plowing levels this microtopography, which is not regained until mature trees begin to fall. Several studies suggest that spatial homogenization may persist in post-agricultural forests for at least 100 years (Wilson et al. 1997, De Keersmaecker et al. 2004, Fraterrigo et al. 2005). If small-scale variation in soil properties contributes to the maintenance of diversity in forest plant communities, then the homogenization caused by agriculture could hinder the recovery of species richness in post-agricultural forests.

Another important limitation on efforts to assess agricultural impacts is the relationship between land-use patterns and pre-existing environmental variation. Since physical factors such as slope and drainage influence which lands people clear and abandon, land use and prior conditions are often confounded (Glitzenstein et al. 1990, Foster 1992, Motzkin et al. 1996, Matlack 1997). In many landscapes, these associations make it difficult to distinguish the effects of land use from inherent site differences. Clearly, the full and long-term consequences of agriculture in forested landscapes remain incompletely understood, and building such knowledge becomes

increasingly important as deforestation for agriculture continues in many parts of the world.

Here we investigate the legacy of agriculture in central New York forests by comparing environmental conditions between forests that developed on plowed fields 85-100 years ago (secondary forests) and forests that were never cleared for agriculture (primary forests, sensu Rackham 1980, Peterken 1981). Our primary goal is to characterize the abiotic environments experienced by herbs and tree seedlings in the two forest types. Thus we cover the principal environmental gradients relevant to understory plants—soil nutrients, water and light availability—and we quantify within-stand variation in these resources. Since the tree canopy mediates all aspects of the environment in the forest understory, we also characterize tree community structure and composition in the two forest types. Previous work emphasized the need to control for initial conditions, as topography and soils strongly influenced the geographical distribution of land uses in this landscape (Flinn et al. 2005). To isolate the effects of agricultural history, we use a paired design where adjacent primary and secondary forests share similar topography and soil types. Past results from central New York also suggested that differences between primary and secondary forest soils may be subtle compared to natural variation across the landscape (Flinn et al. 2005). Thus we designed a more comprehensive study of tree communities, soil physical and chemical properties and light availability, replicated across a heterogeneous landscape representative of much of the northeastern United States.

STUDY AREA

Climate, topography, soils and vegetation

We conducted this study throughout Tompkins County, which occupies 1250 km² in central New York (42°26' N, 76°30' W). The region has a humid, continental

climate with a mean annual temperature of 8°C and a mean annual precipitation of 90 cm (Northeast Regional Climate Center 2005). The land lies on the rolling Allegheny Plateau, with elevations ranging from 120 to 640 m above sea level. The Devonian bedrock and glacial till are predominantly shale, siltstone and sandstone, but also contain some limestone. Soils include loamy, mixed, mesic Alfisols and Inceptisols that range in pH from about 4 to 7 (Neeley 1965). Most are moderately fertile silt loams. The vegetation falls into the Allegheny section of Braun's (1950) hemlock-white pine-northern hardwoods region. Mesic, upland forests dominated by *Acer saccharum* and *Fagus grandifolia* cover much of the landscape (Mohler et al. in press).

Land-use history

Tompkins County was almost completely forested prior to European settlement in 1790 (Marks and Gardescu 1992). Clearing for agriculture accelerated after 1850, reducing forest cover to 19% of the land area in 1900, at the height of agricultural activity (Smith et al. 1993). Dairy farming was the predominant form of agriculture. In 1930, for example, 21% of the county's land area was devoted to pasture, 21% to hay, 18% to other crops, 34% to woods, brush and fallow, and 6% to other uses such as villages, houses and roads (Lewis 1934). Widespread farm abandonment in the early 1900s allowed forests to reclaim much of the landscape, and by 1995 forests covered 54% of the county (Flinn et al. 2005).

METHODS

Sites

During the 2004 growing season, we characterized environmental conditions in 20 pairs of adjacent primary and secondary forests. We chose mesic, upland sites

where the two stands had a similar slope, aspect, elevation and soil type (Singleton et al. 2001, Appendix 1). Many of the land-use boundaries coincided with property lines, further suggesting that ownership patterns rather than environmental discontinuities determined differences in land-use history within these sites. Aerial photographs from 1936-38 and subsequent years allowed us to distinguish primary from secondary forests and to select secondary forests 85-100 years old (Smith et al. 1993).

We follow Rackham (1980) and Peterken (1981) in defining primary forests as sites that have remained continuously wooded throughout the historical period, while secondary forests originated on former agricultural land. Most primary forests are not old-growth. Though never cleared for agriculture, virtually all primary forests in the central New York landscape have been selectively cut, and some were grazed by livestock, primarily cattle. However, the primary forests we studied were neither logged nor grazed so heavily that they lacked a closed tree canopy in 1936-38 and subsequent aerial photographs. We also avoided stands that showed evidence of logging within the past 20 years. These primary forests therefore represent the least-disturbed forests that allow for the paired, replicated comparisons we conduct here. The crucial difference between the forest types in this study is that the primary forests, while disturbed to some extent, remained as forests, whereas the secondary forests were fully cleared, plowed and converted to agricultural fields.

All of the secondary forests we selected had once been plowed. We identified previously plowed areas by the complete absence of treefall pits and mounds. In this region, upland forests have distinctive pit-and-mound topography, so the sharp, linear transition to a perfectly smooth forest floor made adjacent plowed sites readily distinguishable. The presence of stone piles or walls, which are relatively uncommon in central New York and occur only where stones have been removed from plowed

fields, often corroborated this interpretation (Marks and Gardescu 2001). It is likely that some or all of the secondary forests were also used as pastures at some time in their history. Farmers often cropped and pastured lands in rotation, and it was common to pasture animals in fields taken out of cultivation before abandoning them completely (Vaughan 1928). However, we excluded sites that had been only pastured and not plowed.

While it is impossible to know which crops were grown on specific fields, county agricultural census records from 1855 to 1925 show that hay (often *Phleum pratense*), oats (*Avena sativa*), buckwheat (*Fagopyrum esculentum*) and corn (*Zea mays*) covered the greatest acreages (Walrath 1927). The fields we studied were abandoned by 1920, before the widespread use of inorganic fertilizers, but they may have received manure, lime or other amendments. Manure applications were probably relatively light, since livestock densities were quite low compared to other landscapes in New England and Europe (e.g., Compton and Boone 2000). During the 1800s and early 1900s, farms in Tompkins County covered an average of 100 acres (0.4 km²) and had an average of 6-10 cattle (Walrath 1927). The tenure of cultivation may have been relatively brief. Secondary forests in this study probably spent less than 50 years in agriculture, as the majority of forest clearing took place after 1850, and widespread abandonment began shortly after 1900. Many of the sites have less favorable topography and soils for farming than nearby areas (Appendix 1, Neeley 1965), so they may have been among the last to be cleared as well as the first to be abandoned (Flinn and Marks 2004, Flinn et al. 2005).

Each stand covered at least one hectare, and we conducted all sampling along four transects perpendicular to the land-use boundary, 100 m long and 20 m apart.

Tree communities

To describe the tree communities, we recorded the species and diameter at breast height (dbh) of all stems ≥ 10 cm dbh in 100-m² circular plots. We sampled 10 plots per stand, at random positions along the four transects, so that the area sampled in each stand summed to 0.1 ha. These data yielded the stem density (stems/ha), basal area (m²/ha) and relative basal area (percentage of total basal area in each stand) of each species.

Soil physical properties

We measured bulk density by the excavation method (Grossman and Reinsch 2002), which is most appropriate for rocky forest soils (Page-Dumroese et al. 1999). Between June 14 and July 8, four small excavations were made in each stand, one on each transect at a random position. Using a wooden frame, a ruler and a machete, we dug a pit 15 × 15 cm wide × 10 cm deep, then dried the excavated soil in ovens at 60°C and weighed it. Next we sieved the soil and measured the weight and volume of rocks to determine the concentration of coarse fragments (mineral particles >2 mm) and the bulk density of the fine-earth fraction.

At the same locations where we sampled bulk density, we described several characteristics of the forest floor. To quantify the amount of leaf litter, we collected all litter within a 0.1-m² frame, oven-dried and weighed it. We also measured the depth of the humus layer on the four faces of the excavated pits. Since exotic earthworms have a major impact on both litter quantity and humus depth (Bohlen et al. 2004), we also noted the presence or absence of earthworm activity, which was visually evident in casts, burrows and midden piles. Earthworm activity at each site was quantified as the number of pits with worms.

Soil chemical properties

Soil samples were collected by removing intact leaf litter (the Oi horizon), then taking cores 2 cm in diameter and 10 cm deep. This depth was chosen because the top 10 cm contain most roots of herbaceous plants and tree seedlings. We collected 20 cores from each stand, evenly spaced along the four transects, from June 14 to July 8.

To determine water content, soil cores were weighed immediately, air-dried for at least one week and weighed again. Soil water contents fluctuate with weather conditions, making them difficult to compare across sites sampled at different times. However, since paired stands were sampled on the same day or on consecutive days, within-pair comparisons are valid. We use the soil moisture measurements only to compare the relative soil moisture status of adjacent, paired stands, not the absolute soil moisture levels of different sites.

To gain a measure of intra-site variability, we calculated coefficients of variation among the 20 individual samples from each stand for both water content and pH. After weighing, we ground each soil core through a Wiley mill with 0.85-mm mesh and measured its pH in a 1:2 soil:water suspension. The cores were then combined into a composite for further analysis.

Total carbon (C) and nitrogen (N) were determined by elemental analyzer (FlashEA 1112, CE Elantech, Lakewood, NJ, USA) using 7 mg of soil. We used the mean of two analyses from each sample. Organic matter content (OM) was measured by loss on ignition at 500°C for 2 h. Though loss on ignition may overestimate organic matter content due to losses of carbonates and structural water from clay minerals, carbonates do not decompose below 750°C (Nelson and Sommers 1996), and loam soils lose minimal amounts of structural water (<4%; Ball 1964), so this method yielded accurate estimates of organic matter content for these soils.

The Cornell Nutrient Analysis Laboratories (Cornell University, Ithaca, New York, USA) analyzed soil samples for extractable nutrient concentrations, including phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), aluminum (Al), iron (Fe), copper (Cu), manganese (Mn) and zinc (Zn). Nutrients were extracted with Morgan's solution (10% sodium acetate in 3% acetic acid, buffered to pH 4.8; Morgan 1941). Nutrient concentrations were determined by atomic absorption spectrophotometry, except phosphorus concentration, which was measured colorimetrically by stannous chloride reduction.

Soil nutrient concentrations were measured on the basis of weight, as the mass of each nutrient per kilogram of dry soil (mg/kg). But nutrient concentrations per volume may have more biological significance, since they represent the amount of nutrients available to root surfaces (Federer et al. 1993). Therefore we used the bulk density measurements to convert gravimetric nutrient concentrations to a volume basis, and we report the mass of each nutrient in the volume of soil in the top 10 cm of one hectare (kg/ha).

Light availability

We quantified understory light availability using hemispherical photographs of the forest canopy. This method gives a precise characterization of canopy structure and allows for estimation of light availability throughout the year (Rhoads et al. 2004). Between August 12 and September 8, we took 20 photographs in each stand, spaced evenly along the four transects. Photographs were taken on overcast days or at dawn or dusk to avoid glare from direct sunlight. For each photograph, the camera was positioned at 0.75 m above the ground, aligned with north and leveled horizontally. We used a Nikon Coolpix 5700 digital camera with a Nikon FC-E9 Fisheye Converter

(0.2× magnification, 180° view angle, 7mm combined focal length; Nikon Corporation, Tokyo, Japan).

We analyzed the digital images with the Gap Light Analyzer program (Frazer et al. 1999). The growing season was specified as May 15 to September 30, and Appendix 1 provides other site attributes the program used (latitude and longitude, slope, aspect and elevation). A single observer analyzed all images to minimize error in threshold determination. For each stand, we calculated the mean amount of radiation transmitted to the understory ($\text{mols} \times \text{m}^{-2} \text{d}^{-1}$) and the coefficient of variation among the 20 measures.

Ordinations

We described patterns of tree community composition with nonmetric multidimensional scaling ordination (NMS) using PC-ORD (McCune and Mefford 1999). NMS is theoretically preferable to other ordination methods (McCune and Grace 2002), though in this case detrended correspondence analysis gave similar results. The ordination used Sørensen (Bray-Curtis) measures of community dissimilarity based on species' relative basal areas, including only species that occurred in >2 stands (i.e., >1 pair). Since it represents relative basal area, the ordination describes vegetation composition independent of its structure. Following McCune and Grace (2002), we first compared 40 iterations with real data and 50 iterations with randomized data to select an appropriate number of dimensions (axes). Then we performed 400 iterations with the chosen dimensionality to find a stable solution with minimal stress.

To summarize variation in the many, interrelated soil chemical properties we measured, we conducted a principal components analysis (PCA; PROC FACTOR in

SAS, SAS Institute, Cary, NC, USA). All variables except pH, Al and Fe were first natural-log transformed to improve normality.

For both ordinations, we rotated the solution with the varimax method, which maximizes the variance of the factor loadings, and we interpreted the axes by calculating Pearson correlations with the original variables.

Statistical analyses

We assessed the effects of agricultural history on vegetation, soils and light availability with analyses of variance (ANOVA; PROC GLM in SAS). First, multivariate tests evaluated overall effects on tree species composition (NMS axes) and soil chemical properties (PCA axes). Where primary and secondary forests differed overall, we proceeded to specify these differences with univariate analyses of variance. In all analyses, the response variables were the differences between the primary and secondary forests at each site, so the intercept term tested the effect of history. This design enabled us to perform multivariate ANOVAs that accounted for the pairing between stands. For univariate tests, it is equivalent to a paired *t*-test or a mixed model with site as a random factor. Since we hypothesized that any effect of history on understory light levels would be mediated by changes in the forest canopy, we also evaluated the dependence of light availability on vegetation structure and composition. This analysis used a mixed model with site as a random factor. We tested all pairwise interactions and dropped nonsignificant terms sequentially.

RESULTS

Tree communities

Primary and secondary forests had a similar stem density, about 580 trees per hectare ($F = 0.47$, $df = 1, 19$, $P = 0.5012$; Table 2.1). Tree size distributions also

Table 2.1. Tree community structure and species composition of primary and secondary forests in central New York, including only stems ≥ 10 cm dbh and species that occurred in >2 stands. Measures include density (stems/ha), basal area (BA; m²/ha) and relative basal area (%). Paired *t*-tests compare the relative basal area of each species between adjacent primary and secondary forests (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

	Primary forests			Secondary forests			<i>t</i>	<i>P</i>
	Density	BA	%	Density	BA	%		
<i>Acer rubrum</i>	80	4.3	14	202	12.7	37	-3.98	0.0008***
<i>Acer saccharum</i>	142	8.0	26	88	2.6	7.6	3.99	0.0008***
<i>Amelanchier arborea</i>	0	0.0	0.0	5	0.2	0.5	-1.90	0.0722
<i>Betula lenta</i>	9	0.2	0.7	22	0.8	2.4	-1.72	0.1012
<i>Betula lutea</i>	3	0.1	0.2	1	0.0	0.0	1.72	0.1013
<i>Carya cordiformis</i>	2	0.1	0.3	23	1.2	3.5	-1.19	0.2486
<i>Carya ovata</i>	5	0.2	0.6	3	0.3	0.8	-0.57	0.5722
<i>Fagus grandifolia</i>	112	5.2	17	7	0.1	0.3	4.09	0.0006***
<i>Fraxinus americana</i>	39	2.4	7.9	86	3.9	11	-1.35	0.1942
<i>Ostrya virginiana</i>	18	0.3	1.0	26	0.3	1.0	-0.45	0.6598
<i>Pinus strobus</i>	1	0.1	0.3	56	6.0	17	-4.44	0.0003***
<i>Populus grandidentata</i>	8	0.5	1.8	6	0.7	1.9	-0.35	0.7332
<i>Populus tremuloides</i>	7	0.5	1.6	15	1.2	3.4	-1.71	0.1043
<i>Prunus serotina</i>	5	0.5	1.7	13	1.5	4.2	-0.83	0.4156
<i>Quercus alba</i>	0	0.0	0.0	2	0.1	0.2	-1.23	0.2321
<i>Quercus rubra</i>	22	3.0	10	22	1.7	4.9	1.73	0.0999
<i>Tilia americana</i>	22	1.7	5.6	4	0.4	1.0	2.32	0.0319*
<i>Tsuga canadensis</i>	87	3.2	11	9	0.3	0.8	3.15	0.0053**
Total	561	30.5		600	34.7			

appeared similar in the two forest types, though secondary forests had more trees of 30-40 cm dbh (Figure 2.1). Secondary forests had basal areas 14% greater, on average, than adjacent primary stands ($F = 5.21$, $df = 1$, 19 , $P = 0.0341$; Table 2.1).

NMS ordination yielded a three-dimensional solution that explained 89% of the variation in tree species composition. High scores on the first axis, which explained 42% of the variation, indicated dominance by *Acer saccharum* ($r = 0.90$) rather than *Acer rubrum* ($r = -0.72$; Figure 2.2a). The second axis, explaining 23% of the variation, described a gradient from *Pinus strobus* ($r = 0.63$) to *Fagus grandifolia* ($r = -0.76$) and *Tsuga canadensis* dominance ($r = -0.50$). Axis 3 primarily represented *Acer rubrum* ($r = 0.69$) vs. *Fraxinus americana* ($r = -0.63$) and *Carya cordiformis* ($r = -0.57$).

Species composition of primary and secondary forests differed markedly overall ($F = 48.3$, $df = 3$, 17 , $P < 0.0001$). Primary and secondary forests separated along both the first ($F = 44.3$, $df = 1$, 19 , $P < 0.0001$) and second axes ($F = 52.5$, $df = 1$, 19 , $P < 0.0001$), though not the third ($F = 0.06$, $df = 1$, 19 , $P = 0.8123$). Relative to the adjacent primary stands, all 20 secondary forests shifted lower on Axis 1 and higher on Axis 2 (Figure 2.2b).

The distinctness of primary and secondary forest communities resulted from differential distributions of many individual species. Primary forests were dominated by *Acer saccharum* (26% of total basal area), with *Fagus grandifolia* (17%), *Acer rubrum* (14%) and *Tsuga canadensis* (10%), whereas *Acer rubrum* and *Pinus strobus* together represented over half of the basal area in secondary stands (Table 2.1). Several species common in primary forests were almost completely absent from secondary stands, including *Fagus grandifolia*, *Tsuga canadensis* and *Tilia americana*.

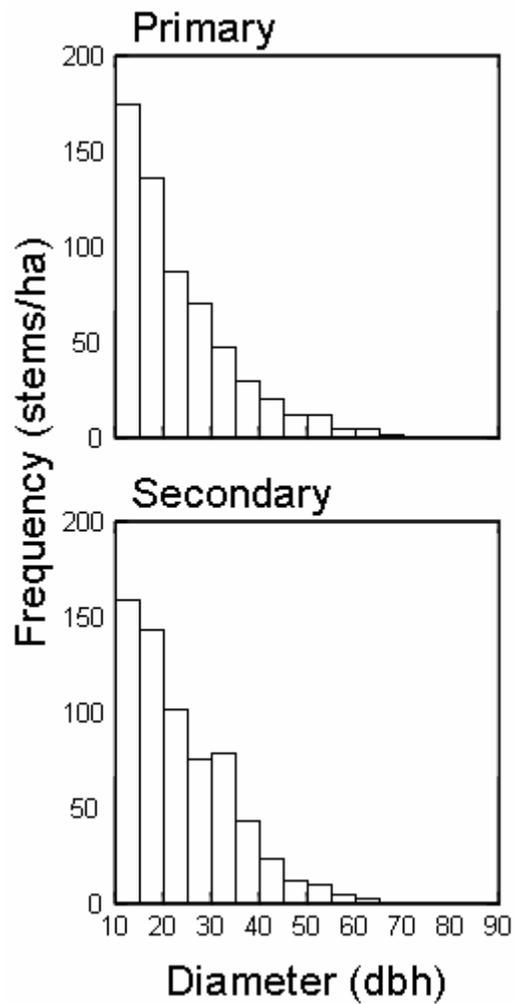


Figure 2.1. Tree size distributions of primary and secondary forests in central New York.

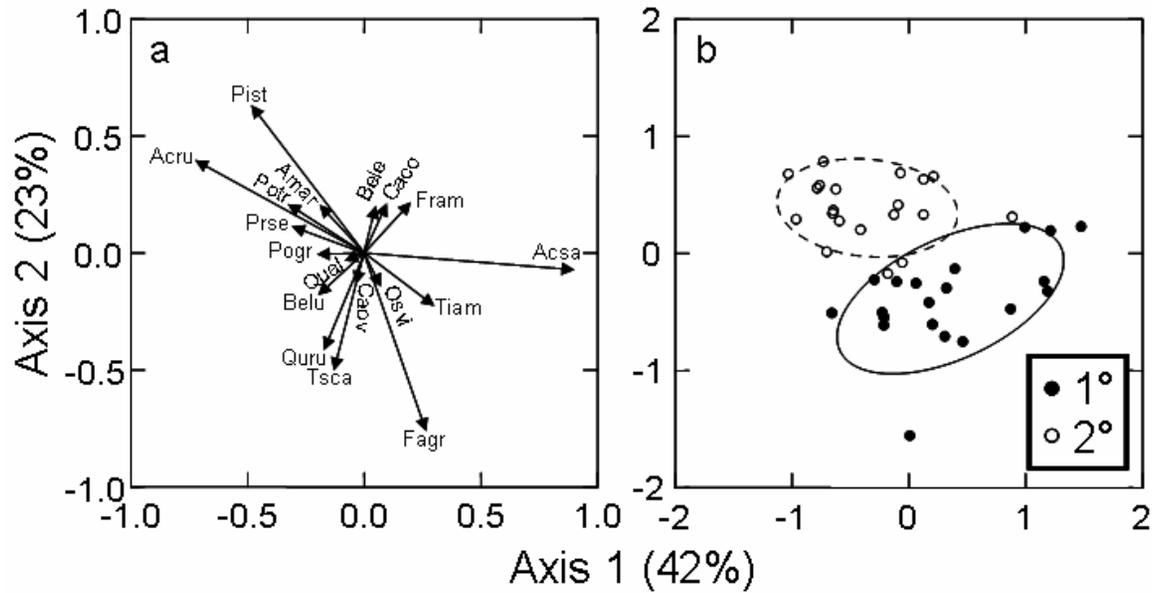


Figure 2.2. NMS ordination of tree species composition. A joint plot (a) shows Pearson correlations between the axes and the species. Species abbreviations are the first two letters of the genus and species names (listed in Table 2.1). A scatterplot of the sites (b) has 68% confidence ellipses for primary forests (solid line) and secondary forests (dashed line). The third axis is not shown.

Soil physical properties

Soil physical properties showed no consistent differences between forest types (Table 2.2). While soil water contents were similar between adjacent primary and secondary forests, they were more variable within stands of primary forest ($F = 23.8$, $df = 1, 19$, $P = 0.0001$; Figure 2.3).

Primary and secondary forests also had similar levels of earthworm activity. Most sites had at least some earthworms present; only five of the 20 sites were completely free of worms. Earthworm activity was associated with increased bulk density ($r = 0.3969$, $P = 0.0112$) and reduced humus depth ($r = -0.7977$, $P < 0.0001$) and litter quantity ($r = -0.3461$, $P = 0.0287$). In fact, 85% of the pits with worms had no humus layer.

Soil chemical properties

Two main gradients in soil chemical properties emerged from the PCA. The first axis represented a pH gradient ($r = 0.94$), also associated with Ca ($r = 0.93$) and Mg ($r = 0.93$), which explained 42% of the variation (Figure 2.4a). The second axis correlated most strongly with C ($r = 0.93$), OM ($r = 0.88$) and N ($r = 0.84$) and explained another 27% of the variation. Since these axes have clear interpretations, we refer to them as pH and OM axes, respectively.

Primary and secondary forest soils were somewhat different overall ($F = 4.50$, $df = 2, 18$, $P = 0.0260$). They overlapped completely on the pH axis ($F = 0.83$, $df = 1, 19$, $P = 0.3745$; Figure 2.4b), and the pH of composite samples from adjacent pairs was similar (Table 2.2). However, within-stand variability in pH was greater in primary forests than in secondary ($F = 21.3$, $df = 1, 19$, $P = 0.0002$; Figure 2.3). The OM axis separated paired forests of different history ($F = 9.30$, $df = 1, 19$, $P = 0.0066$; Figure 2.4b), with secondary forest soils having on average 15% less OM than

Table 2.2. Physical and chemical properties of primary and secondary forest soils (mean \pm se). Bulk densities are expressed in g/cm^3 , humus depth in cm and litter quantity in g/m^2 . Both coarse fragment concentration and water content are volumetric. Chemical properties include pH, OM and volumetric nutrient concentrations in the top 10 cm (kg/ha). For OM, C and N, measurements represent total contents, whereas for all other nutrients they are extractable concentrations. Asterisks highlight properties that differ between adjacent primary and secondary forests, according to paired *t*-tests (*, $P < 0.05$; **, $P < 0.01$).

	Primary forests		Secondary forests		<i>t</i>	<i>P</i>
<i>Physical properties</i>						
Whole-soil bulk density	0.92	± 0.04	0.97	± 0.04	-1.36	0.1896
Coarse fragment concentration	10.5	± 1.54	12.4	± 1.40	-1.52	0.1461
Fine-earth bulk density	0.72	± 0.03	0.75	± 0.04	-0.68	0.5058
Water content	40.7	± 2.19	36.8	± 1.72	1.48	0.1554
Humus depth	1.97	± 0.36	2.03	± 0.39	-0.11	0.9119
Litter quantity	511	± 49	484	± 45	0.34	0.7378
<i>Chemical properties</i>						
pH	4.68	± 0.12	4.75	± 0.14	-0.96	0.3510
OM	103015	± 5911	87276	± 3464	2.64	0.0162*
C	52107	± 2952	43804	± 1638	3.25	0.0042**
N	3276	± 224	2965	± 161	1.65	0.1159
P	3.9	± 0.58	2.7	± 0.40	2.31	0.0320*
K	75	± 4.2	77	± 4.8	-0.59	0.5654
Ca	976	± 227	842	± 205	1.11	0.2829
Mg	129	± 23	115	± 21	0.83	0.4191
Al	214	± 25	198	± 18	0.99	0.3351
Fe	101	± 15	57	± 5.2	3.74	0.0014**
Cu	1.4	± 0.23	1.2	± 0.21	0.98	0.3378
Mn	89	± 10	70	± 4.9	1.90	0.0731
Zn	2.8	± 0.21	2.6	± 0.20	0.82	0.4227

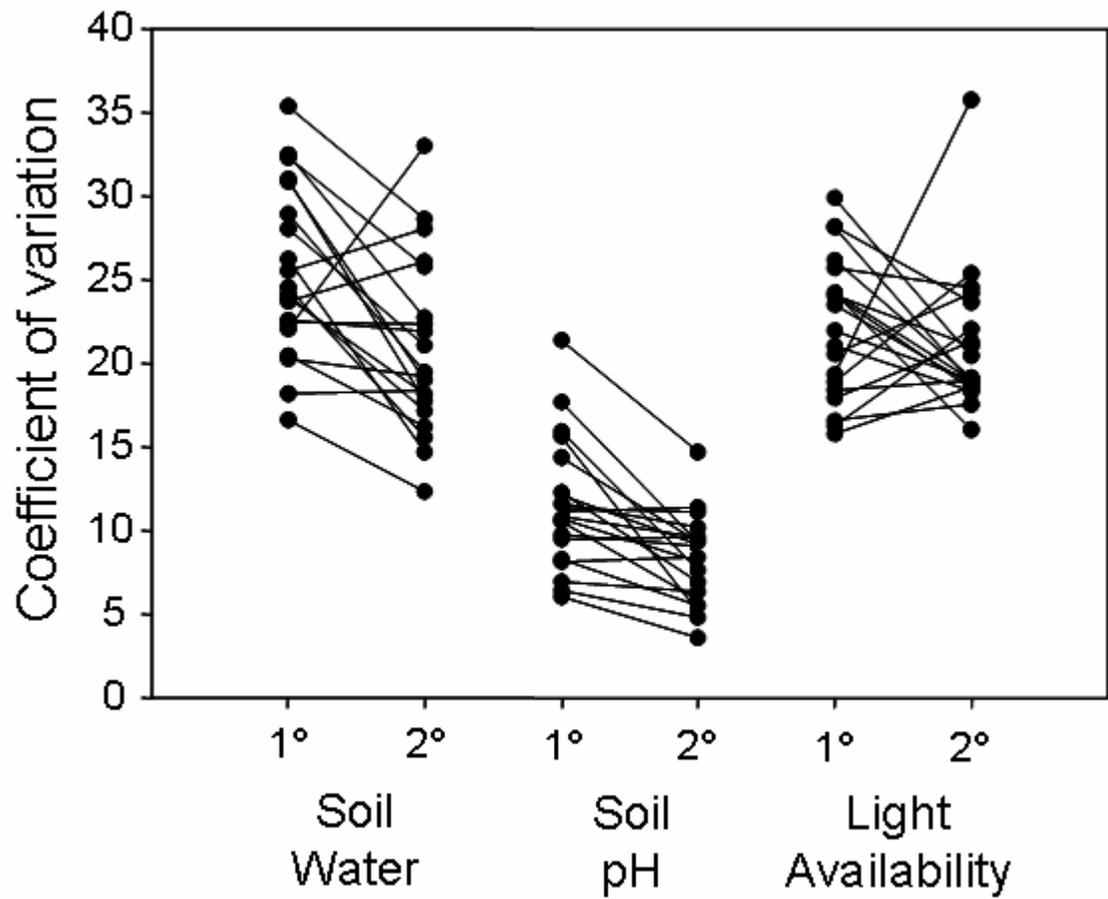


Figure 2.3. Within-stand variability in soil water content, pH and light availability, showing coefficients of variation for primary and secondary forests. Lines connect adjacent, paired stands.

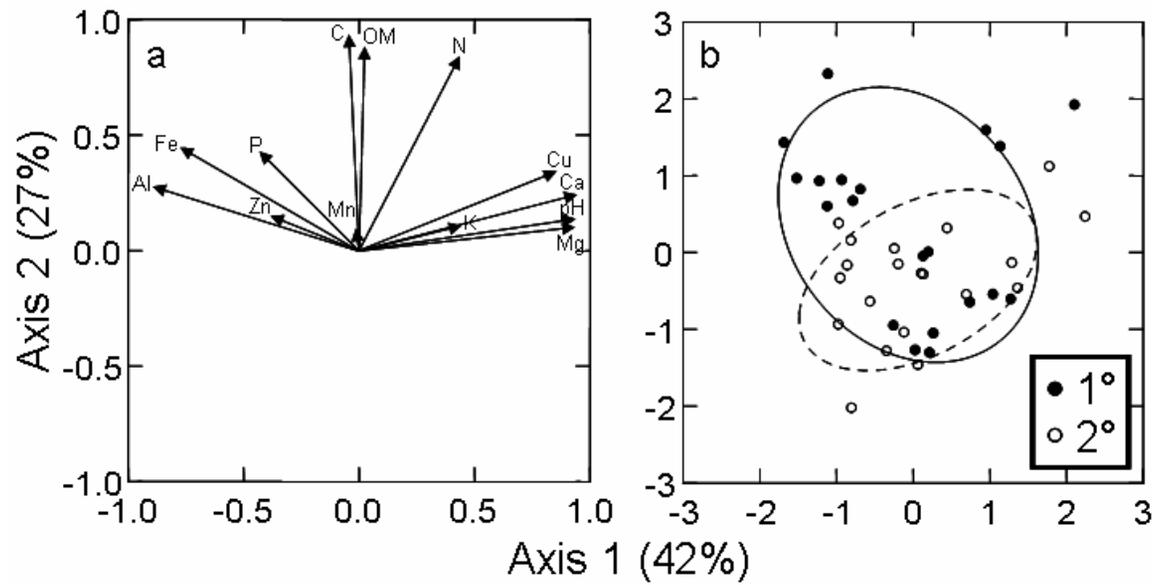


Figure 2.4. Chemical properties of forest soils summarized by PCA, with (a) correlations between the axes and the measured variables and (b) confidence ellipses for primary and secondary forests, as in Figure 2.2.

adjacent primary stands (Table 2.2). Total soil C averaged 16% lower in secondary forests, and extractable P was 29% lower (Table 2.2). Still, most secondary forests fell within the range spanned by primary forests along the OM axis, which exceeded any differences between paired stands (Figure 2.4b).

Light availability

Understory light levels in primary and secondary forests were similar both in means ($F = 0.31$, $df = 1, 19$, $P = 0.5813$) and coefficients of variation ($F = 0.69$, $df = 1, 19$, $P = 0.4159$; Figure 2.3). Primary forest floors received a mean of 6.67 ± 0.29 $\text{mols} \times \text{m}^{-2} \text{d}^{-1}$, and secondary forests 6.47 ± 0.23 . Light availability in the understory depended primarily on tree species composition; for example, stands with high proportions of *Fagus grandifolia* and *Tsuga canadensis* (i.e., low scores on the second vegetation axis) had lower understory light levels (Table 2.3).

DISCUSSION

While agriculture had lasting effects on vegetation and soils in central New York forests, environmental conditions in forests on former agricultural lands also show a substantial degree of recovery. In 100 years, plowed fields have developed many attributes indistinguishable from adjacent forests that were never cleared. Trees in post-agricultural stands have reached a density and size distribution comparable to uncleared forests, and surpassed them in total basal area. This similarity in canopy structure apparently produces similar light regimes in the forest understories. Previously plowed soils have regained the characteristics of soils in uncleared forests in all of the physical properties and many of the chemical properties we measured. In particular, agriculture had no detectable effect on soil properties associated with pH,

Table 2.3. Mixed model showing the effects of agricultural history, vegetation structure and composition on understory light availability. The model explains 80% of the variation in light availability. The random effect of site is not shown.

Dependent variable: Radiation transmitted to the understory ($\text{mols} \times \text{m}^{-2} \text{d}^{-1}$)					
Effect	Direction	df	Type III SS	<i>F</i>	<i>P</i>
Agricultural history	–	1	2.02	3.19	0.0929
Basal area	–	1	1.57	2.49	0.1340
Vegetation Axis 2	+	1	3.45	5.47	0.0327
Vegetation Axis 3	–	1	4.60	7.28	0.0158

a principal control on soil fertility and a dominant gradient of environmental variation across the landscape.

Present environmental conditions may have converged in part because intervening disturbances and shifts in species composition now exert a stronger influence than more distant history. For example, periodic, selective harvesting has reduced the stem density and basal area of almost all primary forests in the region, making them more similar to the developing stands. Neither forest type in this study has the structural characteristics of the old-growth stands they replaced, which would likely have supported similar total basal areas (about 30 m²/ha) but fewer, larger trees (about 400 stems/ha \geq 10 cm dbh; Keddy and Drummond 1996, McGee et al. 1999). Another factor likely to have facilitated the rapid recovery of basal area in post-agricultural forests is their species composition. Post-agricultural forests had a greater abundance of tree species that tend to attain disproportionately large diameters for their age and height, especially when open-grown, such as *Pinus strobus*, *Fraxinus americana* and the *Populus* species. Dominance by *Pinus strobus* probably contributed to the development of post-agricultural forest floors as well, since conifers tend to accumulate thicker, more massive litter and humus layers than hardwood stands (Lutz and Chandler 1946). Similar forest floors in the two forest types may also result from similar levels of earthworm activity. Exotic earthworms now occur throughout adjacent forests regardless of past land-use boundaries, and they may have a dominant impact on forest-floor characteristics (Bohlen et al. 2004).

The most striking legacy of agriculture is the change in tree species composition. As in many other landscapes, past land use still controls much of the variation in present vegetation (Glitzenstein et al. 1990, Foster 1992, Motzkin et al. 1996, Dupouey et al. 2002). Tree species distributions across habitats of different history followed long-known patterns. By 1860, Thoreau recognized *Acer rubrum* and *Pinus*

strobus as common invaders of cleared and cultivated lands in southern New England. These species have since been seen to dominate post-agricultural communities across the northeastern United States, whereas *Fagus grandifolia* and *Tsuga canadensis* have been notably slow to colonize abandoned agricultural lands (Glitzenstein et al. 1990, Foster 1992, Motzkin et al. 1999, Mohler et al. in press). As a result, tree communities in the two forest types had entirely distinct compositions (Figure 2.2b), indicating that agricultural disturbance has created plant communities with novel combinations and relative abundances of species.

Historical agriculture also caused persistent reductions in surface-soil OM, C and P contents. If cultivation reduced soil C by 30% (Johnson 1992, Davidson and Ackerman 1993, Murty et al. 2002), then post-agricultural forest soils have so far regained about half of the amount they lost. A deficit of this magnitude is still larger than the small and variable, usually <10% changes in soil OM and C caused by forest harvesting alone (including the experimental, whole-tree clear-cut at Hubbard Brook; Johnson et al. 1991, Johnson 1992). Many other studies have likewise found that soil OM and C continue to accumulate on formerly cultivated lands for as many as 100 years (Billings 1938, Thorne and Hamburg 1985, Richter et al. 1994, Hooker and Compton 2003). In this study, however, soil OM in post-agricultural forests generally remained within the range of uncleared forests (Figure 2.4b). Though not equal to amounts in adjacent, unplowed soils, OM levels in previously plowed soils were comparable to other unplowed soils in the landscape.

The reduced P in post-agricultural forest soils in central New York contrasts with several findings that soils remain enriched in P hundreds of years after abandonment from agriculture, evidently due to organic amendments (Koerner et al. 1997, Compton and Boone 2000, Dupouey et al. 2002, De Keersmaecker et al. 2004). Given that P increases from manuring can persist for at least 100 years (as in the long-term field

experiments at Rothamsted; Catt 1994), and that comparable central New York soils show lasting P enrichment where animal densities were high, such as in former barnyards (E.L. Stone, personal communication), this result suggests that manure additions must have been small or absent in the former plowed fields we studied. Rather, removing vegetation and harvesting crops would have reduced P inputs to the soil, and the physical mixing of soil horizons by plowing may have accelerated the cycling and leaching of otherwise relatively immobile P.

Erosion could also account for the losses of OM, C and P. Though rocks would have been removed from plowed fields, coarse fragment concentrations were slightly but not significantly higher in post-agricultural soils, suggesting that some erosion of fine soil may have occurred. If so, soil from the more OM- and nutrient-rich surface layers would have been lost, and deeper, less-rich layers exposed. It is also possible that plowing redistributed fine soil in situ, shifting OM, C and P to deeper soil horizons (Motzkin et al. 1996). A full account of land-use impacts on soil OM and nutrient contents would require deeper sampling, as well as measurements of nutrient transformation rates. But regardless of their cause, the lower OM and nutrient levels we observed in surface soils could hinder the growth and survival of some herbaceous plants and tree seedlings in post-agricultural forests.

Another important legacy of cultivation is the spatial homogenization of soil properties. The reduced within-stand variability in the pH and water content of post-agricultural forest soils corroborates previous observations that cultivation homogenizes soil pH and other properties (Wilson et al. 1997, De Keersmaecker et al. 2004, Fraterrigo et al. 2005). Though not unexpected, given the mechanical soil mixing inherent in plowing and the uniform litter inputs from crop monocultures, this consistent result has often been overlooked in studies that rely on composite samples or focus on mean resource supply. Reductions in small-scale heterogeneity have

potentially large biological significance for understory plant communities. Altered patterns of resource availability can affect population structure, diversity and community composition by changing the performance of individual species and the outcome of competitive interactions (Beckage and Clark 2003, Day et al. 2003, Hutchings et al. 2003). For example, the more homogeneous environments in post-agricultural forests could exclude species that require specific regeneration niches or depend on resource-poor patches as refuges from competition.

Implications for understory plant communities

Environmental features other than those we considered may well be critical to certain species. The importance of the biotic environment, such as interactions with mycorrhizae, herbivores, pollinators and pathogens, also remains an open question (Flinn and Vellend 2005). But to the extent that we measured relevant environmental gradients, the results of this study suggest that agricultural legacies in forest environments may play an important role in plant community recovery. Since the ranges of environmental conditions within the two forest types broadly overlap, plants could experience the same levels of light, water and nutrient availability in either post-agricultural or uncleared forests across the central New York landscape. The environmental differences we observed would thus be insufficient to explain a species' exclusion from one of the forest types. However, the lasting soil OM, C and P depletion and the elimination of extreme microsites in post-agricultural forests could contribute to reductions in the frequency and performance of some species and the diversity of understory communities.

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CHAPTER THREE
REPRODUCTIVE BIOLOGY OF THREE FERN SPECIES MAY
CONTRIBUTE TO DIFFERENTIAL COLONIZATION SUCCESS
IN POST-AGRICULTURAL FORESTS

Abstract. Since selfing enables a single individual to reproduce in a new location, the ability to self-fertilize should enhance plants' capacity for colonization. This study examined whether selfing ability correlated with colonization success in three fern species, *Dryopteris carthusiana* (Villars) H. P. Fuchs, *Dryopteris intermedia* (Muhlenberg ex Willdenow) A. Gray and *Polystichum acrostichoides* (Michaux) Schott (Dryopteridaceae), which vary in their ability to colonize forests on abandoned agricultural lands in central New York, USA. *Polystichum acrostichoides* is much more frequent in forests that were never cleared for agriculture; *D. carthusiana* is more frequent in forests that developed on former fields; and *D. intermedia* is equally frequent in the two forest types. To test the hypothesis that selfing ability is greater in better-colonizing species and in post-agricultural forest populations, I assessed the sporophyte production of gametophytes grown in isolation and in pairs of varying relatedness. *Dryopteris carthusiana* had the highest reproductive success and selfing ability, and *P. acrostichoides* the lowest. These results support the hypothesis that selfing may facilitate colonization in these species. They also exemplify the general pattern that polyploid fern species self-fertilize more than related diploids, since the allotetraploid *D. carthusiana* had greater selfing ability than both diploid species.

INTRODUCTION

Understanding how life history traits relate to colonization ability can reveal the processes underlying natural patterns of plant distribution, and help to predict species'

responses to human introduction, extirpation and habitat alteration. One trait long thought to facilitate colonization is the ability to self-fertilize (Lloyd 1980). Darwin (1876) discussed the suggestion that hermaphroditic and monoecious plants should spread more easily than dioecious species, since a single individual could found a reproductive population. On the same principle, Baker (1955, 1967) proposed that self-compatibility should facilitate long-distance dispersal, an idea Stebbins (1957) called “Baker’s Law.” In fact, self-fertilization should be favored not only in migration across long distances, but in any landscape with frequent local colonization and extinction (Pannell and Barrett 1998). Despite the logical appeal and theoretical support of this hypothesis, it remains unclear how often range expansions and establishment events actually depend on selfing.

Most of the empirical evidence for Baker’s Law comes from large-scale, biogeographic patterns, such as the prevalence of self-compatible species in island floras (Carlquist 1974, McMullen 1987, Webb and Kelly 1993, Anderson et al. 2001). In many cases, selfing taxa occur at the range margins of outcrossing sister taxa (Solbrig and Rollins 1977, Wyatt 1986, Barrett and Shore 1987, Barrett et al. 1989, Moeller and Geber 2005). These patterns suggest an association between selfing and historical colonization, but few studies have directly measured both selfing ability and colonization success during ongoing migrations. For example, species introductions have allowed for comparisons of selfing abilities among congeners of varying invasiveness (Gerlach and Rice 2003), and between established and recently colonized populations (Schueller 2004).

Like the spread of invasives, the recolonization of restored habitats by native species provides an ideal opportunity to study the role of selfing in contemporary colonization. Among the most common restored habitats worldwide are forests on abandoned agricultural lands (Williams 1989, Ball 2001). As forests regrow,

herbaceous plants vary widely in their ability to recolonize post-agricultural sites (reviewed by Flinn and Vellend 2005). While several studies have explored relationships between migration rates and life history traits, especially those associated with dispersal (Matlack 1994, Verheyen et al. 2003), none have examined how plant mating systems may affect the recolonization of post-agricultural forests.

Here I use a post-agricultural landscape in central New York to investigate whether selfing ability may contribute to the differential colonization success of three fern species. Ferns and other homosporous plants are particularly interesting in this context because their mating systems potentially include outcrossing, intergametophytic selfing (analogous to selfing in seed plants) and intragametophytic selfing (which has no analog in seed plants and yields fully homozygous progeny; Klekowski 1969). Outcrossing occurs between gametophytes from different sporophytes; intergametophytic selfing occurs between two gametophytes from the same sporophyte; and intragametophytic selfing occurs when two gametes from the same gametophyte unite. Though all homosporous plants have the potential to produce bisexual gametophytes, most maintain outcrossing mating systems through several primary mechanisms (Soltis and Soltis 1992). Gametophytes may become unisexual by developing male and female function either exclusively or sequentially. In many species, mature female gametophytes enhance opportunities for outcrossing by releasing antheridiogen, a pheromone that stimulates spore germination and induces maleness in neighboring gametophytes (Näf 1979). When gametophytes do undergo intragametophytic selfing, deleterious recessive alleles may hinder the survival of the completely homozygous sporophytes (Klekowski 1969). Ferns' great capacity for dispersal via windblown spores presumably facilitates outcrossing by increasing mate availability in many habitats. In order to mate, however, two gametophytes must establish simultaneously within about 5-10 cm of one another, an

unlikely event after long-distance dispersal (Schneller et al. 1990, Greer and McCarthy 1997, Peck et al. 1990). Selfing may thus be as important to colonization in ferns as in seed plants.

This study focuses on the ferns *Dryopteris carthusiana* (Villars) H. P. Fuchs, *Dryopteris intermedia* (Muhlenberg ex Willdenow) A. Gray and *Polystichum acrostichoides* (Michaux) Schott (Dryopteridaceae), which are wintergreen, herbaceous perennials common in mesic, upland forests and native to eastern North America (Montgomery and Wagner 1993, Wagner 1993). The range of *D. carthusiana* also extends throughout Eurasia. Despite similar patterns of spore dispersal (unpublished data), these three species show contrasting distributions across forests that were never cleared for agriculture (i.e., primary forests) and forests that established on plowed fields 85-100 years ago (i.e., secondary forests, sensu Rackham 1980, Peterken 1981). In central New York, *P. acrostichoides* is among the herb species most restricted to primary forests; *D. intermedia* is equally frequent in the two forest types; and *D. carthusiana* is more frequent in secondary forests (Singleton et al. 2001; unpublished data). I hypothesized that, if selfing facilitated colonization, then the species that are more successful colonists should have greater selfing ability than the species that are less successful colonists. Thus I expected *D. carthusiana* to have greater selfing ability than *D. intermedia*, and *D. intermedia* to have greater selfing ability than *P. acrostichoides*. In addition, if populations in secondary forests were recently founded through selfing, then plants from secondary forests should have greater selfing ability than plants from primary forests. To test these hypotheses, I conducted an experiment in which I grew gametophytes either in isolation or in pairs, allowing different levels of inbreeding, and compared rates of sporophyte production.

MATERIALS AND METHODS

Study sites

Spores for this experiment came from fern populations in three pairs of adjacent primary and secondary forests, located on mesic uplands in Tompkins County, New York, USA. The secondary forests were abandoned from agriculture 85-100 years ago, according to 1936-38 aerial photographs. Field evidence showed they had been plowed, eliminating all native vegetation. In central New York, both the *Dryopteris* species and *Polystichum acrostichoides* occur in tree and shrub thickets on sites plowed 20-40 years before (Stover and Marks 1998). Therefore, fern populations in the oldest secondary forests may have established as many as 80 years ago, whereas populations in primary forests could have continuously occupied the sites for the last several thousand years.

Spore collection

To obtain spores, I collected fertile fronds of the three species between 30 June and 11 July 2003. Using transects to stratify samples across 1 ha, I took fronds from 20-30 plants of each species from each forest stand. The fronds were sealed in glassine envelopes and dried in ovens at 35°C for 1 wk to promote spore release.

Gametophyte culture

I sowed the spores from each sporophyte on nutrient medium in a 60 × 15 mm petri dish by piercing the glassine envelopes with an insect pin, making holes just large enough to sift out spores without pieces of frond, indusia or sporangia (D.R. Farrar, Iowa State University, personal communication). The medium contained Parker's macroelements and Thompson's microelements solidified with 1% agar (Klekowski 1969). To minimize contamination, I autoclaved the medium at 121°C for

15 min and added the fungicide Nystatin at 50 mg/L. The dishes were sealed with Parafilm (American National Can, Chicago, Illinois, USA) and placed in a growth chamber under 14 h light at 26°C and 10 h dark at 16° C.

Experimental crosses

After 2 wk, I established crosses by transplanting gametophytes onto fresh medium with a dissecting microscope and a scalpel, placing pairs 1 cm apart. To compare reproductive success at four potential levels of inbreeding, gametophytes grew either in isolation; paired with another gametophyte from the same sporophyte; paired with a gametophyte from a different sporophyte in the same population; or paired with a gametophyte from a sporophyte in a different population, at least 2 km away. Pairs were randomly matched within the appropriate pool. Isolated gametophytes could only reproduce through intragametophytic selfing, whereas paired gametophytes could either self-fertilize or outcross. The four inbreeding levels were crossed with the three species and the two forest types in a fully factorial design. Replicating the experiment across three sites and 20 plants per population therefore yielded 1440 crosses involving 2520 gametophytes. I maintained the cultures for 18 mo, watering gametophytes with an eyedropper to facilitate fertilization and examining them monthly for the presence of sporophytes.

Statistical analysis

I assessed the effects of inbreeding level, species, forest history and their interactions on the likelihood of sporophyte production with maximum-likelihood analysis (PROC CATMOD in SAS; SAS Institute, Cary, North Carolina, USA). An additional factor accounted for site effects. I tested all possible two- and three-way interactions and dropped from the final model those not significant at $P < 0.05$. This

analysis considered only the 953 gametophytes that survived to sexual maturity, at least 1 mo after transplanting. To make maximum use of the available information, the analysis included sporophyte production from each member of pairs.

RESULTS

Gametophytes had modest reproductive success overall. Of gametophytes that survived to sexual maturity, 39% formed sporophytes. The three species had significantly different rates of sporophyte production (Table 3.1). Across all treatments, *Dryopteris carthusiana* had the highest reproductive success, with 50% of gametophytes forming sporophytes; *Dryopteris intermedia* was intermediate, with 31%; and *Polystichum acrostichoides* had the lowest reproductive success, with 21%.

Sporophyte production did not differ consistently among the four potential levels of inbreeding (Table 3.1). However, the three species responded differently to the different inbreeding levels (Table 3.1, Figure 3.1). *D. carthusiana* had high reproductive success across all levels of inbreeding. In fact, 63% of isolated gametophytes formed sporophytes in this species, a higher rate than when outcrossing was possible. Likewise, the sporophyte production of *D. intermedia* was fairly consistent across inbreeding levels, ranging from 25-38%. For *P. acrostichoides*, by contrast, reproductive success increased dramatically as gametophytes had greater access to outcrossing. Only 11% of isolated gametophytes produced sporophytes via intragametophytic selfing, whereas 50% of crosses between different populations produced sporophytes.

Plants from primary and secondary forests did not show consistent differences in rates of sporophyte production, nor did they perform differently across levels of inbreeding, as indicated by the lack of interaction between forest history and inbreeding level (Table 3.1). Rather, the effect of forest history varied among the

Table 3.1. Maximum-likelihood analysis of the effects of species, inbreeding level, forest history and their interactions on sporophyte production, for three fern species colonizing post-agricultural forests in central New York. An additional factor accounts for the three replicate sites.

Effect	df	Wald χ^2	<i>P</i>
Intercept	1	46.37	<0.0001
Site	2	45.16	<0.0001
Species	2	36.73	<0.0001
Inbreeding level	3	4.60	0.2037
Forest history	1	0.42	0.5155
Species × inbreeding level	6	27.00	0.0001
Species × forest history	2	9.42	0.0090
Likelihood ratio	50	86.14	0.0011

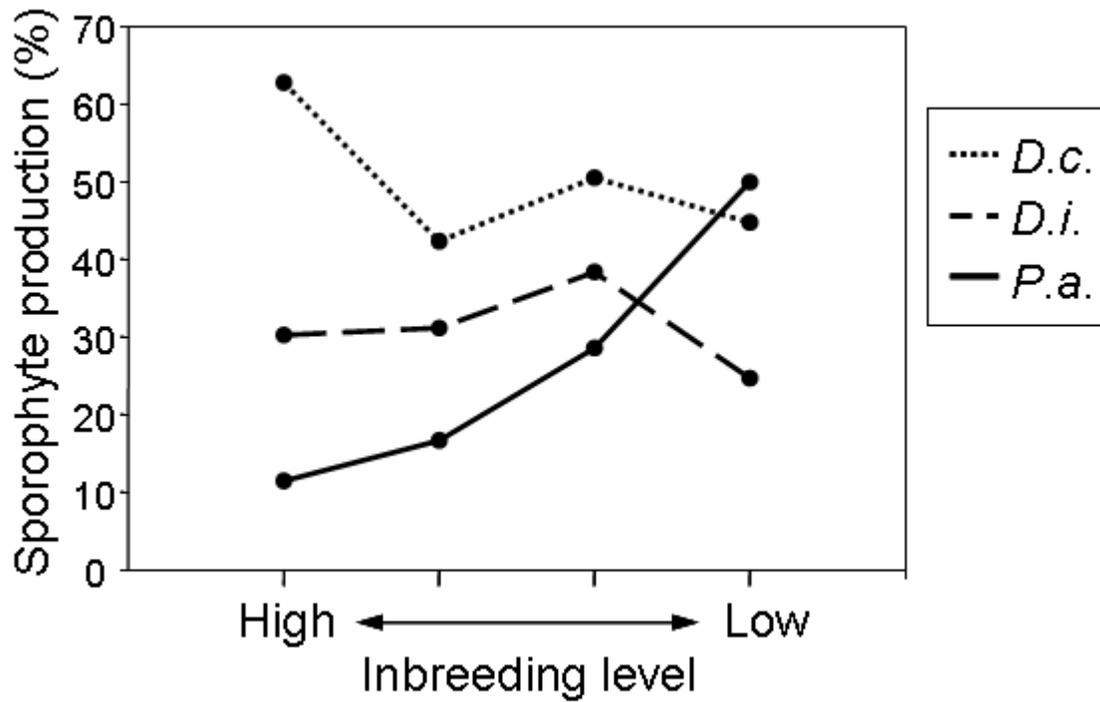


Figure 3.1. Sporophyte production across four levels of inbreeding for three fern species: *Dryopteris carthusiana* (dotted line), *Dryopteris intermedia* (dashed line) and *Polystichum acrostichoides* (solid line). Ranging from high to low, the potential levels of inbreeding included intragametophytic selfing, intergametophytic selfing, within-population outcrossing and among-population outcrossing (see Materials and Methods, Experimental crosses).

three species (Table 3.1). *D. carthusiana* plants from primary and secondary forests had equally high rates of sporophyte production, near 50%. In *D. intermedia*, reproductive success was slightly higher among plants from secondary forests, 36%, than from primary forests, 27%. *P. acrostichoides* showed the opposite trend, with the proportion of gametophytes forming sporophytes over twice as high among plants from primary forests as from secondary forests, 24% versus 10%.

DISCUSSION

This experiment revealed differences among species in gametophyte reproductive biology that may play important roles in the colonization of post-agricultural forests by homosporous ferns. The most successful colonist, *Dryopteris carthusiana*, had the greatest reproductive success overall, whereas the least successful colonist, *Polystichum acrostichoides*, had the lowest. In fact, gametophytes were over twice as likely to form sporophytes in *D. carthusiana* as in *P. acrostichoides*. Even in the absence of other differences, such consistently higher rates of sporophyte production could speed the colonization process and possibly explain the species' distributions. In addition, the species' responses to inbreeding were consistent with the hypothesis that selfing ability may facilitate colonization. The potential for self-fertilization was greater in *D. carthusiana* than in *D. intermedia*, and in *D. intermedia* than in *P. acrostichoides*.

These laboratory results agree with previous characterizations of the species' mating systems based on patterns of genetic variation in natural sporophyte populations. For example, populations of *D. carthusiana* had severe heterozygote deficiencies at polymorphic loci, suggesting high selfing rates (C.R. Werth, deceased, and C.H. Haufler, University of Kansas, unpublished data cited in Xiang et al. 2000). By contrast, *D. intermedia* appears to outcross predominantly, as indicated by

genotype frequencies in accord with Hardy-Weinberg equilibrium (C.R. Werth, deceased, unpublished data cited in Xiang et al. 2000). Allozyme data also demonstrated that *P. acrostichoides* and five other North American *Polystichum* species are highly outcrossing (Soltis and Soltis 1990). In seven populations across the eastern United States, *P. acrostichoides* maintained high levels of genetic variation within populations, with inbreeding coefficients ranging from 0.007-0.084 and intragametophytic selfing rates (estimated from genotype frequencies according to Holsinger 1987) ranging from 0-12% (Soltis and Soltis 1990, Soltis et al. 1990). The 11% intragametophytic selfing rate documented here for *P. acrostichoides* thus appears representative of selfing rates in natural populations.

Previous studies of gametophyte ontogeny suggest that sex expression patterns may contribute to the reproductive outcomes observed in this experiment. Growing isolated *D. carthusiana* gametophytes on agar, Peck (1985) found that 86% were bisexual, indicating a high potential for self-fertilization. In denser laboratory cultures on soil (1-3 gametophytes cm⁻²), both *D. carthusiana* and *D. intermedia* had mostly female gametophytes, 59-70%, with 17-27% male and 13-14% bisexual (Cousens 1975). It is unknown whether *D. carthusiana* produces or responds to pheromones, but sex expression in *D. intermedia* can be influenced by antheridiogen (C.R. Werth, deceased, unpublished data cited in Xiang et al. 2000). For *P. acrostichoides*, Greer and McCarthy (1997, 1999) reported that isolated gametophytes grown on soil invariably became female and remained unisexual, forming antheridia only on lobes separated from the meristem by necrosis. This pattern of sex expression, mediated by antheridiogen (Näf 1979, Greer and McCarthy 1997), would explain the species' highly outcrossing mating system.

The development of gametophytes in laboratory cultures, especially in isolation and on agar, may differ from growth patterns in denser populations and under field

conditions (Rubin and Paolillo 1983, Ranker and Houston 2002). Likewise, the low overall reproductive success of gametophytes in this experiment, though comparable to rates seen in many other species (Peck et al. 1990), may reflect the cultural regime. In this case, however, results of the laboratory tests so far appear consistent with the available information from natural populations.

The species' contrasting mating systems also seem to support theoretical predictions about the evolutionary consequences of polyploidy. Polyploid species are expected to self-fertilize more often than diploids because newly formed polyploids, lacking mates, could only reproduce through selfing; and because genome duplication should reduce genetic load and inbreeding depression (Stebbins 1950, Lande and Schemske 1985). In the case study presented here, the allotetraploid *D. carthusiana* had a greater selfing ability than *D. intermedia*, one of its diploid progenitors (Walker 1961), or *P. acrostichoides*, another closely related diploid. This example thus adds to the growing number of cases in which polyploid fern species tend to self-fertilize more than their diploid relatives (Hedrick 1987, Masuyama and Watano 1990, Soltis and Soltis 2000, Chiou et al. 2002), though the relationship between polyploidy and inbreeding in seed plants remains much less clear (Husband and Schemske 1997, Cook and Soltis 1999, Mable 2004; B.C. Barringer, Cornell University, unpublished manuscript).

Within species, I found no evidence for an association between the history of populations and their selfing ability. One plausible explanation for this result is that, contrary to the original hypothesis, the foundation of fern populations in post-agricultural forests did not involve elevated rates of self-fertilization. Since the post-agricultural forests in this study were adjacent to continuously forested areas, fern populations may have spread gradually across the land-use boundaries, remaining contiguous with areas of higher plant density that allowed for outcrossing. The

proximity to source populations also makes the simultaneous arrival of multiple spores more likely. In fact, I have documented substantial spore banks in the soil of post-agricultural forests adjacent to but not containing sporophyte populations of these species (unpublished data). Similar situations may be common in the region, as about 90% of the area in secondary forest is contiguous with older stands (Smith et al. 1993).

Alternatively, even if populations did establish through selfing, they may have grown sufficiently old and large that evidence of founder events involving selfing is no longer detectable. Rather, existing plants' selfing abilities could depend more strongly on mating patterns at current population densities than on a population bottleneck that may have occurred as many as 80 years ago. To obtain sufficient sample sizes for the experiment, I chose sites where all three species had population densities of at least 20 plants ha⁻¹ in each forest stand. The effects of a founder event might be more evident at other sites in the region where population densities remain lower, or in more isolated or more recently established populations. If in fact fern populations in forests of different history have similar selfing rates, the genetic consequences of post-agricultural forest colonization may be comparable to those seen for *Trillium grandiflorum* (Michx.) Salisb. in the same central New York landscape; primary and secondary forest populations did not differ in inbreeding coefficients or observed heterozygosity, though allelic richness and expected heterozygosity were slightly lower in secondary forests (Vellend 2004).

Several other studies have related mating systems to colonization ability in ferns, at either the species or the population level. Based on observations of gametophyte development and reproduction, Holbrook-Walker and Lloyd (1973) and Lloyd (1974) suggested that Hawaiian fern species frequently found on newly formed lava flows, though primarily outcrossing, retained a greater ability to self-fertilize than species of late-successional habitats. In two species of Hawaiian *Sadleria* Kaulf., however,

Ranker et al. (1996) later found that even populations on recent lava flows had genotype frequencies indicative of outcrossing and gametophytes with primarily unisexual development, antheridiogen systems and very little ability to form sporophytes in isolation. Among three South Asian ferns, Singh and Roy (1977) found a greater capacity for self-fertilization in the more widely distributed, generalist species. Ranker et al. (2000) noted that the four fern species for which genetic evidence suggests a mixed mating system occupy both disturbed places and more stable habitats. A high capacity for self-fertilization may also have facilitated the spread of two invasive fern species in Florida (Lott et al. 2003).

While fewer studies have addressed mating-system variation among fern populations, Cousens (1979) found a higher incidence of bisexuality and a greater ability to self-fertilize in gametophytes from a disjunct population than from the central range of *Blechnum spicant* (L.) J. Sm. Similarly in *Asplenium platyneuron* (L.) Oakes, geographically disjunct, solitary plants on recent coal spoils had greater selfing ability than plants from dense populations in the center of the species' range (Crist and Farrar 1983). Peck et al. (1990) contrasted the selfing and colonization abilities of *A. platyneuron* with *Adiantum pedatum* L., which had a very low rate of sporophyte formation by isolated gametophytes, and which had failed to colonize the coal spoils from adjacent populations for 50 years. Together with these studies, the patterns of fern reproductive biology documented here suggest that selfing ability may often be an important component of population establishment following long-distance dispersal.

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CHAPTER FOUR

RECRUITMENT LIMITS FERN COLONIZATION OF POST-AGRICULTURAL FORESTS

INTRODUCTION

Plant population dynamics and species distributions may depend primarily on the availability of propagules or on the availability of suitable habitats, and the relative importance of these processes remains controversial. The prevalence of niche differentiation would suggest that predictable habitat requirements largely determine species distributions, and that the local abundance of microsites conducive to germination and establishment limits recruitment rates (Harper 1977, Crawley 1990). However, recent theoretical and empirical evidence increasingly emphasizes the influence of stochastic colonization and extinction events (Bell 2001, Hubbell 2001). Seed supply and dispersal appear to limit recruitment more often than previously appreciated, leaving many suitable habitats unoccupied (Tilman 1997, Clark et al. 1998, Hubbell et al. 1999).

Disturbances introduce elements of both dispersal and establishment limitation into natural communities. By definition, they remove vegetation from suitable sites, and where they also destroy seed banks, create unoccupied habitats that colonists must reach from outside (Pickett and White 1985). Disturbances also modify environmental conditions, potentially favoring the establishment of distinct sets of species. Communities recovering from disturbance thus present an ideal context for examining the relative strengths of neutral and selective forces in community assembly. Forests growing on abandoned farmland are particularly conducive because agriculture imposes a relatively uniform disturbance across well-defined areas; in plowed fields, cultivation completely eradicates native vegetation and leaves a

radically altered environment. Extensive farm abandonment in Europe and eastern North America during the last several centuries (Rackham 1986, Williams 1989) has thus opened a major opportunity to discover what roles dispersal and establishment play as forests regrow. Of prime concern during this process is the recovery of herbaceous plant communities, since they represent the majority of plant diversity in temperate forests. Even centuries after reforestation, understory communities in forests that developed on old fields consistently show lower species richness than those of forests that were never cleared for agriculture (reviewed by Flinn and Vellend 2005).

Several lines of evidence suggest that dispersal limitation controls the recovery of forest herb diversity in post-agricultural communities. For example, species dispersed by animals and wind often recolonize faster than those dispersed by ants or no special mechanism (Matlack 1994, Bellemare et al. 2002). A dominant role for dispersal seems reasonable in this context, since most forest herbs have low fecundity and lack adaptations for long-distance dispersal (Whigham 2004). In fact, seed-sowing experiments indicate that seed availability limits many forest herb populations even in undisturbed habitats (Ehrlén and Eriksson 2000, Turnbull et al. 2000). However, environmental interactions may also shape the distinctive composition of post-agricultural forests by determining colonization success once propagules arrive. Legacies of agriculture may persist in the nutrient status of forest soils for as long as 2000 years (Dupouey et al. 2002), for example, and where habitats in post-agricultural stands remain altered, they can either enhance or depress the performance of understory plants (Donohue et al. 2000, Endels et al. 2004, Fraterrigo et al. 2005, Vellend 2005). Individual species' responses to post-agricultural habitats may become increasingly important as forests mature, and could prove crucial to the full recovery of these communities.

One common feature of post-agricultural forests that dispersal limitation fails to explain is that species with similar dispersal abilities vary widely in colonization success. For example, several species of shade-tolerant, perennial ferns common in the deciduous forests of eastern North America show distinct distribution patterns across habitats of different history (Whitney and Foster 1988, Singleton et al. 2001, Bellemare et al. 2002). Ferns and other spore-bearing plants have long been thought to have an equivalent capacity to migrate great distances, via wind dispersal of their dustlike spores (Tryon 1970, Smith 1972). Since ferns also have fewer biotic interactions than seed plants, as with pollinators, seed vectors or herbivores, their distributions should more directly reflect interactions with the abiotic environment (Barrington 1993). However, recent studies have shown joint roles for environmental gradients and spatial structure, representing limited dispersal, in determining the composition of fern communities (Tuomisto et al. 2003, Karst et al. 2005). Species' unique distributions in post-agricultural forests thus suggest that ferns may have species-specific environmental interactions with these habitats, but an attempt to specify these interactions must consider all life stages, including dispersal.

An equally compelling reason to focus on ferns is the general lack of information about fern population ecology. Despite their ecological importance in diverse communities worldwide, we know remarkably little about how fern populations establish, reproduce and maintain themselves (Werth and Cousens 1990, Sheffield 1996). The assumption of ubiquitous spore dispersal remains largely untested (Peck et al. 1990). While seed banks are widely known and well-studied (Leck et al. 1989), the existence of soil spore banks has only recently been recognized (Dyer and Lindsay 1992). Numerous laboratory studies have investigated fern gametophyte development *in vitro* (Miller 1968, Dyer 1979), but field observations remain mostly anecdotal (exceptions include Cousens et al. 1988, Peck et al. 1990). Like many studies of rare

plants, attempts to study natural populations of fern gametophytes confront the challenge of yielding low sample sizes from objective sampling designs (Cousens et al. 1985). Fern gametophytes present the additional problem of being quite small (<5 mm) and difficult or impossible to identify at the species level (Farrar and Gooch 1975, Cousens et al. 1985, Werth and Cousens 1990). In addition, simple experiments sowing fern spores in natural habitats have not been successfully carried out. Yet safe sites for establishment could prove particularly crucial to fern distributions, and these early life stages would seem critical to any account of the life history or ecology of ferns (Page 2002).

This study presents feasible methods for studying fern spore dispersal, spore germination, gametophyte survival and sporophyte establishment in natural habitats. It applies these methods to compare the demography of three fern species with contrasting distributions across the post-agricultural landscape of central New York, addressing two main questions. First, which life stages limit the colonization of post-agricultural forests and the growth of populations? Second, what characteristics of the species explain their varying colonization success in habitats of different history? At the same time, this study works toward the more general goal of understanding the life history and reproductive biology of ferns in relation to the abiotic environment. It uses a combination of descriptive and experimental approaches to quantify the effects of land-use history and environmental conditions on all stages of the fern life cycle. Among the three fern species and between forests with different histories, I compare the size and fecundity of adult plants; the availability of spores deposited by the wind and stored in the soil; the rates of germination and establishment in various microsites; and the distribution of juvenile plants across these microsites.

METHODS

Sites

Tompkins County, in the Finger Lakes region of central New York (42°26' N, 76°30' W), is an ideal location to study the effects of past agriculture on present vegetation. Almost completely forested before European settlement in 1790, the county lost much of its forest land to agriculture by 1900, when forest cover reached a minimum of 19% (Marks and Gardescu 1992, Smith et al. 1993). With farm abandonment, forests grew to cover 54% of the county's land area by 1995 (Flinn et al. 2005). Thus the current landscape consists of a patchwork of remaining open lands, forests that were never cleared for agriculture (primary forests), and forests that established on former agricultural lands (secondary forests, sensu Rackham 1980, Peterken 1981). Comparisons between the forest types are made possible by previous work, which reconstructed the land-use history of each forest stand throughout the county (Smith et al. 1993, Flinn et al. 2005).

I conducted this study in 20 pairs of adjacent primary and secondary forests spread across Tompkins County. All sites were located in mesic, upland forests, and placed so that the adjacent stands had a similar slope, aspect, elevation and soil type (Appendix 1, Flinn and Marks in review). Based on aerial photographs and field evidence including the lack of pit-and-mound microtopography, I chose sites where the secondary forests had developed on plowed fields 85-100 years ago. Each stand covered at least one hectare. Flinn and Marks (in review) describe the tree communities of these forests, as well as physical and chemical properties of the soils and light availability in the understory. To relate environmental conditions in each stand to the performance of the three fern species, I use two axes from a principal components analysis of soil chemical properties, representing gradients in soil pH and

organic matter content (OM), and a measure of light levels, the mean amount of radiation transmitted to the understory ($\text{mols} \times \text{m}^{-2} \text{d}^{-1}$; Flinn and Marks in review).

Species

This study focuses on three wintergreen, perennial fern species native to the temperate deciduous forests of eastern North America: *Dryopteris carthusiana* (Villars) H. P. Fuchs, *Dryopteris intermedia* (Muhlenberg ex Willdenow) A. Gray and *Polystichum acrostichoides* (Michaux) Schott. *D. carthusiana* is an allotetraploid derivative of the diploid *D. intermedia* and an extinct *D. "semicristata"* (Walker 1961, Wagner 1970), and it has a circumboreal range, whereas *D. intermedia* and *P. acrostichoides* occur only in eastern North America (Montgomery and Wagner 1993, Wagner 1993). These species are the most common ferns in mesic, upland forests of central New York (Wiegand and Eames 1926, Mohler et al. in press). I chose these three species because they have contrasting distributions across forests of different history, despite their close relationship and ecological similarity. In central New York, *D. carthusiana* is more frequent in secondary forests than in primary; *D. intermedia* is equally frequent in the two forest types; and *P. acrostichoides* is among the herbaceous species most strongly associated with primary forests (Singleton et al. 2001).

In all three species, adult sporophyte plants consist of leaf clusters growing from a short, creeping rhizome. *P. acrostichoides* has a slightly greater capacity for clonal spread than the *Dryopteris* species, but individuals do not extend more than several meters. A new flush of leaves unfurls in late May, as the canopy leafs out. The undersides of leaves bear sori containing the spores, which mature in late June and have no inherent dormancy (personal observation). Spores germinate to form heart-shaped gametophytes a single cell thick. Each gametophyte has the potential to

become bisexual, though the species have varying rates of self-fertilization (Flinn in review). The flagellated sperm need free water to reach the egg, and when fertilization occurs, the newly formed sporophyte begins to produce leaves.

Adult plant performance

To compare the performance of adult plants in forests of contrasting history, I quantified the density, size and fecundity of individuals in 20 pairs of adjacent primary and secondary stands. Along four transects perpendicular to the land-use boundary, 20 m apart, 100 m long and 2 m wide, I counted and measured all individuals of the three fern species. Where densities were low, I searched the remainder of the hectare until I had measured at least 40 plants or all that I found. Plants not physically connected by rhizomes were considered separate since functional rather than genetic individuals were of interest. For each plant, I noted the number of leaves and the number of leaves with sori, and measured the length and width of the largest leaf and the length and width of the largest part of a leaf with sori. Having developed regression equations to estimate total leaf area, leaf area with sori and spore production from these measurements (Appendix 2), I used total leaf area as a measure of plant size and leaf area with sori as a measure of fecundity. Each square centimeter of leaf area with sori represents spore production of approximately 29,000 for *D. carthusiana*, 24,000 for *D. intermedia*, and 84,000 for *P. acrostichoides* (Appendix 2).

I compared population density in primary and secondary forests using mixed models with land-use history as the independent variable and site as a random factor (SAS Proc Mixed; SAS Institute, Cary, NC, USA). In the absence of other independent variables, this analysis is equivalent to a paired *t*-test. In this and all subsequent models, land-use history was a binary variable with primary forest = 0 and

secondary forest = 1. Population density was natural-log transformed after adding one individual.

Komolgorov-Smirnov two-sample tests compared the size distributions of plants in primary and secondary forests, pooled across sites. For sites with at least five individuals in both primary- and secondary-forest populations ($N = 11$ pairs for *D. carthusiana*, 16 for *D. intermedia* and 10 for *P. acrostichoides*), I compared individual plant size between the forest types using mixed models with land use as the independent variable and site as a random factor. Similar logistic models with an additional factor to account for total leaf area evaluated the odds of producing spores for individual plants of a given size in primary and secondary forests (SAS Proc Logistic). Likewise, I used mixed models with a covariate for plant size to evaluate the effects of land-use history on individual fecundity. Individual size and fecundity were natural-log transformed.

I also compared performance at the population level by calculating median leaf area, the proportion of plants that produced spores, and among plants producing spores, the median leaf area with sori. To assess the relative influences of land-use history and stand-level environmental conditions on population performance, I used mixed models with site as a random factor and history, soil pH, soil OM and light availability as independent variables, again including only those sites with at least five individuals in each stand. I tested all pairwise interactions and dropped those not significant at $\alpha = 0.05$. One site (WG3) was a statistical outlier in that its population performance measures were exceptionally high for its low light levels, and it was excluded from the analyses relating population performance to environmental conditions. This site had a dense understory of woody plants below a relatively open canopy.

Spore dispersal and the soil spore bank

To measure spore dispersal from primary-forest populations into adjacent secondary forests, as well as within stands, I focused on two sites where *P. acrostichoides* was restricted to the primary forests (DD7 and WV13). At these sites, *D. intermedia* plants were about half as dense in the secondary forests as in the primary forests, and *D. carthusiana* was uncommon. I used microscope slides coated with petroleum jelly and clipped to pigtail stakes 20 cm above the ground to trap airborne spores (Peck et al. 1990, Penrod 1994, Hill 1996). At each site, spore traps were placed along three transects perpendicular to the land-use boundary, at 0, 1, 2, 3, 5, 10 and 25 m into both stands. As spores of these species mature in late June in central New York (personal observation), I set out fresh spore traps every two weeks from June 26 to October 2, 2001.

After collecting each slide, I systematically searched the area of a 22 × 22 mm coverslip for fern spores using the Vernier scale of a compound microscope at 100X magnification. I developed a key to identify spores by making voucher slides of spores collected directly from reproductive plants of all fern species at the sites.

To quantify the soil spore bank, I counted germinants from soil cores collected at the same locations where spore traps were placed. Cores were taken on both June 26 and October 2, 2001, to reflect spore abundance in the soil both before and after the season's spore deposition (Penrod and McCormick 1996). Using a bulb planter, I took cores of 6 cm diameter and 6 cm depth and placed them directly into pots. Leaf litter was removed from the surface, but the soil was not otherwise disturbed. To facilitate germination, the pots were covered with transparent plastic lids, placed in a growth chamber and watered as necessary. The growth chamber provided 13 hours of day and 11 of night, temperatures ranging from 15 to 27° C and light intensities from 0.29

to 46.47 $\mu\text{E}/\text{m}^2/\text{s}$. I harvested sporophytes as they became identifiable, through December 2002.

I used mixed models with site as a random factor and sampling date as a repeated measure to compare spore density in the air and soil of primary and secondary forests. This analysis modelled the covariance among samples from the same location with an autoregressive covariance structure, in which correlations within locations decrease with time between measures (Littell et al. 1998). Using similar models with an additional factor for distance from the land-use boundary, I also tested whether spore density within secondary forests declined with distance from primary forests. Samples from the boundary between the two forest types were excluded from all analyses.

Spore germination, gametophyte survival and sporophyte establishment

I conducted a field experiment to compare germination and establishment rates between forest types, among species and under varying microhabitat conditions. In three pairs of primary and secondary forests, I sowed spores of the three fern species and left control plots unsown on three different forest-floor substrates and at ambient and elevated humidity, in a fully factorial design. For the experiment, I again chose sites (DD7, WV3 and WV13) where adult plants were present in the primary forests, but rare or absent in the secondary forests, so that sowing spores represented a reintroduction into unoccupied habitat. The three substrates included leaf litter, left undisturbed; humus, with leaf litter removed; and mineral soil, with leaf litter and humus removed and the soil turned with a trowel. I created the microhabitat treatments and sowed spores on July 31 and August 1-2, 2002, at a time when spores could naturally be deposited, and followed the resulting gametophyte and sporophyte plants through May 2005.

I included the elevated humidity treatment because, based on growing conditions of fern gametophytes in natural habitats and in culture, humidity appeared potentially critical to fern spore germination and gametophyte survival (Page 2002). In addition, previous attempts to sow fern spores in forests without covers to maintain high humidity had failed to produce germination (Glaves 1991). Lindsay and Dyer (1992) successfully followed gametophyte development in the field by sowing spores on sterilized soil in pots in the laboratory, covering the pots with transparent plastic lids and transplanting them to woodlands. In this experiment, I maintained elevated humidity by covering plots with 14 × 14 cm transparent plastic food storage containers, fastened down with ground staples through holes drilled in the corners. To quantify the effect of this treatment, I set out six adjacent pairs of Hobo data loggers (Onset Computer Co., Bourne, Massachusetts, USA), one of each pair under a cover, the other in the open. The data loggers recorded the temperature and relative humidity every 10 minutes from July 25 to November 5, 2003. Mean humidity under the covers was 12% higher than in the open, remaining near 96% (paired *t*-test, $t = 8.77$, $P = 0.0003$). Ambient humidity during this period ranged from 2-104%, with a mean of 84% (relative humidities >100% occur during condensation). Humidity was also significantly less variable under the covers (based on coefficients of variation, $t = -2.69$, $P = 0.0435$). Mean temperatures under the covers were also higher and less variable, but by only 0.3°C (means, $t = 11.91$, $P < 0.0001$; coefficients of variation, $t = -18.64$, $P < 0.0001$). Though artificial, the elevated humidity treatment was intended to simulate naturally moist, protected microhabitats, such as the crevice between a rotten log and the forest floor, a cavity formed by exposed roots at the base of a tree, or a clump of moss.

To obtain spores for sowing, I collected fertile leaves from 20-30 plants of each species in forests contiguous to each site, and dried them in ovens at 35°C to promote

spore release. I combined the released spores into a composite spore source for each species at each site. To ensure a uniform sowing density, I weighed 1.0 g of spores into a glassine envelope for sowing into each plot. Trial sowings in pots had indicated that this quantity of spores was sufficient to saturate the area.

At each site, I located five 1×1.5 m blocks at random positions within both the primary and secondary stands. Within the blocks, the species, humidity and substrate treatments were fully crossed and completely randomized in 4×6 arrays of 25×25 cm plots. Spores were sown from the glassine envelopes into a 9×9 cm frame in the center of the plots, first moistening the soil and then rinsing out the envelopes with water to help the spores adhere to the surface. Throughout the experiment, I maintained the substrate and humidity treatments by removing leaf litter from litterless plots, replacing broken covers and clipping any seedlings and root sprouts. I sampled the plots at the beginning of every month from May to November, the season when plants were not covered by snow. Since the size and density of gametophytes and sporophytes made marking and following individuals impossible, I quantified the percentage cover of gametophytes in the 9×9 cm area using a 25-cell grid, and counted the number of sporophytes.

These response variables had distributions with many zeroes, few moderate values and some extremely high values. For statistical analysis, I treated the presence of gametophytes and sporophytes as binary variables. In addition to the effects of land-use history, humidity, substrate, and species of spores sown, if any, fixed factors tested the effects of year, month, and month within year. Random factors accounted for the pairing between stands at each site, the blocks within each stand and the repeated sampling of each plot. To incorporate random effects with categorical responses, I used generalized linear mixed models (SAS Proc Glimmix). I tested all effects on the presence of gametophytes in a single model. For plots with gametophytes, I then

tested treatment effects on the presence of sporophytes. Only 5% of plots at ambient humidity formed sporophytes, however, making it impossible to analyze the effects of humidity and the other treatments simultaneously. Thus I separately analyzed the effect of ambient or elevated humidity on the presence of sporophytes in all plots with gametophytes, and the effects of the other treatments only in plots with gametophytes at elevated humidity. Across all plots, I also evaluated the effects of all treatments on the odds of having surviving sporophytes at the end of the experiment in May 2005. For plots having sporophytes at any time, I tested the effects of all treatments on the number of sporophytes using a model with a Poisson-distributed response and a log link function. In all models, I dropped interactions not significant at $\alpha = 0.05$.

Juvenile plant distribution in relation to microhabitat

While sampling adult plant populations at the 20 pairs of adjacent primary and secondary forests, I also searched for juvenile plants along the four 2 m-wide transects through each stand. Sporophytes formed during the present or the previous growing season can be distinguished from older plants and identified to species by their distinctive juvenile leaves, which I recognized by comparison to plants raised from spores (Peck 1980). I documented the distributions of juvenile sporophytes rather than gametophytes because gametophytes of closely related species cannot be distinguished from one another in the field (Farrar and Gooch 1975, Cousens et al. 1985).

For each young sporophyte, I recorded the substrate it grew on, whether leaf litter, humus, mineral soil, wood, moss, grass or stone; and whether the substrate was associated with a larger feature, such as a rotten log, a tree root, a fresh or old treefall pit or mound, or a pool or rivulet of water. I quantified the cover of these substrates and features on primary and secondary forest floors by noting which was present at every meter of the four transects, for 400 point samples per stand. I compared the

proportions of substrates occupied by juvenile plants to the proportions of substrates available on forest floors using G tests for goodness of fit.

RESULTS

Adult plant performance

Land-use history influenced the distribution and abundance of the three fern species in different ways. Across all sites, the average population density of *Dryopteris carthusiana* was about seven times higher in secondary forests than in primary (Figure 4.1), and population densities tended to be greater in secondary forests than in adjacent primary forests (Table 4.1). *Dryopteris intermedia* had nearly equal average population densities in the two forest types (Figure 4.1), but primary forests had significantly higher population densities than adjacent secondary forests (Table 4.1). For *Polystichum acrostichoides*, average population density was over three times greater in primary forests than in secondary (Figure 4.1), and populations were consistently more dense in primary forests than in adjacent secondary forests (Table 4.1).

By all measures, adult plant performance was either comparable or enhanced in secondary forests relative to primary. Plant size distributions differed between primary and secondary forests in *D. carthusiana* ($D = 0.1258$, $P = 0.0010$) and *P. acrostichoides* ($D = 0.1911$, $P < 0.0001$), with median plant size larger in secondary forests, while the overall size distribution of *D. intermedia* plants was similar in the two forest types (Figure 4.2).

Individual plants of all three species were larger and more likely to produce spores in secondary forests than in adjacent primary forests (Table 4.2). In *D. carthusiana* and *P. acrostichoides*, plants of a given size had over 50% higher odds of producing spores in secondary forests than in adjacent primary forests. While *Dryopteris*

Table 4.1. Population densities of different life stages in primary and secondary forests, for three fern species in central New York (individuals m⁻²; mean ± se).

	Primary	Secondary	<i>F</i>	<i>P</i>
<i>Dryopteris carthusiana</i>				
Adult plants	0.0068 ± 0.0023	0.0484 ± 0.0218	3.53	0.0758
Spores produced	14820 ± 6295	183500 ± 92770	0.20	0.6612
Spores deposited	1205 ± 381	918 ± 239	0.46	0.4969
Spores in soil	147 ± 65	108 ± 33	0.31	0.5755
Juvenile plants	0.0003 ± 0.0003	0.0015 ± 0.0010	1.61	0.2201
<i>Dryopteris intermedia</i>				
Adult plants	0.0763 ± 0.0169	0.0733 ± 0.0288	5.38	0.0317*
Spores produced	321600 ± 105100	306400 ± 114900	5.76	0.0266*
Spores deposited	13890 ± 3993	5108 ± 635	7.00	0.0084**
Spores in soil	3026 ± 570	2348 ± 489	1.18	0.2793
Juvenile plants	0.0051 ± 0.0022	0.0090 ± 0.0034	0.08	0.7801
<i>Polystichum acrostichoides</i>				
Adult plants	0.0774 ± 0.0206	0.0229 ± 0.0123	19.7	0.0003***
Spores produced	81010 ± 21060	50500 ± 24220	16.5	0.0007***
Spores deposited	32540 ± 6318	8781 ± 1271	22.9	<0.0001***
Spores in soil	2810 ± 487	1867 ± 352	2.79	0.0972
Juvenile plants	0.0023 ± 0.0022	0.0001 ± 0.0001	1.30	0.2678

Notes. Mixed models with site as a random factor compare population densities between pairs of adjacent primary and secondary forests, with asterisks for significant differences: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. For these analyses, adult and juvenile plant density and spore production were natural log-transformed after adding one individual. Adult and juvenile plant density and spore production estimates represent sampling of 20 primary-secondary forest pairs. Comparisons of spore deposition and the soil spore bank included an additional factor to account for repeated samples over the season. The spore deposition and soil spore bank estimates represent 503 slide-trap samples and 144 soil-core samples at two pairs of primary and secondary forests.

Table 4.2. Effects of land-use history on individual plant size, reproductive status and fecundity of three fern species in central New York forests.

<i>Dryopteris carthusiana</i>			<i>Dryopteris intermedia</i>			<i>Polystichum acrostichoides</i>		
Source	F/χ^2	P	Source	F/χ^2	P	Source	F/χ^2	P
Size (ln Leaf area, cm ²)								
History +	16.3	<0.0001***	History +	23.7	<0.0001***	History +	64.0	<0.0001***
Odds of reproduction								
History +	4.72	0.0298*	History +	2.74	0.0976	History +	11.3	0.0008***
Size (ln)+	265	<0.0001	Size (ln)+	612	<0.0001	Size (ln)+	281	<0.0001
Fecundity (ln Leaf area with sori, cm ²)								
History +	0.04	0.8438	History +	1.78	0.1829	History +	33.3	<0.0001***
Size (ln)+	305	<0.0001	Size (ln)+	952	<0.0001	Size (ln)+	238	<0.0001

Notes. In mixed models with site as a random factor accounting for pairing between adjacent stands, history was a binary variable with 0 = primary forest and 1 = secondary forest. Thus, a positive effect of history indicates a higher value in secondary forests. Asterisks mark significant effects of land-use history: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The analyses include only sites with ≥ 5 individuals in both stands ($N = 11$ pairs for *D. carthusiana*, 16 for *D. intermedia* and 10 for *P. acrostichoides*).

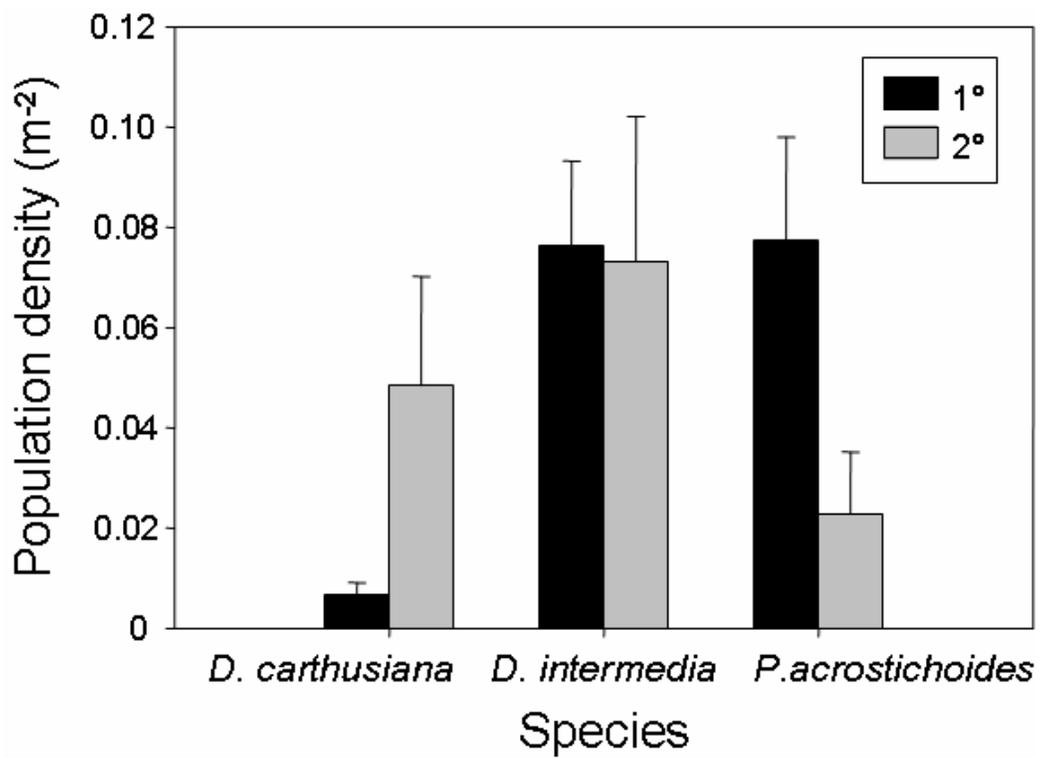


Figure 4.1. Population density of three fern species in primary and secondary forests of central New York (mean \pm se; $N = 20$ pairs of adjacent primary and secondary forests).

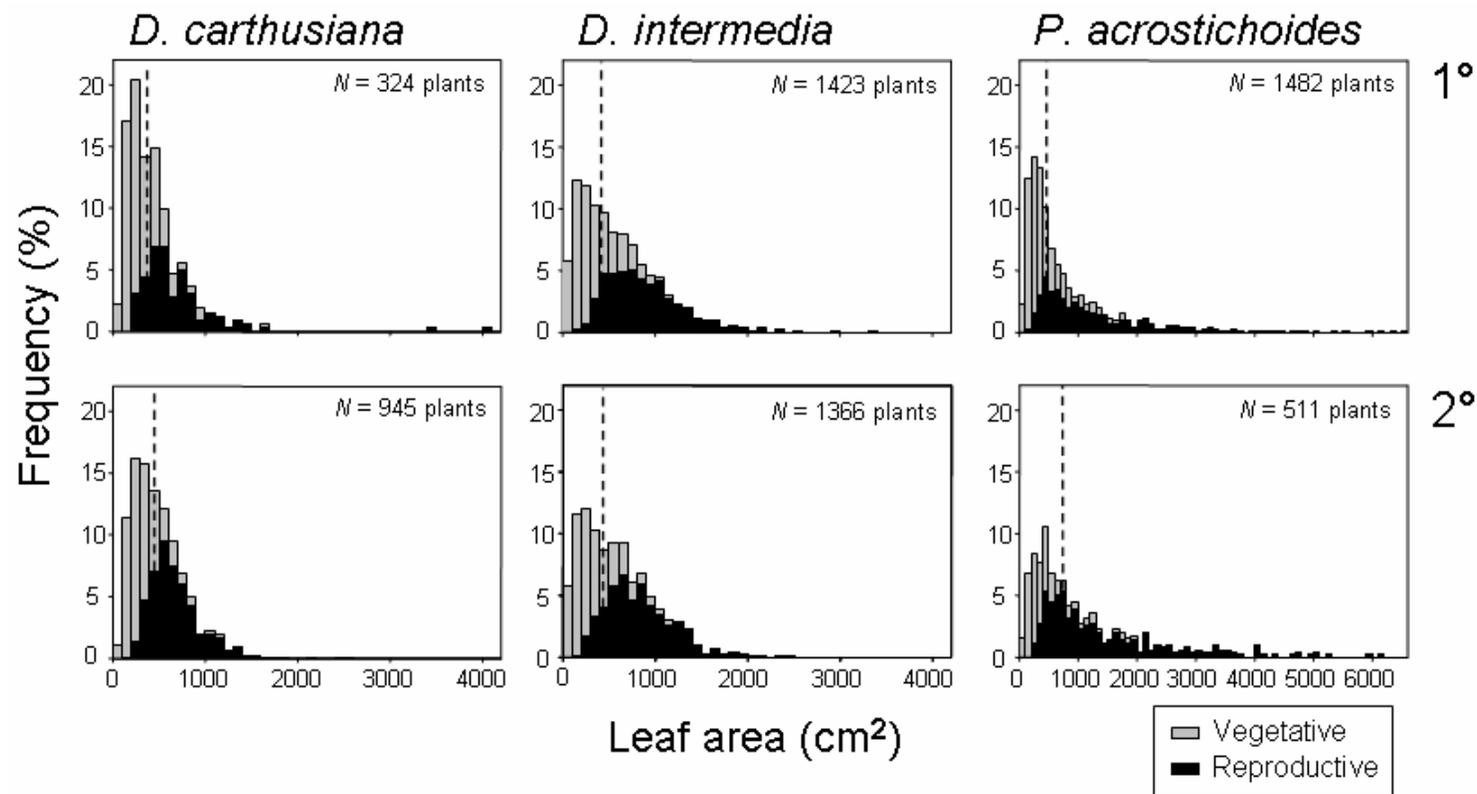


Figure 4.2. Size distributions of vegetative and reproductive individuals of three fern species in primary and secondary forests, with leaf area in 100-cm² size classes. Note that scales for leaf area differ between the *Dryopteris* species and *Polystichum acrostichoides*. One *P. acrostichoides* plant in a primary forest, with leaf area 8753 cm², is not shown.

individuals had similar fecundity in the two forest types, reproductive plants of *P. acrostichoides* with the same total leaf area had one-third more leaf area with sori in secondary forests than in primary (Table 4.2, Figure 4.3).

Accounting for variation in soil nutrients and light availability, populations of all three species had similar median plant sizes in adjacent primary and secondary forests (Table 4.3). In fact, present light availability had a greater influence than past land use on median plant size. However, the proportion of individuals that produced spores was higher in secondary-forest populations of all three species. Forest history had a greater impact than light availability on the reproductive proportion of populations in both *Dryopteris* species, whereas for *P. acrostichoides*, the proportion of reproductive plants depended most strongly on light and soil OM. The median fecundity of *D. carthusiana* populations increased with light levels and did not vary with forest history, but history had a stronger impact than light availability on median fecundity in both *D. intermedia* and *P. acrostichoides*. *D. intermedia* populations had 20% higher median fecundity, and *P. acrostichoides* populations had 50% higher median fecundity, in secondary forests than in primary. Despite greater population or individual fecundity, however, no species had greater total spore production in secondary forests, due to lower population densities there (Table 4.1). In fact, *D. intermedia* and *P. acrostichoides* produced more spores per area in primary forests (Table 4.1).

Relationships between population density and population performance differed among the three species. In *D. carthusiana*, density did not relate to performance. *D. intermedia* population density showed positive, marginally significant correlations with median size ($\rho = 0.34$, $P = 0.0550$) and median fecundity ($\rho = 0.33$, $P = 0.0658$). By contrast, the density of *P. acrostichoides* populations was negatively correlated

Table 4.3. Effects of land-use history and environmental conditions on population performance of three fern species in central New York forests. Measures of population performance include median plant size, the proportion of plants that were reproductive, and the median fecundity of reproductive plants.

<i>Dryopteris carthusiana</i>			<i>Dryopteris intermedia</i>			<i>Polystichum acrostichoides</i>					
Source	F	P	Source	F	P	Source	F	P			
Median size (Leaf area, cm ²)											
History	+	1.53	0.2621	History	+	2.34	0.1542	History	+	1.62	0.2597
pH	-	0.43	0.5369	pH	+	0.31	0.5884	pH	+	0.78	0.4178
OM	+	0.44	0.5308	OM	+	2.13	0.1721	OM	+	5.72	0.0623
Light	+	4.34	0.0823	Light	+	4.92	0.0484*	Light	+	3.79	0.1091
Proportion reproductive (%)											
History	+	10.7	0.0172*	History	+	12.0	0.0053**	History	+	11.4	0.0198*
pH	-	1.60	0.2534	pH	-	1.07	0.3226	pH	-	3.32	0.1282
OM	+	0.79	0.4082	OM	+	2.46	0.1450	OM	+	21.3	0.0058**
Light	+	8.26	0.0283*	Light	+	1.47	0.2513	Light	+	28.4	0.0031**
Median fecundity (Leaf area with sori, cm ²)											
History	-	0.05	0.8285	History	+	6.44	0.0275*	History	+	14.0	0.0135*
pH	-	0.56	0.4831	pH	+	0.03	0.8610	pH	-	0.04	0.8554
OM	+	1.43	0.2768	OM	+	1.47	0.2511	OM	+	5.18	0.0720
Light	+	13.5	0.0104*	Light	+	2.65	0.1319	Light	+	11.1	0.0209*

Notes. Mixed models included site as a random factor to account for pairing between adjacent stands, and history as a binary variable with 0 = primary forest and 1 = secondary forest. Thus, a positive effect of history indicates a higher value in secondary forests. Asterisks mark significant effects: *, P < 0.05; **, P < 0.01; ***, P < 0.001. There were no significant interactions. The analyses include only sites with ≥5 individuals in both stands, and exclude one site with exceptionally high performance measures for its low light levels (N = 10 pairs for *D. carthusiana*, 15 for *D. intermedia* and 9 for *P. acrostichoides*).

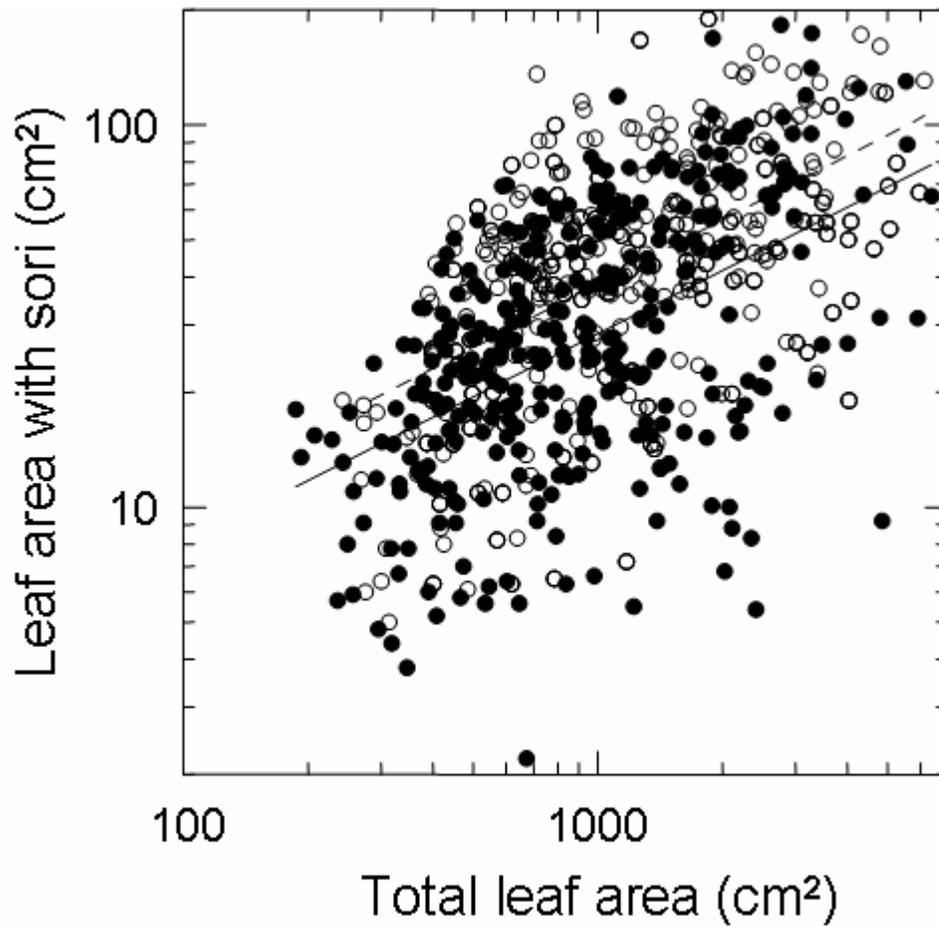


Figure 4.3. Fecundity of *Polystichum acrostichoides* plants relative to their size, in primary (filled circles, solid line) and secondary forests (open circles, dotted line). The scatterplot includes all reproductive plants at the 10 sites with at least 5 individuals in both primary and secondary forest ($N = 656$ plants).

with median plant size ($\rho = -0.47$, $P = 0.0369$), the proportion of plants that were reproductive ($\rho = -0.63$, $P = 0.0029$) and median fecundity ($\rho = -0.44$, $P = 0.0541$).

Spore dispersal and the soil spore bank

Fern spores were abundant and nearly ubiquitous throughout the forests, arriving at 91% of the slide traps and 80% of the soil cores. Over the 2001 growing season, 1534 spores of seven fern species landed on the slides, at a rate of about 500 fern spores $\text{m}^{-2} \text{day}^{-1}$. *D. carthusiana*, *D. intermedia* and *P. acrostichoides* spores represented 74% of the total deposition, with 91% of these falling between June 26 and July 24. The soil cores produced 2935 sporophytes of ten fern species, including *D. carthusiana*, *D. intermedia* and *P. acrostichoides*, demonstrating that their spores can remain viable in the soil over at least one winter.

D. carthusiana had low levels of spore deposition throughout the two sites (Table 4.1, Figure 4.4). Both *D. intermedia* and *P. acrostichoides* deposited about three times as many spores in primary forests as in secondary (Table 4.1). Within secondary forests, spore abundance appeared to decline with distance from the land-use boundary (for *D. intermedia*, $F = 3.69$, $P = 0.0560$; for *P. acrostichoides*, $F = 2.87$, $P = 0.0914$; Figure 4.4). Still, an average of 5100 *D. intermedia* and 8800 *P. acrostichoides* spores m^{-2} reached 25 m into secondary forests where adult plants were sparse or absent.

In the soil, *D. carthusiana* and *D. intermedia* had similar numbers of spores throughout the primary and secondary forests (Table 4.1, Figure 4.4). The density of *P. acrostichoides* spores, however, averaged twice as high in primary forest soils as in secondary (Table 4.1) and tended to decrease with distance from the primary forests ($F = 3.22$, $P = 0.0772$; Figure 4.4). Soils in secondary forests without adult plants still produced an average of 1900 *P. acrostichoides* sporophytes m^{-2} , or 4-5 orders of magnitude more than adult population densities.

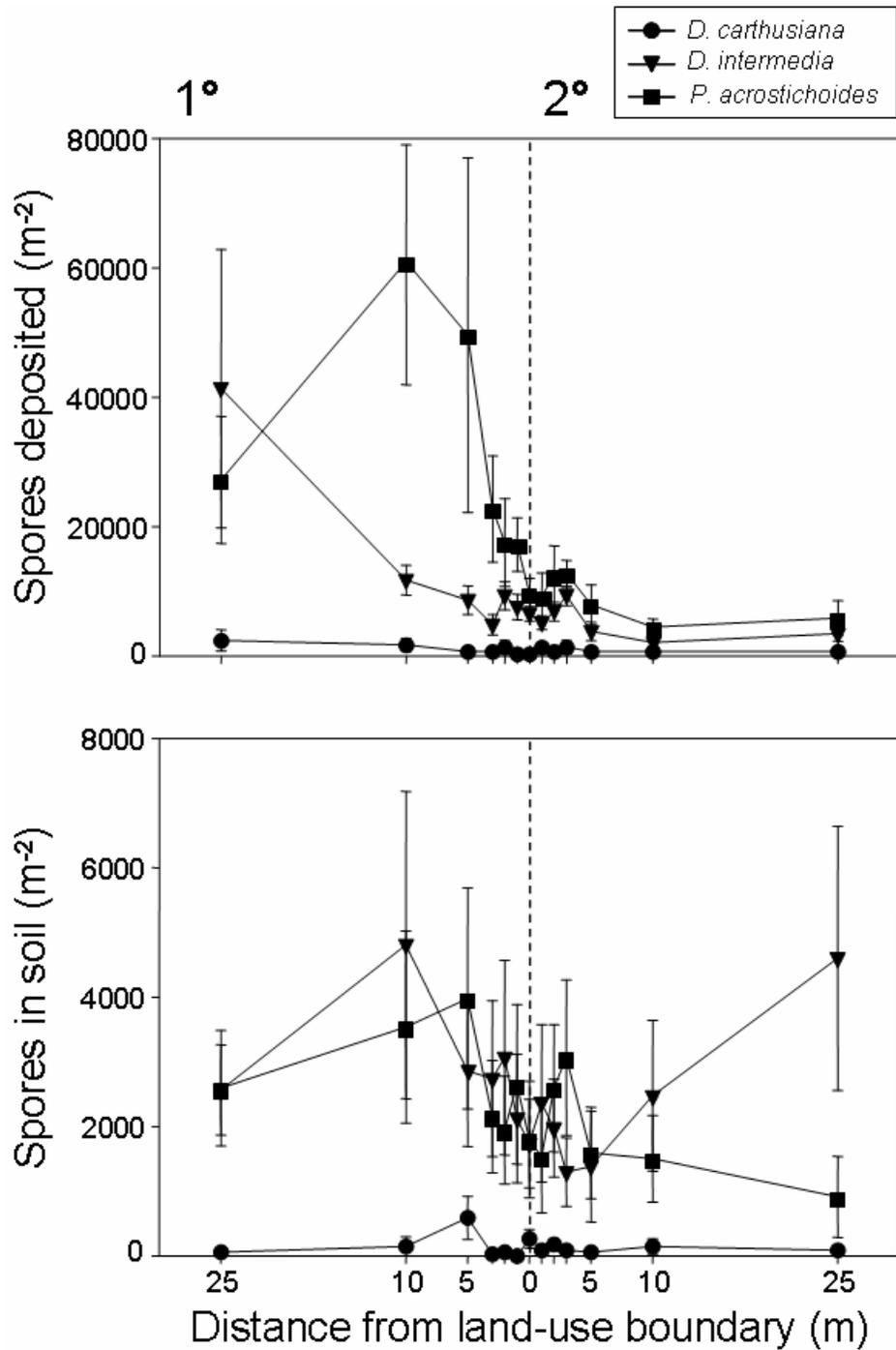


Figure 4.4. Spore deposition and the soil spore bank of three fern species in two pairs of adjacent primary and secondary forests. At varying distances from the land-use boundary, symbols for each species show the density of spores deposited over one full growing season, and the density of sporophytes produced by soil cores (mean \pm se). Note the tenfold difference between the scales.

Spore germination, gametophyte survival and sporophyte establishment

In the field experiment, spore germination began shortly after sowing in August 2002, with gametophytes clearly visible by October. After an initial flush of germination during the fall and spring of the first year, the cover of gametophytes remained relatively constant over time, increasing over each growing season and declining modestly over each winter (Figure 4.5). This pattern demonstrates that spore germination occurred continuously during both growing seasons of the experiment, and that most of the gametophytes must have survived. The first sporophytes formed during the summer after sowing, in July 2003, and sporophyte establishment continued throughout that growing season and the next. Like gametophytes, sporophytes appeared to have relatively high survival rates once established, as sporophyte numbers mostly increased over time (Figure 4.5). The presence of covers providing elevated humidity had the greatest impact on the formation and maintenance of both gametophytes and sporophytes (Table 4.4, Figure 4.6). Accounting for all other factors, plots at elevated humidity were about 4000 times more likely to have gametophytes, and plots with gametophytes at elevated humidity were 60 times more likely to have sporophytes, than plots at ambient humidity. Of plots at elevated humidity, 84% had gametophytes and 51% formed sporophytes, whereas only 12% of open plots had gametophytes and 5% formed sporophytes. The next largest influence on whether plots produced gametophyte and sporophyte plants was the substrate. Spore germination was 33 times more likely on mineral soil than on humus, and 11 times more likely on humus than on leaf litter. Likewise, given gametophytes at elevated humidity, sporophyte formation was 380 times more likely on mineral soil than on humus, and 20 times more likely on humus than on leaf litter. Where sporophytes were present, plots with elevated humidity, mineral soil and humus also formed greater numbers of sporophytes (Table 4.4,

Table 4.4. Generalized linear mixed models predicting the presence of gametophytes and sporophytes, and the number of sporophytes, in a three-year field experiment.

Factor	df	<i>F</i>	<i>P</i>
Odds of having gametophytes; <i>N</i> = 11520			
Humidity	1, 805	612	<0.0001
Substrate	2, 448	157	<0.0001
Species	3, 409	7.71	<0.0001
History	1, 26	0.25	0.6209
Year	3, 11497	312	<0.0001
Month	6, 11497	83.8	<0.0001
Year*Month	6, 11497	8.23	<0.0001
For plots with gametophytes, odds of having sporophytes; <i>N</i> = 4485			
Humidity	1, 237	20.8	<0.0001
Year	2, 4471	266	<0.0001
Month	6, 4471	67.9	<0.0001
Year*Month	4, 4471	5.10	0.0004
For plots with gametophytes at elevated humidity, odds of having sporophytes; <i>N</i> = 3913			
Substrate	2, 218	92.6	<0.0001
Species	3, 176	2.50	0.0614
History	1, 22	0.00	0.9981
Year	2, 3894	231	<0.0001
Month	6, 3894	59.1	<0.0001
Year*Month	4, 3894	6.01	<0.0001
Odds of having sporophytes in May 2005; <i>N</i> = 720			
Humidity	1, 712	124	<0.0001
Substrate	2, 712	48.3	<0.0001
Species	3, 712	1.48	0.2184
History	1, 22	0.40	0.5340
For plots with sporophytes, number of sporophytes; <i>N</i> = 1506			
Humidity	1, 237	65.4	<0.0001
Substrate	2, 185	66.3	<0.0001
Species	3, 170	5.60	0.0011
History	1, 27	0.51	0.4814
Year	2, 1486	619	<0.0001
Month	6, 1486	368	<0.0001
Year*Month	4, 1486	276	<0.0001

Notes. The random factors accounting for sites, blocks and repeated measures are not shown. There were no significant interactions.

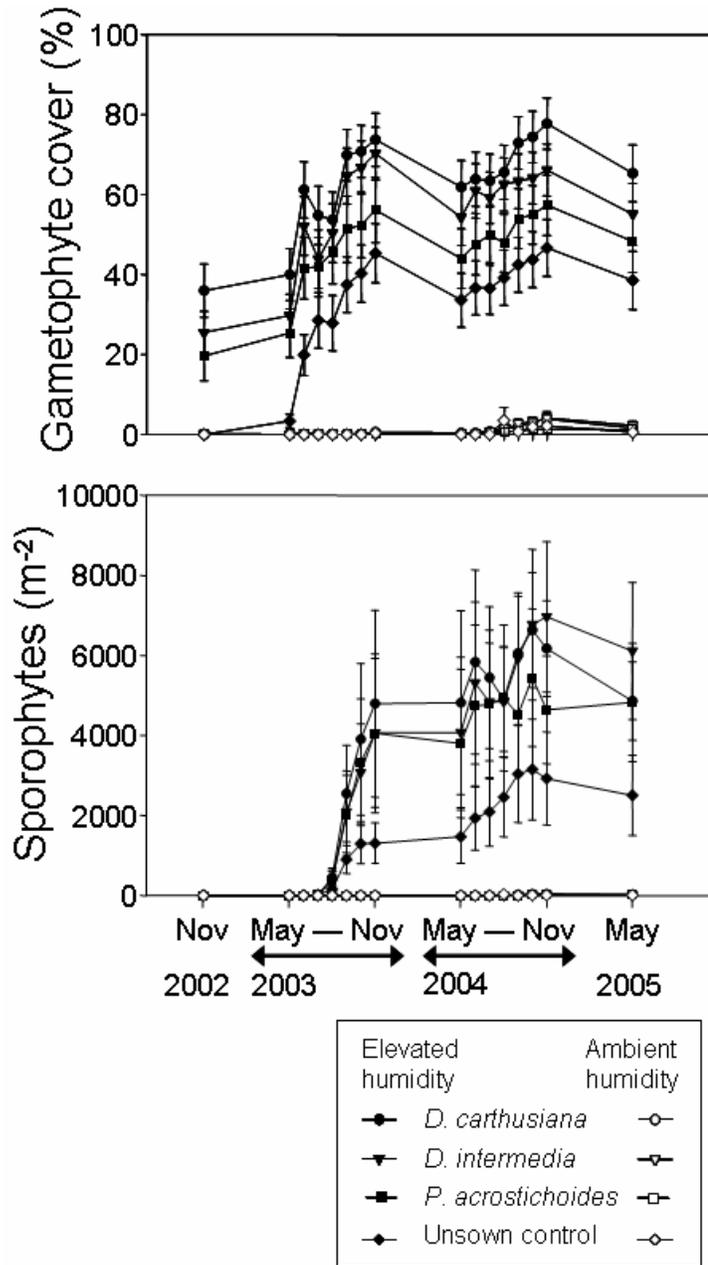


Figure 4.5. Gametophyte cover and sporophyte density during a three-year field experiment, in plots sown with spores of three fern species and unsown control plots, at either elevated or ambient humidity (mean \pm se). For clarity, the graph shows only plots on mineral soil (N = 240). Plots were sampled at the beginning of each month from May to November. At ambient humidity, both gametophyte cover and sporophyte density were low but nonzero.

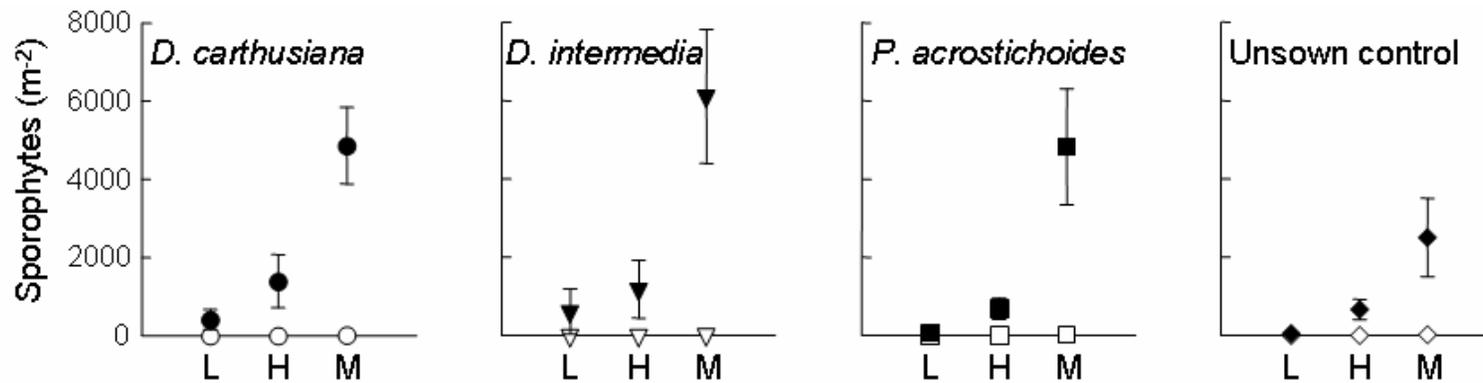


Figure 4.6. Sporophyte establishment at the end of a three-year field experiment in May 2005, for three fern species and an unsown control, on leaf litter (L), humus (H) or mineral soil (M), at elevated (filled symbols) or ambient humidity (open symbols; mean \pm se; N = 720 plots). At ambient humidity, sporophytes did not occur on leaf litter, and sporophyte density was low but nonzero on humus and mineral soil.

Figure 4.6). Thus, humidity had the dominant influence on the presence and number of both gametophytes and sporophytes, but it had a stronger effect on spore germination and gametophyte survival than it did on sporophyte establishment, whereas substrates had a stronger effect on sporophytes than on gametophytes.

Though the effects of sowing spores were 1-3 orders of magnitude smaller than the effects of humidity and substrate, germination and establishment rates differed significantly among the three species (Table 4.4). Plots with added *D. carthusiana* or *D. intermedia* spores were 2-4 times more likely to have gametophytes than either *P. acrostichoides* or unsown control plots. Pairwise contrasts showed no significant differences in spore germination between *D. carthusiana* and *D. intermedia*, or between *P. acrostichoides* and the unsown control. *D. carthusiana* also had the highest rate of sporophyte formation, followed by *D. intermedia*, *P. acrostichoides* and unsown plots. Given gametophytes at elevated humidity, *D. carthusiana* was 4-6 times more likely to have sporophytes than either *P. acrostichoides* or the unsown control, while other species pairs did not differ significantly. Thus, adding spores enhanced germination rates in *D. carthusiana* and *D. intermedia*, and sporophyte establishment rates in *D. carthusiana*, but had no effect on either for *P. acrostichoides*. By May 2005, after three years, unsown control plots were no less likely to have sporophytes than plots where spores of any species had been added. Among plots with sporophytes, however, all species' spore-sown plots had higher sporophyte numbers, an average of 4000 m⁻², than the unsown control, with 2500 m⁻² (Figure 4.6). Still, this value shows that, given suitable conditions, areas without added spores had the capacity to produce stands of sporophytes 4-5 orders of magnitude more dense than adult fern populations in these forests (Table 4.1). Sporophyte numbers were similar among the three species, though *D. carthusiana* plots had marginally higher

numbers of sporophytes than *P. acrostichoides* (pairwise contrast, $F = 3.37$, $P = 0.0682$).

Forest history had no effect on spore germination, gametophyte survival or sporophyte establishment (Table 4.4). The analysis also did not detect any significant interactions among the treatments—indicating, for example, that elevated humidity enhanced the odds of germination and establishment on all substrates equally, and that the three species and the unsown control responded similarly to the humidity levels and substrates.

Juvenile plant distribution in relation to microhabitat

In surveys of all sites, natural densities of juvenile plants were on average one order of magnitude less than adult plant densities, and were not significantly different in primary and secondary forests for any species (Table 4.1). The proportions of juvenile ferns occupying different substrates differed radically from the proportions of substrates available on the forest floor ($G = 1859$, $df\ 6$, $P < 0.0001$; $N = 534$; Figure 4.7). The three species also had significantly different distributions across the substrates ($G = 120.3$, $df\ 12$, $P < 0.0001$; Figure 4.7). Though leaf litter covered more than three-quarters of the area on forest floors (Table 4.5), no juvenile plants were found on leaf litter. Rather, *D. carthusiana* occurred preferentially on mineral soil, wood, and in moss ($G = 120.2$, $df\ 6$, $P < 0.0001$; $N = 37$); and *D. intermedia* occurred preferentially on humus, mineral soil, wood, and in moss ($G = 796.7$, $df\ 6$, $P < 0.0001$; $N = 253$). *D. carthusiana* and *D. intermedia* had similar distributions across the substrates, with most juvenile plants growing on wood (40%) or mineral soil (33%). In *D. carthusiana* and *D. intermedia*, 48% of juvenile plants were associated with rotten logs, and an additional 29% with living tree roots, whether directly on the wood or in a crevice created by it. Only 5% grew on treefall mounds and 5% on substrates

Table 4.5. Paired t-tests comparing the proportions of primary and secondary forest floors covered by various substrates and features (percentage, mean \pm se), based on 16000 point samples in 20 pairs of adjacent primary and secondary forests.

	Primary	Secondary	<i>t</i>	<i>P</i>
Substrate				
Leaf litter	77.4 \pm 2.65	76.2 \pm 4.47	0.34	0.7361
Humus	4.06 \pm 0.42	1.66 \pm 0.35	5.22	<0.0001
Mineral soil	6.54 \pm 1.62	10.64 \pm 3.59	-1.67	0.1117
Wood	8.26 \pm 0.59	8.65 \pm 0.64	-0.59	0.5644
Stone	1.49 \pm 0.47	0.68 \pm 0.24	1.43	0.1697
Moss	2.18 \pm 0.63	2.16 \pm 0.51	0.02	0.9806
Grass	0.13 \pm 0.09	0.04 \pm 0.03	0.92	0.3672
Feature				
Logs	7.10 \pm 0.59	8.15 \pm 0.68	-1.67	0.1118
Tree roots	3.41 \pm 0.49	2.19 \pm 0.22	2.41	0.0261
Pits and mounds	3.21 \pm 0.48	0.23 \pm 0.09	6.09	<0.0001
Water	2.60 \pm 0.77	0.60 \pm 0.35	2.41	0.0264

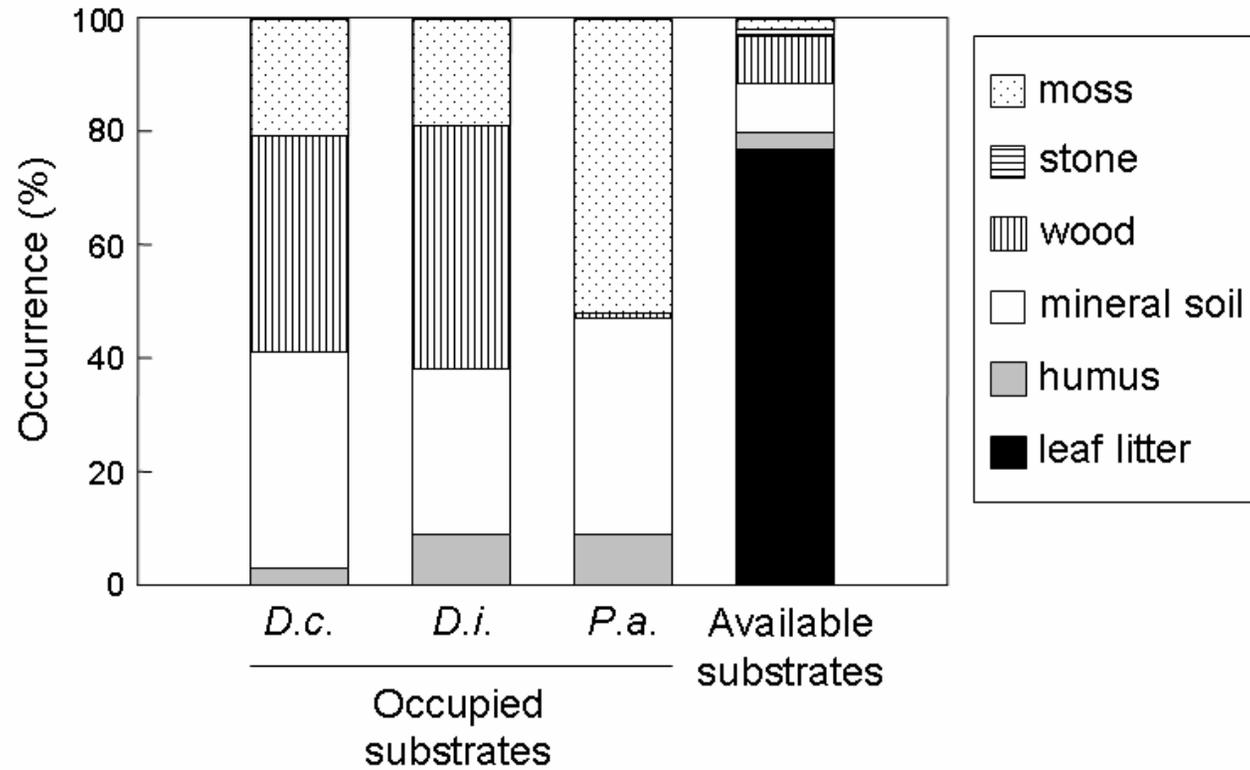


Figure 4.7. Proportions of juvenile plants of three fern species occupying various substrates, relative to proportions of available substrates on the forest floor. For juvenile plants, $N = 37$ *Dryopteris carthusiana*, 253 *Dryopteris intermedia* and 244 *Polystichum acrostichoides*; for forest floors, $N = 16000$ point samples in 20 pairs of adjacent primary and secondary forests.

exposed by a pool or rivulet of water. In contrast, *P. acrostichoides* occurred preferentially on humus, mineral soil and with moss, and less often than expected on wood ($G = 1111$, $df\ 6$, $P < 0.0001$; $N = 244$). Most juvenile *P. acrostichoides* plants grew in moss (51%) or on mineral soil (38%). While 18% were associated with rotten logs and 11% with tree roots, 21% occurred on treefall mounds, and 16% on substrates exposed by water.

The proportions of forest floors covered by various substrates differed significantly between primary and secondary forests ($G = 385.2$, $df\ 6$, $P < 0.0001$). Substrates and features more common in primary forests included humus, tree roots, treefall pits and mounds, and ephemeral pools and rivulets of water (Table 4.5).

DISCUSSION

Which life stage limits colonization of secondary forests?

Contrary to predictions based on their distribution, adult plants of all three fern species had similar or greater size and fecundity in secondary forests than in primary forests. This pattern could arise in two ways: either plants in secondary forests are older, plants of the same age are larger and more reproductive, or both. Since populations in secondary forests would likely have established within the last 80 years, whereas populations in primary forests may have persisted for thousands of years, it seems unlikely that plants in secondary forests would be consistently older. A lack of recruitment in secondary forests could contribute to a lower proportion of small, pre-reproductive individuals in secondary forest populations. However, an age difference cannot fully account for the observed performance variation, since individual plants also differed in allocation patterns between the forest types. In both *D. carthusiana* and *P. acrostichoides*, plants of the same size were more likely to produce spores in secondary forests, and in *P. acrostichoides*, reproductive plants of the same size

produced more spores. These patterns demonstrate that plants respond differently to habitats created by past agriculture, and suggests that some aspect of the environment improves performance in secondary forests relative to adjacent primary stands.

Among the measured environmental variables, light availability had the greatest impact on all aspects of population performance for all three species. Light is often the limiting resource in forest understories (Neufeld and Young 2003), and can control growth and sexual reproduction in forest herbs such as *Aster acuminatus* (Pitelka et al. 1980, Ashmun and Pitelka 1984, Hughes et al. 1988) and the forest fern *Dennstaedtia punctilobula* (Hill and Silander 2001). However, adjacent primary and secondary forests have similar understory light availability in these 20 pairs of stands, as well as similar soil physical properties, moisture status and pH (Flinn and Marks in review). The principal difference in the abiotic environments of the two forest types is a 15% reduction in soil OM in secondary forests relative to adjacent primary stands, which would seem unlikely to promote greater growth or fecundity. Evidently these plants provide a more sensitive bioassay of environmental differences between the forest types than direct measurements (Fowler and Antonovics 1981, Antonovics et al. 1987, Bell et al. 2000), responding to an undetected difference in one of the measured environmental variables, or to some unmeasured aspect of the biotic or abiotic environment. It is also possible that current performance represents a fixed response to past environmental conditions, such as the previously high light levels in developing secondary forests.

Regardless of its cause, the apparently enhanced performance of adult plants in secondary forests clearly cannot explain the limited colonization of these stands. Rather, lower densities of adult plants must result from lower recruitment, whether due to reduced spore availability or reduced rates of germination and establishment. Previous studies have shown that most fern spores disperse within several meters of

the parent plant (Peck et al. 1990, Penrod 1994), and in fact, *D. intermedia* and *P. acrostichoides* produced and deposited fewer spores in secondary forests where adult plants were rare or absent. However, this study documented that spores arrive and remain viable in the soil of unoccupied habitats in numbers far in excess of maximum recruitment rates, so that sowing additional spores had relatively little effect. The increased germination rate with added spores of *D. carthusiana* and *D. intermedia*, and the increased sporophyte establishment of *D. carthusiana*, are likely to be biologically redundant in an area that would eventually support only one adult plant. In the end, unsown plots produced sporophytes as often as plots with added spores of any species, and at densities 5-6 orders of magnitude greater than observed densities of juvenile plants (Table 4.1). This result demonstrates that the availability of suitable sites for establishment, not spores, limits recruitment in these populations. In Harper's analogy, taking a cupful of beans from a sack of beans, the number of beans in the cup does not depend on the number of beans in the sack, above a threshold value (Harper et al. 1965). In addition, equal rates of germination and establishment in the two forest types, given similar microhabitat conditions, indicate that no other factor reduces recruitment in secondary forests.

Thus, the lower abundance of some species in secondary forests most likely reflects a lack of sites suitable for establishment. Natural densities of juvenile plants were not significantly higher in primary forests than in secondary forests, though this may reflect their general rarity. In fact, safe sites may be sufficiently rare everywhere that, in 100 years, secondary forests simply have not accumulated population densities comparable to the continuously forested primary stands. However, the lower cover of humus, tree roots, treefall pits and mounds, and ephemeral pools and rivulets has the potential to reduce recruitment of all three fern species in secondary forests. These categories only coarsely characterize the available microhabitats; certainly, for

example, not all wood on the forest floor provides similar conditions. Still, the different proportions of substrates suggest a subtle but potentially critical difference between the forest types. Even substrates now as frequent in secondary forests as in primary may have been less common in the recent past. For example, post-agricultural sites often develop a dense thicket of trees or shrubs within 20-40 years of abandonment, in which leaf litter can form a thick and uniform cover. Only larger and older trees have elevated bases and exposed roots that rise above the litter layer (though secondary forests now have similar tree stem density and slightly greater basal area than primary forests; Flinn and Marks in review). Plowing leaves the soil surface of secondary forests flat and homogenous, with reduced within-stand variability in soil moisture and pH (Flinn and Marks in review). Not until many canopy trees die and fall will these stands begin to redevelop the microtopography typical of long-forested areas. On environmental gradients and spatial scales relevant to most forest plants, and to adult plants of the three fern species, secondary forests appear to provide suitable habitats. In a type and scale of environmental conditions rarely considered, however, persistent legacies of agriculture may continue to hinder the establishment of ferns.

What characteristics explain the species' contrasting distributions?

At most life stages, the three fern species showed largely similar responses to land-use history and environmental conditions. What then explains their contrasting distributions across habitats of different history? Several results suggest that *Polystichum acrostichoides* may have more specific habitat requirements than the *Dryopteris* species. First, its population performance showed greater sensitivity to soil conditions, increasing with soil OM. The current, 15% soil OM deficit in secondary forests does not appear to hinder plant size or fecundity, since both were greater in

secondary forests than in primary. However, cultivation would have initially reduced soil OM by about 30%, and soils may have only recently regained current OM levels (Davidson and Ackerman 1993, Murty et al. 2002). The response of *P. acrostichoides* to this gradient could suggest that soil conditions have been less favorable for this species during the development of post-agricultural forests. Second, though the spore-sowing experiment did not detect differences among species in establishment requirements, the natural distribution of juvenile plants suggested that *P. acrostichoides* had a stronger association with mineral soil and moss than the *Dryopteris* species, which occurred equally frequently on wood. Mineral soil and moss were equally common on primary and secondary forest floors, but this pattern could reflect a greater specificity in the response of *P. acrostichoides* gametophytes or juvenile sporophytes to other aspects of their microhabitat.

Whether or not the three fern species have different interactions with post-agricultural forest environments, the species' different distributions may also reflect intrinsic life history characteristics. In the spore-sowing experiment, the species' germination and establishment rates fell in the rank order predicted by their distributions, with *D. carthusiana* consistently having the highest rates of spore germination and sporophyte formation, and *P. acrostichoides* the lowest. Sporophyte establishment rates could also depend on gametophyte mating patterns, which I assessed by growing gametophytes in isolation and in pairs of varying relatedness (Flinn in review). This laboratory experiment yielded very similar results to those from plants grown in forest habitats. *D. carthusiana* gametophytes again had the greatest sporophyte production across all treatments, as well as the greatest potential for self-fertilization, while *P. acrostichoides* had the lowest reproductive success and the lowest tolerance for inbreeding. It appears that high germination and establishment rates, including the ability to self-fertilize, facilitate rapid colonization

in *D. carthusiana*. Lower rates of germination and sporophyte formation, due in part to a predominantly outcrossing mating system (Flinn in review, Soltis and Soltis 1990), slow the colonization process for *P. acrostichoides*. The current distributions of *D. carthusiana* and *D. intermedia* appear to match their performance, whereas the negative correlations of plant density with adult performance in *P. acrostichoides* suggest that its distribution has not reached an equilibrium with the environment. Together, these results indicate that, on a fast-slow continuum of life history (Franco and Silvertown 1996), *D. carthusiana* is the fastest of the three species, *D. intermedia* is intermediate, and *P. acrostichoides* is simply slower. The basic life history constraints and reproductive biology of these species could provide a sufficient explanation for their relative colonization success.

Implications for the recovery of post-agricultural forest communities

Since adult survival and growth have the greatest influence on population growth rates in long-lived, perennial plants (Franco and Silvertown 1996), parity in adult performance is an important condition for population persistence in secondary forests. Most forest understory plants investigated so far have similar or better performance in secondary forests relative to primary (Singleton 1998, Donohue et al. 2000, Verheyen and Hermy 2004), and some species show higher growth rates (Fraterrigo et al. 2005) or greater reproductive output (Endels et al. 2004). Also as in this study, Fraterrigo et al. (2005) found different allocation patterns between the forest types, with plants in previously farmed stands allocating proportionately more to leaves versus stems. By contrast, *Trillium grandiflorum* plants at high-pH sites in central New York were smaller and less likely to flower in secondary forests than in primary (Vellend 2005). Even within the same landscape, therefore, individual species can have unique responses to the legacies of past agriculture. The accumulated evidence demonstrates

that the effects of agriculture on forest understory plants may include not only a reduction in species richness, but also a selective, environmental filter that shapes the composition of recovering communities.

Though previous studies of herbaceous species in forests regrowing after agriculture have overwhelmingly focused on dispersal limitation, this study reveals a greater role for environmental interactions in the process of recolonization. Perhaps the strongest evidence for seed supply limiting the distributions of other forest herbs comes from experiments comparing the germination and establishment of seeds planted in primary and secondary forests. For most species, adding seeds increased recruitment at least as much in secondary forests as in primary (Singleton 1998, Graae et al. 2004, Verheyen and Hermy 2004), supporting the view that seed availability generally limits site occupancy in forest herbs, especially those lacking adaptations for long-distance dispersal (Ehrlén and Eriksson 2000, Turnbull et al. 2000). Even in ferns, spore availability could prove more limiting at greater distances from source populations, as all secondary stands studied here were contiguous with primary forests. However, the situation documented by this study may be more common than previously appreciated, with 90% of secondary forests in the region adjacent to older stands (Smith et al. 1993). By providing a counter-example to the pattern shown by other species, the population biology of the ferns described here shows that dispersal limitation is not universal among plants of forest understories. Restoring all species typical of these communities may require specific habitat modifications, in addition to the arrival of seeds and spores.

The population ecology of ferns

The present results advance our understanding of fern population ecology by beginning to specify the conditions necessary for establishment and reproduction in

natural habitats. First, they clearly point to moisture availability as a critical requirement for both the germination and survival of gametophytes, and the formation of sporophytes. The experimental results corroborate a phenomenon long known in horticulture, that high and constant humidity promotes gametophyte germination and survival. Early methods of raising ferns from spores used cloches, bell jars or glass cases (Ward 1842), and ferns often appear in glass bottles left in woods or gardens (Benham 1924). Though some fern gametophytes have been shown to withstand desiccation (Pickett 1914, Farrar 1985), it would seem logical that moist environments facilitate the growth of gametophytes, which consist of a single cell layer without a cuticle or vascular system, and the formation of sporophytes, since fertilization requires free water (Page 2002). However, this experiment is the first to demonstrate the primary importance of humidity to the establishment of ferns in natural habitats.

The methods used to create humid microclimates proved highly effective and potentially applicable in other studies. In fact, the covers may have elevated humidity beyond levels usually encountered, as well as creating a greenhouse-like environment when direct sunlight reached them. They also provided some measure of protection from mechanical disturbances, such as rainstorms. Thus, the sporophyte densities produced under the covers may represent maximum potential rates of germination and establishment. However, they are commensurate with estimates reported from naturally dense gametophyte populations (Farrar and Gooch 1975, Peck 1980, Cousens 1981). In general, the elevated humidity treatment appeared to provide a reasonable approximation of the conditions juvenile plants would experience in the damp, sheltered places where they naturally occurred, and it made feasible the experimental study of the early stages of the fern life cycle under field conditions.

Further evidence for a dominant role of moisture availability comes from patterns of mortality in the spore-sowing experiment. Most mortality of both gametophytes

and sporophytes apparently resulted from either drying or flooding. Desiccation appeared to cause declines in gametophyte cover and sporophyte numbers, especially during dry periods in June and October 2004. The 2003 and 2004 growing seasons otherwise had above-average precipitation; in fact, 2004 had the fourth wettest summer since 1879 (Northeast Regional Climate Center 2006). Plants in several plots washed out during the spring snowmelt and rains of April and May, and during the unusually rainy month of July 2004. Others were overgrown by bryophytes or fungi. Desiccation, erosion and bryophyte competition were also the principal sources of mortality Peck et al. (1990) observed in following natural gametophyte populations.

Many of the microsites preferentially occupied by juvenile plants have a constant supply of moisture (Groninger and McCormick 1992). Rotten wood, for example, holds water, and bryophyte mats trap humidity. Just as cliffs seep moisture, tiny ledges can provide a source of subsurface runoff. Extremely small crevices, hollows and variations in the soil surface can create moist, moderated microclimates. In seed-sowing experiments on soil surfaces of varying microtopography, for example, Harper et al. (1965) found much more germination on rougher soils, but covers maintaining high humidity compensated for the effect of microtopography, allowing similar germination rates on smooth and rough soil surfaces.

At the same time, sites such as logs, tree bases, treefall mounds and other small rises serve to elevate plants above the blanket of leaf litter. In both the spore-sowing experiment and juvenile habitat surveys, tree leaf litter represented a major impediment to establishment. While perhaps more strict in ferns, the preference for areas free of litter is shared by many other herbaceous understory plants (Sydes and Grime 1981, Facelli and Pickett 1991, Eriksson 1995, Xiong and Nilsson 1999, Vellend et al. 2000). For example, Sydes and Grime (1981) documented that many species tended to occur on small hummocks, stones or fallen trees that provided a

refuge from litter, but bryophytes were most strongly restricted to locally elevated situations.

Though not previously quantified, the preferential occurrence of fern gametophytes and young sporophytes on disturbed mineral soil confirms numerous anecdotal reports (Pickett 1914, Schneller 1979, Cousens 1981, Watson and Vazquez 1981, Cousens et al. 1985, Groninger and McCormick 1992). Several field observers have also noted the tendency for fern gametophytes to grow on rotten wood (Pickett 1914, Schneller 1979) and amongst bryophytes (Pickett 1914, Willmot 1985, Groninger and McCormick 1992). For example, Cousens et al. (1988) found *Lorinseria areolata* gametophytes and young sporophytes on the bare soil of hummocks in Florida bayhead forests, and on the rotten wood of stumps and fallen branches in slash pine flatwoods. In a river canyon in central Iowa, fern gametophyte populations occurred on sandstone, soil slumps and alluvial soil, substrates often freshly exposed by rainstorms (Peck et al. 1990). In fact, though they did not directly observe juvenile plants, several studies have documented associations of the *Dryopteris* species with treefall pits and mounds (Beatty 1984, Collins and Pickett 1982, Peterson and Campbell 1993, Palmer et al. 2000), and McGee (2001) found that *Dryopteris intermedia* had densities twice as high on rotten logs as on the rest of the forest floor in Adirondack forests.

What processes create suitable microsites for fern establishment? Most owe their existence to some form of disturbance (Werth and Cousens 1990). In this study, larger-scale disturbances associated with juvenile plants included the falling of live and dead trees and branches, and soil scouring by water. In the spore-sowing experiment, extremely small-scale soil erosion both created and destroyed suitable habitats by exposing new patches of bare soil and burying or dislodging small plants. Likewise, earthworms could promote spore germination, by removing leaf litter and

turning fresh mineral soil, and increase mortality, by continually churning the surface; ants and small mammals occasionally played a similar role. Cousens et al. (1985) discovered several fern gametophyte populations on crayfish chimneys, which probably provide habitats analogous to earthworm burrows. Other disturbances known to create substrates pioneered by fern gametophytes include volcanic eruptions (Docters van Leeuwen 1936, Ranker et al. 1996), fires (Conway 1949, Gliessman 1978), flash floods (Peck et al. 1990) and log skidding (Groninger and McCormick 1992). The available evidence thus suggests a tight coupling between fern recruitment and disturbance events, even within relatively stable forest habitats (Grubb 1988).

Though habitat requirements often change with plant development (Grubb 1977, Parrish and Bazzaz 1985, Schupp 1995, Eriksson 2002), these fern species seem to present an extreme case of niche differentiation between life stages, where the essentially ruderal habit of the gametophyte phase contrasts with the long-lived, stress-tolerant sporophyte generation (Grime 1979). In fact, the two generations of a single fern species may have a wholly distinct ecology, life history and even geographic range (Farrar 1967, Rumsey et al. 1998). For the three fern species in this study, specific requirements for gametophyte germination and establishment appear to exclude plants from habitats otherwise favorable for the sporophyte generation, and may largely determine population growth rates and species distributions.

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Appendix 1. Site characteristics of 20 pairs of adjacent primary (P) and secondary (S) forests in central New York, including latitude (°N) and longitude (°W), elevation (m), slope (°), aspect (°) and soil type.

Site	Quadrangle	History	Latitude	Longitude	Elev.	Slope	Aspect	Soil type
AP5	Alpine	P	42°20'18"	76°39'28"	436	15.1	280	Bath channery silt loam
		S	42°20'22"	76°39'28"	436	12.4	263	Bath channery silt loam
AP6	Alpine	P	42°19'14"	76°38'43"	471	15.9	311	Bath, Valois and Lansing
		S	42°19'16"	76°38'37"	487	15.8	328	Bath, Valois and Lansing
DD5	Dryden	P	42°27'02"	76°19'58"	565	2.71	218	Lordstown channery silt loam
		S	42°26'59"	76°19'59"	562	1.69	163	Lordstown channery silt loam
DD7	Dryden	P	42°25'50"	76°18'20"	514	8.05	303	Volusia channery silt loam
		S	42°25'54"	76°18'20"	506	7.87	305	Volusia channery silt loam
LV1	Ludlowville	P	42°37'11"	76°30'59"	281	1.87	241	Lima silt loam
		S	42°37'11"	76°30'54"	285	1.98	250	Lima silt loam
MB2	Mecklenburg	P	42°27'25"	76°39'40"	414	2.27	205	Langford channery silt loam
		S	42°27'25"	76°39'35"	419	2.64	265	Langford channery silt loam
MB3	Mecklenburg	P	42°24'25"	76°40'49"	488	11.9	195	Lordstown channery silt loam
		S	42°24'25"	76°40'54"	480	14.5	325	Lordstown channery silt loam
MB4	Mecklenburg	P	42°23'20"	76°40'32"	570	10.6	134	Lordstown channery silt loam
		S	42°23'20"	76°40'37"	576	16.0	22	Lordstown channery silt loam
SV1	Speedsville	P	42°22'24"	76°21'53"	467	10.7	89	Lordstown channery silt loam
		S	42°22'20"	76°21'53"	466	8.17	103	Lordstown channery silt loam
SV5	Speedsville	P	42°21'24"	76°20'13"	515	3.44	279	Lordstown channery silt loam
		S	42°21'24"	76°20'18"	509	3.72	294	Volusia channery silt loam
SV7	Speedsville	P	42°18'52"	76°17'16"	475	4.21	113	Bath channery silt loam
		S	42°18'52"	76°17'20"	481	2.61	140	Bath channery silt loam
TB2	Trumansburg	P	42°30'43"	76°41'01"	301	2.44	304	Howard gravelly loam
		S	42°30'45"	76°40'56"	303	2.50	218	Howard gravelly loam

Appendix 1 (Continued).

Site	Quadrangle	History	Latitude	Longitude	Elev.	Slope	Aspect	Soil type
WD8	West Danby	P	42°19'13"	76°37'00"	509	6.57	250	Volusia channery silt loam
		S	42°19'16"	76°37'00"	514	6.71	244	Volusia channery silt loam
WG2	West Groton	P	42°32'02"	76°26'47"	375	4.12	301	Lordstown channery silt loam
		S	42°31'59"	76°26'47"	383	5.40	270	Lordstown channery silt loam
WG3	West Groton	P	42°30'29"	76°27'39"	341	0.56	253	Erie channery silt loam
		S	42°30'24"	76°27'39"	341	0.23	flat	Erie channery silt loam
WG9	West Groton	P	42°36'22"	76°23'24"	434	6.17	49	Erie channery silt loam
		S	42°36'18"	76°23'25"	443	5.47	51	Erie channery silt loam
WV10	Willseyville	P	42°19'44"	76°29'25"	425	5.29	51	Bath and Valois gravelly silt loams
		S	42°19'48"	76°29'25"	420	7.82	75	Bath and Valois gravelly silt loams
WV12	Willseyville	P	42°19'01"	76°28'26"	419	6.65	281	Bath and Valois gravelly silt loams
		S	42°19'01"	76°28'31"	408	8.49	286	Bath and Valois gravelly silt loams
WV13	Willseyville	P	42°19'18"	76°25'20"	451	20.5	84	Lordstown channery silt loam
		S	42°19'14"	76°25'19"	457	13.2	60	Lordstown channery silt loam
WV3	Willseyville	P	42°21'29"	76°22'30"	547	13.5	110	Lordstown channery silt loam
		S	42°21'33"	76°22'29"	558	12.4	135	Lordstown channery silt loam

Notes. Site names are consistent with Singleton et al. (2001), and quadrangle names indicate 7.5-minute topographic maps (USGS, Reston, Virginia). Soil types follow the county soil survey (Neeley 1965).

Appendix 2. Regression equations to estimate total leaf area, leaf area covered by sori and spore production for individual plants of three fern species.

Species, Regression equations	<i>N</i>	<i>R</i> ²
<i>Dryopteris carthusiana</i>		
total leaf area (cm ²) = 48.94 (# leaves) + 6.431 (# leaves with sori) + 0.9595 (length × width of largest leaf)	25	0.94
leaf area with sori (cm ²) = 34.85 (# leaves with sori) + 0.8534 (length × width of largest leaf part with sori)	22	0.93
spore production = (17.43 (leaf area with sori) = # sori) × (25.63 ± 1.333 sporangia/sorus) × (64 spores/sporangium)	20	0.95
<i>Dryopteris intermedia</i>		
total leaf area (cm ²) = 29.05 (# leaves) + 4.457 (# leaves with sori) + 1.497 (length × width of largest leaf)	25	0.89
leaf area with sori (cm ²) = 8.915 (# leaves with sori) + 1.400 (length × width of largest leaf part with sori)	17	0.84
spore production = (19.88 (leaf area with sori) = # sori) × (18.73 ± 1.139 sporangia/sorus) × (64 spores/sporangium)	16	0.95
<i>Polystichum acrostichoides</i>		
total leaf area (cm ²) = 43.39 (# leaves) – 4.976 (# leaves with sori) + 1.464 (length × width of largest leaf)	20	0.97
leaf area with sori (cm ²) = 3.398 (# leaves with sori) + 0.6831 (length × width of largest leaf part with sori)	15	0.93
spore production = (53.87 (leaf area with sori) = # sori) × (24.22 ± 1.169 sporangia/sorus) × (64 spores/sporangium)	19	0.92

Notes. Leaf areas were measured with a LI-3100 Area Meter (LI-COR Inc., Lincoln, Nebraska, USA). The regression equations apply to adult, not juvenile, plants. All leptosporangiate ferns have 64 spores per sporangium.