

Land-use history and plant performance in populations of *Trillium grandiflorum*

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Abstract

Many forest herbs show reduced frequency in forests growing on former agricultural land (secondary forests) relative to forests that were never cleared for agriculture (primary forests). To explain this pattern, studies of secondary forest colonization by forest herbs have stressed the role of limited seed dispersal, though environmental conditions may also limit colonization. Here I demonstrate that adult plant performance of *Trillium grandiflorum* is significantly reduced in secondary vs. primary forests in central New York State, USA. Comparing primary and secondary sites both with relatively high soil pH, *T. grandiflorum* populations were more dense, and individual plants were larger and more likely to be flowering in primary than secondary forests. Using counts of annual leaf scars on the rhizome, I demonstrate that this result is not due to secondary populations being younger than primary populations. Age-specific leaf area was significantly greater in primary than secondary stands at high soil pH, and the data suggest slightly reduced seed set in secondary stands as well. These results point to a more important role for environmental conditions in limiting forest-herb colonization of secondary forests than has been previously appreciated. Restoration and conservation of forest herbs in post-agricultural forests will require more than simply overcoming dispersal limitation.

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1. Introduction

Plant distributions in deciduous forests of Europe and eastern North America have been profoundly influenced by human land-use history (e.g., Peterken and Game, 1984; Singleton et al., 2001; Bellemare et al., 2002; Honnay et al., 2002; Vellend, 2003; Verheyen et al., 2003; Flinn and Marks, 2004). Over the past several centuries, massive clearance of forest for agriculture has been followed by widespread abandonment of fields, and subsequent forest recovery (Whitney, 1994; Kirby and Watkins, 1998). In contemporary landscapes, we recognize primary forests as those that have never been cleared for agriculture, and secondary forests as those

that are growing on abandoned agricultural lands (Rackham, 2003).

The observation that species richness of forest herbs is reduced in secondary vs. primary forests (e.g., Singleton et al., 2001; Bellemare et al., 2002; Vellend, 2003; Flinn and Marks, 2004) has raised the issue of whether colonization of secondary forests is limited largely by seed dispersal or by environmental conditions. If colonization is limited largely by seed dispersal, restoration and conservation of forest herbs may be achieved by simply introducing seeds to suitable, but presently unoccupied sites; otherwise, conservation efforts may additionally require improvement of site conditions, a far more laborious undertaking. The overwhelming emphasis in the literature thus far has been on dispersal limitation, and two principal lines of evidence support this hypothesis. First, secondary forests that are distant from

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primary forests are often less likely to be colonized than forests in close proximity to older forests (e.g., Peterken and Game, 1984; Flinn and Marks, 2004). Second, in at least a few studies species with dispersal modes thought to result in short-distance movement (e.g., via ants or gravity) tend to be poorer colonizers than species with more mobile seeds (e.g., via wind or vertebrate ingestion) (e.g., Matlack, 1994; Verheyen et al., 2003).

The dispersal- and environmental-limitation hypotheses are not mutually exclusive, and relatively little attention has been paid to explicitly testing for environmental limitation. For example, if the performance of forest-herb individuals and populations is reduced in secondary vs. primary stands, this would point to a potentially important role for environmental limitation in slowing colonization of secondary forests. In an experimental introduction of both seeds and ramets of four species of forest herbs, Verheyen and Hermy (2004) found that plant performance was equal or greater in recent vs. ancient forests in Belgium. Using observations of established individuals of three forest-herb species, Endels et al. (2004) found better adult plant performance in recent vs. ancient forests in Belgium, and Donohue et al. (2000) found performance in *Gaultheria procumbens*, a short-statured woody species, to be enhanced in secondary relative to primary forests in Massachusetts. These studies strongly support the dispersal limitation hypothesis for the species that were studied, though some components of performance were slightly reduced for certain species in recent vs. ancient forests. The generality of these results across species remains uncertain. In this paper, I report evidence revealing reduced performance of *Trillium grandiflorum* (Michaux) Salisb. populations in secondary vs. primary forests.

I analyzed population density, plant size distributions, and flowering frequency in *T. grandiflorum* from primary and secondary forests of Tompkins County, New York. These surveys were followed up with more detailed analyses in selected primary–secondary pairs of stands. In these analyses, I first used annual leaf scars on *T. grandiflorum* rhizomes to test the hypothesis that plant size and flowering frequency might be reduced in secondary stands simply because these populations are younger. I then harvested mature fruits to analyze seed set (relative numbers of seeds and ovules) in the two stands types. Stands were sampled to avoid environmental differences between primary and secondary forests that may predate agricultural land use.

2. Methods

2.1. Study area and species

Tompkins County covers about 1300 km² in central New York State (Fig. 1) and Smith et al. (1993) have

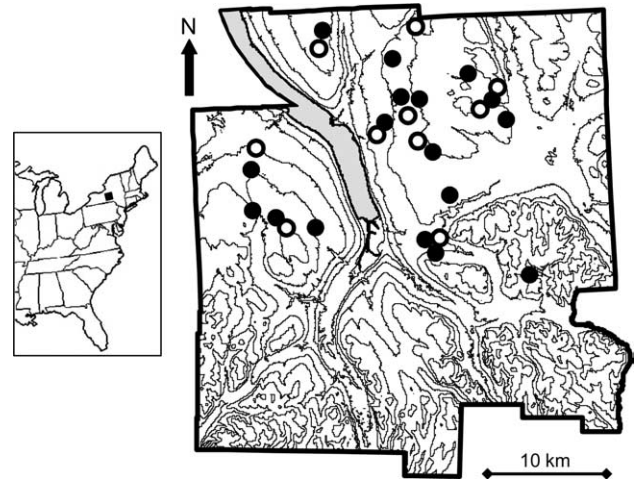


Fig. 1. Map of Tompkins County, New York, showing the locations of 17 primary (closed circles) and 10 secondary (open circles) forests used in this study. Contour lines are separated by 200 feet (~60 m), and the southern end of Cayuga Lake is shown in gray; the inset shows the location of Tompkins County in the eastern United States. Circle size does not represent the actual area of stands (i.e., none were physically adjacent).

reconstructed the history of forests in this county. European settlement began in the 1790's, prior to which >99% of the landscape was covered with a mixed deciduous forest; forest cover was reduced to <20% by 1900 via agricultural land use, and by 1995 forest cover had risen to >50% via abandonment of agriculture (Smith et al., 1993).

T. grandiflorum is a relatively common forest herb in Tompkins County, though it is present far more often in primary than secondary forests (Singleton et al., 2001; Vellend, 2004). Its distribution extends from Minnesota, Ontario and Québec in the north to Georgia and Alabama in the south (Gleason and Cronquist, 1991). It is a long-lived perennial with a rhizome that may grow to about 10 cm long; seedlings and younger plants bear a single leaf, while adults bear three leaves (Patrick, 1973). One shoot (occasionally two) emerges from a rhizome in early spring, and each shoot may (or may not) bear a single flower. Bees are the principal pollinators (Irwin, 2000), and individuals are largely self-incompatible, though some seeds can be produced by self-pollination (Sage et al., 2001). The single capsule produced by each flower contains about 15–30 seeds, and each seed bears an elaiosome to which ants are attracted. Ants are the primary agent of seed dispersal, though seeds can occasionally be moved up to several km via ingestion and defecation by white-tailed deer (Vellend et al., 2003). There is no long-term seed bank (Hanzawa and Kalisz, 1993).

Twenty-seven forest stands – 17 primary and 10 secondary – were sampled (Fig. 1; see also Vellend, 2004). All secondary stands were 70–100 years old, and in addition to the presence of *T. grandiflorum*, two criteria were

used in site selection. First, only “isolated” stands were sampled, in that each stand was surrounded on all sides by either fields, or younger secondary forests. This allowed an unambiguous delineation of *T. grandiflorum* populations. Second, once secondary stands were selected, primary stands were chosen to represent an equivalent range of soil associations as the secondary stands (based on maps from Neeley, 1965, and Tompkins County Planning Department, 2000). An analysis of soil nutrient data from these stands revealed no significant differences between primary and secondary forests (Vellend, 2004).

2.2. Population surveys

The density, leaf area, and reproductive status of *T. grandiflorum* plants were estimated during 2001–2003 in all 27 populations. A principal components analysis of soil nutrient data from these stands revealed one major axis of variation, and this axis was used as a potential predictor of *T. grandiflorum* performance (details provided in Vellend, 2004). This axis explained 49% of the variation, and represents a pH gradient. Numeric values of this axis are arbitrary, and range from about -2 (pH ~ 4.5) to 2 (pH ~ 6.5).

In a sample of plots from each stand, I counted and measured ≥ 100 plants, or all that I could find if < 100 . Only three-leaved plants were measured because of difficulties in reliably finding small, one-leaved individuals in plots with relatively dense vegetation. For each plant, I measured the length and width of a randomly chosen leaf, and recorded whether or not the plant was flowering. Using a sample of 90 plants from outside the study plots, I estimated leaf area using an LI-3100 Area Meter (LI-COR Inc., Lincoln, Nebraska), and then derived a regression equation for calculating total leaf area (of all three leaves) based on the length and width of one leaf (Total Leaf Area = $1.684 \times \text{Length} \times \text{Width}$, $r^2 = 0.99$).

The size and arrangement of plots in each stand were tailored to the spatial distribution of individuals. In larger stands where *T. grandiflorum* was evenly distributed, three 2×100 m belt transects were positioned at random along evenly spaced lines traversing the stand. Shorter transects were used in the smallest stands. Where density was high, 8–10 positions were chosen at random along each transect, and all individuals were measured in 0.5 – 2 m² plots at these positions. Where density was low, all individuals were counted and measured in the entire area of each belt transect. Where *T. grandiflorum* was present in only a small area (or areas) of the stand, random 1 m² plots were sampled within these areas until at least 100 individuals had been measured. I counted and measured all the individuals I could find in the stands with the two smallest populations.

For each population, three measures of performance were calculated: population density per m², the proportion of individuals that were flowering, and the median individual leaf area (cm²). Population density was averaged over the entire area of each stand. I used general linear models (SAS PROC GLM, SAS Institute, Cary, North Carolina) to assess the influence of land-use history and the soil pH axis on performance.

2.3. Plant age, size, and seed set

Analyses across the 27 stands suggested that *T. grandiflorum* performance was reduced in secondary vs. primary populations at high pH sites, but not at low pH sites (see Section 3). To ask whether this was due to secondary populations simply being comprised of younger individuals, I selected two primary–secondary pairs of stands at high pH for more in-depth analysis. The two stands in each pair were within 1 km of one another, had similar soil pH, and occurred on the same soil association (more details provided in Section 3). In each stand, 20 individuals representing the full range of above-ground sizes were excavated. In the two primary stands – where *T. grandiflorum* was quite abundant – a 100 m transect was laid down the middle of the stand, and five random points were chosen along the transect; at each point, the largest, smallest, and two intermediate-sized individuals were chosen for excavation. In the two secondary stands – where the distribution of *T. grandiflorum* was quite restricted – individuals were selected haphazardly to represent the full range of above-ground sizes. The number of leaf scars on each rhizome was counted as an estimate of minimum plant age (Hanzawa and Kalisz, 1993). Rhizome length and maximum and minimum widths were measured to the nearest 0.1 mm using a digital caliper, and rhizome volume was estimated assuming a cylindrical shape with diameter equal to the mean of the maximum and minimum widths. Leaf area was estimated as described above. General linear models (PROC GLM) were used to test for the effects of land use history and plant age on leaf area and rhizome volume in each stand pair separately. The interaction between land use and age was not significant in any of these analyses ($p > 0.05$), and was dropped from all models.

Secondary populations tended to be smaller than primary populations (Vellend, 2004), and population size may have important consequences for plant reproduction (Ellstrand and Elam, 1993). For three primary–secondary pairs of populations (at low, medium, and high pH), I estimated seed set in a sample of 20–22 fruiting individuals from each population in 2003. Estimated numbers of flowering individuals per hectare in the secondary stands (from low to high pH) were 17, 169, and 39; in the primary stands these were 2200, 6500, and 397,000. Populations within each pair of stands were

sampled on the same day; the secondary stand was sampled first (as described above for the age analysis), and individuals were chosen within the primary stand (at five random points on a 100 m transect) to ensure overlap in plant sizes (leaf area) between the two stands. Leaf area was estimated for each plant, and fruits were harvested and stored in 70% ethanol prior to analysis. Seeds and unfertilized (or aborted) ovules were counted under a dissecting microscope, and seed set was expressed as # seeds/(# seeds + # unfertilized ovules). General linear models were used to test for effects of land use and leaf area on the total number of ovules per fruit and on seed set in each stand pair separately. The interaction between land use and leaf area was dropped from each model as it was not significant in any analysis ($p > 0.05$).

3. Results

Performance of *T. grandiflorum* was influenced by both land-use history and the soil pH gradient (Fig. 2; Table 1). One primary stand was an outlier in that leaf area and flowering proportion were far higher than in other stands at comparably low pH (Fig. 2(b) and (c)). At this site, a fairly strong discontinuity in the vegetation associated with *T. grandiflorum* density (personal observation) strongly suggested that the low pH averaged across the whole stand was not representative of the area that encompassed most of the *T. grandiflorum* population. Therefore, this stand was dropped from all statistical analyses (though it is shown in Fig. 2).

Population density, the proportion of individuals flowering, and median leaf area all increased from low to high pH sites (Fig. 2; Table 1). Population density was significantly lower in secondary than primary populations (Fig. 2(a)), and there was a significant interaction between the effects of land-use history and pH on flowering and leaf area. At high pH sites, flowering and leaf area were greater in primary than secondary stands, though there was no such difference at low pH sites (Fig. 2(b) and (c); Table 1). The striking distinctness of *T. grandiflorum* populations in primary forests at high pH is seen clearly in size distributions of all individuals found at low (<0.2) vs. high (>0.2) values on the pH axis in the two forest types (Fig. 3). Both primary and secondary populations at low and high pH show a wide range of plant sizes, though far more large flowering individuals are found in primary forests at high pH (Fig. 3).

T. grandiflorum plants in primary stands at high pH sites are not particularly large simply because they are older than plants in secondary sites. Plants of a given age tended to have smaller leaf area (though not smaller rhizome volume) in secondary than primary stands; both pairs of stands showed the same patterns (Fig. 4; Table 2). However, Fig. 4 suggests that maximum age

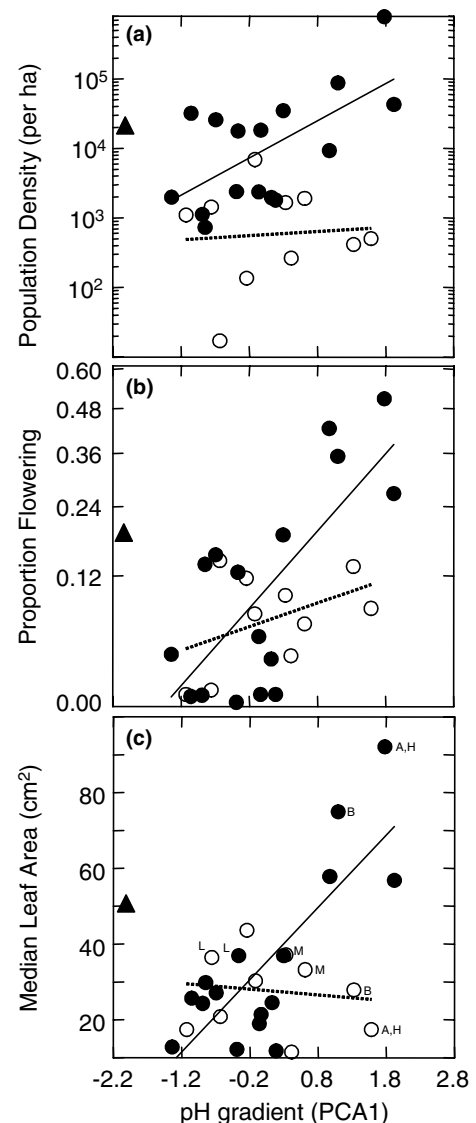


Fig. 2. Effects of soil pH and land-use history on *Trillium grandiflorum* population density (a), proportion of individuals flowering (b), and median leaf area (c) in 17 primary (filled symbols, solid line) and 10 secondary (open symbols, dashed line) forests in Tompkins County, New York. Soil pH is represented by the first axis of a principal components analysis (PCA) using data on several soil properties; actual pH ranges from about 4.5 to 6.5. The triangular symbol indicates the outlier excluded from statistical analysis of these data (see text for details). The letters in (c) indicate the pairs of stands in which rhizomes were excavated (A, B), and where seed set data were taken (L = low, M = medium, and H = high pH sites).

may be slightly greater in primary than secondary stands. To ask whether this is due to population age or some unmeasured aspect of the environment, I excavated 20 of the largest plants in a primary population at low pH, where it is reasonable to assume that population age does not place an upper limit on plant age. The maximum age of these plants was 25 (full data set not shown) – lower than the maximum observed in the secondary stands (see Fig. 4) – indicating that plant ages

Table 1
Results of general linear models (SAS PROC GLM) predicting measures of *Trillium grandiflorum* performance with land-use history and an axis of soil pH in 16 primary and 10 secondary forests of Tompkins County, New York

Source (direction of effect)	df	Type III SS	F	p
Dependent variable: log Population density				
Land use (–)	1	47.3	18.0	0.0003
pH axis (+)	1	12.8	4.9	0.0376
Land use × pH (–)	1	5.7	2.2	0.1558
Dependent variable: sqrt Proportion flowering				
Land use (–)	1	0.022	1.2	0.2903
PH axis (+)	1	0.175	9.5	0.0054
Land use × pH (–)	1	0.058	3.2	0.0884
Dependent variable: sqrt Median leaf area				
Land use (–)	1	1.1	18.0	0.3824
pH axis (+)	1	22.0	4.9	0.0006
Land use × pH (–)	1	12.0	2.2	0.0069

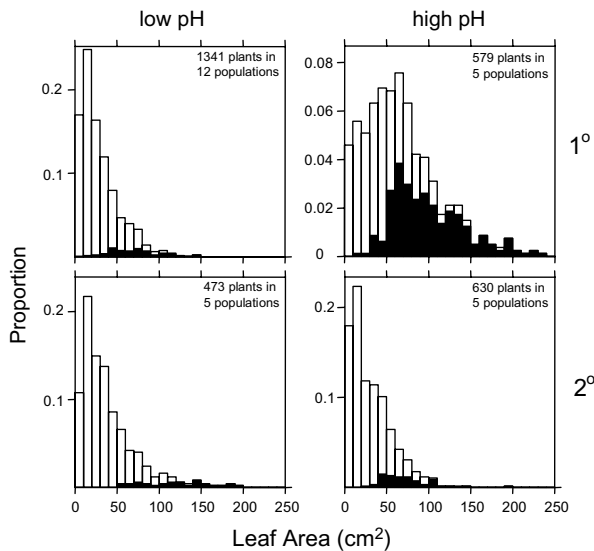


Fig. 3. Histograms of plant leaf area in populations of *Trillium grandiflorum* in primary (1°) and secondary (2°) forests at low and high pH for flowering (filled bars) and non-flowering (open bars) individuals. The cutoff between low and high values on the pH gradient was set at 0.2 (see Fig. 2) to emphasize differences.

are unlikely to be different in secondary and primary stands.

Larger plants produced more ovules than smaller plants. Ovule production did not differ significantly between primary and secondary forests in any of the three stand pairs, though there was a trend for greater ovule production in the secondary stand at medium pH ($p = 0.057$, Fig. 5; Table 3). In contrast, proportional seed set was not influenced by plant size, and at medium pH seed set was lower in the secondary than the primary stand ($p = 0.036$, Fig. 5; Table 3). The number of seeds produced per fruiting plant consequently did not differ between primary and secondary forests in any of the stand pairs ($p > 0.15$; data not shown).

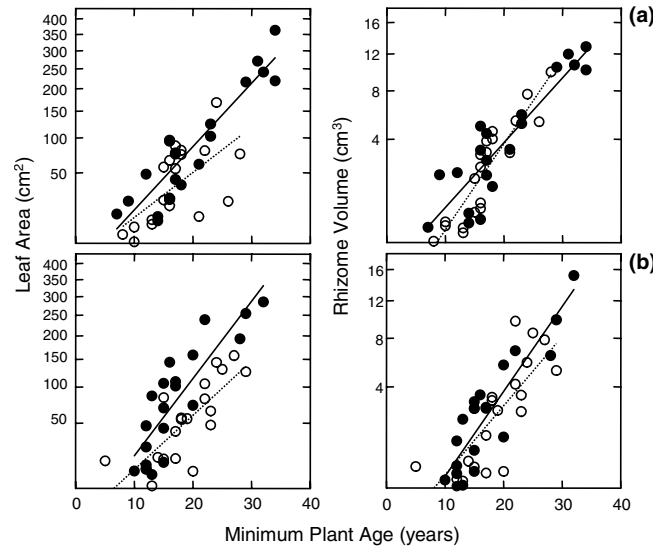


Fig. 4. Leaf area and rhizome volume of *Trillium grandiflorum* plants in relation to plant age in primary (filled symbols, solid line) and secondary (open symbols, dashed line) forests at relatively high pH. Each pair of populations (A and B, see Fig. 2) occurred within 1 km of one another, and on the same soil series.

Table 2
Results of general linear models predicting *Trillium grandiflorum* leaf area and rhizome volume with plant age and land-use history in two primary–secondary pairs of stands at high pH

Stand pair	Source (direction of effect)	df	Type III SS	F	p
Dependent variable: sqrt Leaf area					
A	Age (+)	1	423.0	84.0	<0.0001
	Land use (–)	1	32.0	6.4	0.0161
B	Age (+)	1	394.7	76.9	<0.0001
	Land use (–)	1	67.8	13.2	0.0008
Dependent variable: sqrt Rhizome volume					
A	Age (+)	1	26.3	146.3	<0.0001
	Land use (–)	1	0.1	0.5	0.4917
B	Age (+)	1	23.7	88.3	<0.0001
	Land use (–)	1	0.4	1.4	0.2489

Letter designations for each stand correspond to those in Fig. 4. Twenty plants were sampled in each stand.

4. Discussion

In discussions of forest-herb distributions in relation to land-use history, the overwhelming emphasis has been on dispersal limitation (see Section 1). The conclusion is that many species are absent from secondary forests for decades or centuries simply because seeds have yet to arrive. The resulting implication for conservation is that forest-herb communities can be restored by introducing seeds into post-agricultural forests. In contrast, the present study has provided clear evidence that the performance of *T. grandiflorum* populations is inhibited

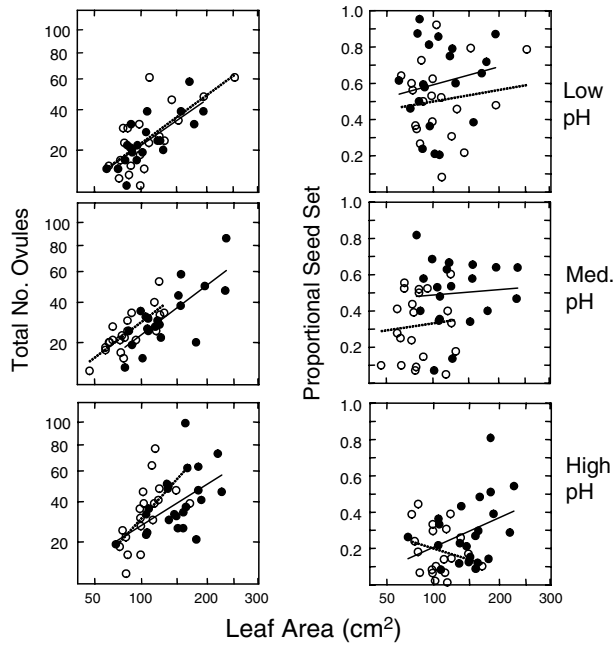


Fig. 5. Ovule production and proportional seed set in *Trillium grandiflorum* plants from primary (filled symbols, solid line) and secondary (open symbols, dashed line) forests at low, medium, and high pH. Each pair of populations occurred within 1 km of one another, and on the same soil series at similar pH (see Fig. 2).

by some aspect of the environment in secondary forests under soil conditions that would otherwise seem to provide optimal growing conditions for this species.

At high pH sites, *Trillium* plants tended to be smaller and less likely to flower in secondary than primary forests (Figs. 2 and 3). Analysis of annual leaf scars on *Trillium* rhizomes allowed the effect of population age to be ruled out as a potential explanation for this pattern (Fig. 4). Though this method of aging individuals provides

only minimum estimates of age due to disintegration of the oldest part of the rhizome (Hanzawa and Kalisz, 1993), I observed no obvious differences between populations in the rhizome morphology to cast doubt on these conclusions. Thus, the observation of fewer and smaller populations of *T. grandiflorum* in secondary relative to primary forests (Singleton et al., 2001; Vellend, 2004) is not fully explained by dispersal limitation. The degree to which this conclusion applies to other forest herbs is unknown, but the present results suggest that environmental limitation may be more important than generally thought.

Understanding the mechanism behind this environmental limitation may have important implications for forest-herb recovery and restoration efforts in post-agricultural forests. The soil nutrient status in these primary and secondary stands is not significantly different (Vellend, 2004). Light levels on the forest floor have not been measured in these stands, but all are closed canopy forests, and small potential differences in light seem unlikely to explain the patterns. This suggests some kind of a biotic limitation in secondary stands, such as herbivory, disrupted mycorrhizal associations, differences in soil pathogens, or competition from herbaceous plants typical of open habitats that have persisted through the period of forest establishment. At present, these are only speculations; the important conclusion is that environmental limitation of some sort depresses the performance of *T. grandiflorum* in secondary forests, and improvement of site conditions would be necessary to promote colonization.

Age-specific leaf area and rhizome volume were both measured as indices of plant performance, but only leaf area showed a reduction in secondary relative to primary forests (Fig. 4). Using experimental defoli-

Table 3

Results of general linear models predicting measures of *Trillium grandiflorum* reproduction with land-use history and leaf area in three primary–secondary pairs of stands varying in soil pH; 20–22 plants were sampled in each stand

Stand pair	Source (direction of effect)	df	Type III SS	F	p
Dependent variable: sqrt Total no. ovules					
Low pH	sqrt Leaf area (+)	1	34.6	40.4	<0.0001
	Land use (+)	1	0.1	0.1	0.7377
Medium pH	sqrt Leaf area (+)	1	31.6	53.9	<0.0001
	Land use (+)	1	2.3	3.9	0.0566
High pH	sqrt Leaf area (+)	1	25.7	18.2	0.0001
	Land use (+)	1	3.0	2.1	0.1542
Dependent variable: Proportional seed set (No. seeds/Total no. ovules)					
Low pH	sqrt Leaf area (+)	1	0.05	0.92	0.3445
	Land use (–)	1	0.09	1.84	0.1834
Medium pH	sqrt Leaf area (+)	1	0.01	0.25	0.6230
	Land use (–)	1	0.16	4.70	0.0365
High pH	sqrt Leaf area (+)	1	0.03	0.99	0.3269
	Land use (–)	1	0.03	1.33	0.2553

ation of *T. grandiflorum* plants, Lubbers and Lechowicz (1989) demonstrated that when a plant's ability to acquire resources is compromised, investment in energy storage in the rhizome is reduced. However, this effect was manifested as reduced rhizome density and non-structural carbohydrate content, not rhizome volume (Lubbers and Lechowicz, 1989). Furthermore, leaf area is a better predictor of whether or not *T. grandiflorum* will flower than is rhizome volume or age (Hanzawa and Kalisz, 1993). Thus, leaf area appears to be the best indicator of overall plant performance. Several studies have demonstrated that above-ground size of *T. grandiflorum* plants in a given year is reduced by herbivory in previous years (Anderson, 1994; Rooney and Waller, 2001), pointing to herbivory as a potential explanation for reduced performance in secondary forests.

Ovule production and seed set were similar in primary and secondary forests, though there was a slight tendency for plants in secondary forest to show greater ovule production, but lower seed set, in one of the three pairs of stands (Fig. 5). When *T. grandiflorum* plants are carbohydrate limited, ovule and seed production occurs at the expense of investment in rhizome storage (Lubbers and Lechowicz, 1989). So even if some aspect of the environment in secondary forests reduces performance, we may not expect this to be manifested in ovule or seed production. Proportional seed set in *T. grandiflorum* is often limited by pollen availability (Griffin and Barrett, 2002); in this study, seed set may have been influenced by pollinator availability. In a pilot study, I found significantly reduced proportional seed set in 16 fruits collected across three small populations (<100 flowering plants per ha) than in 22 fruits from two large populations (>2000 flowering plants per hectare); there was no difference in ovule number. All of these stands were primary forests, suggesting that the reduction in proportional seed set observed in the medium pH secondary stand may have been a result of relatively low population density, and consequent reduced pollinator visitation (e.g., Jennersten, 1988).

Individuals in small secondary-forest populations may be expected to show poor performance due to genetic factors such as drift or inbreeding. Indeed allelic richness and expected heterozygosity for allozyme and microsatellite loci in *T. grandiflorum* were slightly lower in primary than secondary forests (Vellend, 2004). However, only the rarest alleles tended to be absent from secondary populations, and the magnitude of difference in expected heterozygosity was quite small (0.44 in primary, 0.40 in secondary). Moreover, primary and secondary populations did not differ significantly either in observed heterozygosity or the inbreeding coefficient. Thus, it is highly unlikely that genetic factors explain the difference in plant performance between secondary and primary populations.

In sum, this paper has provided evidence of a potential environmental limitation to forest-herb colonization of post-agricultural forests, in contrast to the many studies pointing to dispersal as the dominant limitation. The rate of population growth in long-lived perennial plants, such as forest herbs, is most sensitive to changes in the survival and growth of adult plants (Franco and Silvertown, 1996), suggesting that reduced adult plant performance in secondary forests may severely slow the expansion of populations once they have established. Almost a century after agricultural abandonment, and at least 30 years since the establishment of *T. grandiflorum*, populations in secondary stands remain much smaller than their counterparts in primary forests. A more mechanistic understanding of the processes underlying this pattern is an important goal for future research, with important implications for restoration and conservation of forest-herb diversity in post-agricultural forests.

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