

# 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 km<sup>2</sup> in central New York State (Fig. 1) and Smith et al. (1993) have

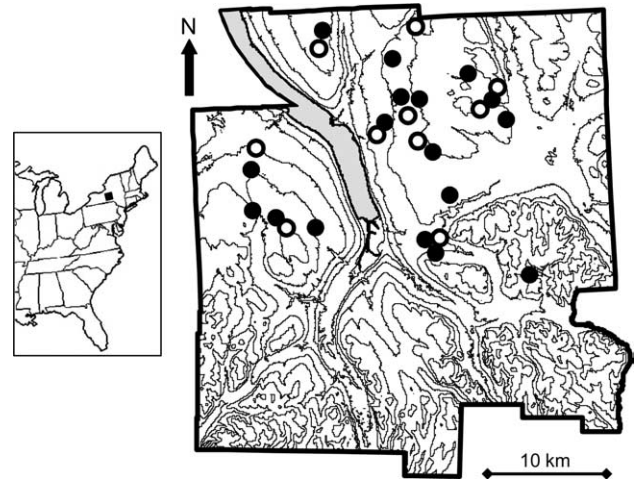


Fig. 1. Map of Tompkins County, New York, showing the locations of 17 primary (closed circles) and 10 secondary (open circles) forests used in this study. Contour lines are separated by 200 feet (~60 m), and the southern end of Cayuga Lake is shown in gray; the inset shows the location of Tompkins County 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

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