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REESTABLISHING DIVERSITY IN OUR HARDWOOD FORESTS: A TRANSPLANT STUDY OF FIVE SPRING-FLOWERING HERBS

A Thesis
Presented to
The Faculty of the Department of Biology
Western Kentucky University
Bowling Green, Kentucky

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

By
Danielle Racke
August 2010

REESTABLISHING DIVERSITY IN OUR HARDWOOD FORESTS:
A TRANSPLANT STUDY OF FIVE SPRING-FLOWERING HERBS

Date Recommended 27 July 2010

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REESTABLISHING DIVERSITY IN OUR HARDWOOD FORESTS:
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Danielle Racke August 2010 75 Pages

Directed by: Dr. Albert J. Meier, Dr. John Andersland and Dr. Michael Stokes

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Herbaceous communities are critical to the functioning of forest ecosystems. They recycle nutrients, help prevent erosion, provide critical microhabitats and maintain biodiversity. In the eastern United States, most hardwood forests are growing on land once entirely cleared or used for some form of agriculture. Although some of these forests are nearly 150 years old, they still have depauperate native herbaceous communities when compared to remaining old-growth forests. This long-term depletion may result from dispersal limitation or environmental limitation.

I tested the hypothesis that dispersal was the primary factor contributing to the absence of five spring-flowering herbaceous species in four secondary mesic hardwood forests. I transplanted adults and sowed fresh propagules into chosen forests. By establishing negative controls, I showed that propagules of experimental species were not incidentally dispersed and would not have been present at the sites had I not introduced them. In all four sites, seeds of three ant-dispersed species germinated and adults of these species survived, flowered and self-sowed viable propagules. These results strongly indicated dispersal limitation in all sites. Another ant-dispersed species showed evidence of being dispersal-limited in at least two sites. The limitations of one gravity-dispersed species were unclear. I discuss results from the first year after transplanting and offer management suggestions to facilitate the return of these species to degraded forests.

Introduction

Eastern hardwood forests once held a diverse array of spring and summer perennial herbs (Braun 1935, 1940, 1942). However, since colonial times, many of these old-growth forests have been extensively logged and cleared for agriculture. In the eastern United States, old-growth forests now constitute as little as 0.5% of remaining forested land (Davis 1996). In some areas, hardwood forests have reestablished on disturbed lands that have been abandoned for more than a few decades. However, in many of these forest stands, herbaceous communities lack the alpha and beta diversity characteristic of primary or old-growth forests (Peterken and Game 1981 and 1984, Duffy and Meier 1992, Wyatt and Silman 2010). Indeed, Dupouey et al. (2002) showed that herbaceous vegetation patterns retained evidence of disturbance history more than 2000 years after lands were abandoned. Researchers have found that herbaceous recovery in secondary forests is limited by both environmental changes caused by disturbance and dispersal characteristics of extirpated species. The current study tested the hypothesis that dispersal factors limit the recovery of spring-flowering herbaceous species in secondary mesic forests of south-central Kentucky.

Terminology

In this paper, I use the term “old-growth forest” to refer to forests of the United States and Europe which have never been clear-cut and which show little or no evidence of past anthropogenic disturbance. Thus, “old-growth forest” is a near synonym for “primary forest.” Environmental limitations are defined as conditions that negatively affect establishment and growth of plant populations where plants or propagules of the

species are present. Other researchers may refer to such environmental conditions as establishment or microsite limitations. I define dispersal limitations as conditions that slow the arrival of a species to a site.

Factors slowing or preventing herbaceous recovery

Native herbaceous species can be both environmentally-limited and dispersal-limited in the same site (Ash et al. 1994). Environmental limitations can include abiotic factors, such as soil moisture, or biotic factors, such as competition from exotic species. Dispersal limitations include factors like long generation times and short dispersal distance per generation.

Abiotic environmental factors

Herbaceous species composition, diversity and richness in secondary forests are greatly influenced by the type and extent of historical land use (Peterken and Game 1984, Matlack 1994, Foster et al. 1998, Motzkin et al. 1999, Flinn and Vellend 2005, Dorrough et al. 2006). Various disturbance regimes can result in environmental changes that limit population survival and growth for some species. Some of these changes include alteration of nutrient and pH levels, decreased soil fertility, compacted soil structure, increased light, increased soil temperature and decreased soil moisture.

Elevated levels of nitrogen and phosphorous are evident in former pastures and crop fields years after abandonment (Yates et al. 2000, Dupouey et al. 2002, Dorrough et al. 2006). Past nutrient enrichment enhances invasion by exotic plant species and is positively correlated with the presence of exotic plants (De Keersmaeker et al. 2004,

Lake and Leishman 2004, Dorrough et al. 2006). Excessive levels of nitrogen and phosphorous also have adverse effects on native plant diversity and species richness (Suding et al. 2005, Dorrough et al. 2006).

Severe and repeated soil disturbance, such as from agricultural tilling, can lead to leaching of soil nutrients (Matson et al. 1997, Hartshorn et al. 2006). Repeated trampling by livestock or use of heavy equipment can result in severe soil compaction and decreased water infiltration rates (Yates et al. 2000). Increased compaction negatively affects seedling establishment, time to penetration, root growth, development of above-ground parts, time to flowering and fruit yield (Nevens and Reheul 2003, Bassett et al. 2005). Increased compaction and decreased water infiltration rates negatively affect soil moisture (Yates et al. 2000).

Habitat disturbance affects plants by altering temperature, photoperiod and irradiance. These environmental changes may alter the structure of herbaceous communities by conveying advantages to some species over others. Interactions of photoperiod and temperature can affect growth rates and time to maturity (Mattson and Erwin 2005). Increased light levels may allow light-loving species to invade (Elemans 2004, Mattson and Erwin 2005, Brooker 2006). Conversely, a reduction in light availability reduces the biomass of light-demanding species regardless of soil nutrient concentration (Elemans 2004). Reduced cover also allows greater irradiation of the forest floor and causes an increase in soil temperature (Nofziger 2003).

Greater soil moisture results in greater biomass for some herbaceous species (Chen et al. 2007). Soil moisture is positively correlated with herbaceous diversity (De Keersmaeker et al. 2004). However, drastic increases in irradiation lead to decreases in

soil moisture. Reductions in soil moisture due to increases in irradiation from vegetation loss will likely lead to loss of some species.

Finally, climatic temperatures can affect phenology and morphological development of herbs. In the presence of competitors, a population can be reduced because of temperature effects (Dunnett and Grime 1999). Phenological changes that are induced by increased temperatures include earlier onset dates of leaf unfolding, flowering, fruit ripening and dormancy for herbaceous species (Gabryszewska 2004, Menzel et al. 2006). Morphologically, increased temperatures can negatively affect shoot formation, shoot growth and leaf emergence (Gabryszewska 2004). Additionally, increased temperatures reduce mean dry weight and sucrose concentration (Parker and Borthwick 1939), increase rates of flower abortion (Kamentsky et al. 2003) and increase seed production (De Frenne et al. 2010).

Biotic environmental factors

In degraded forest habitat, biotic factors that limit herbaceous reestablishment may include an increase in herbivory, a loss of soil microorganisms and invertebrates, a loss of mutualist species, a loss of environmental heterogeneity and invasion by exotic species.

Nitrogen-enrichment of plants positively influences herbivore and pest preference (Matson et al. 1997, Stiling and Moon 2005, Lu et al. 2007). This results in larger pest populations and reduced plant productivity (Matson et al. 1997, Lu et al. 2007). Elevated levels of soil N also negatively influence diversity of soil microbes and invertebrates (Lavelle 1996, Barbercheck et al. 2009). Soil microbes and invertebrates contribute to

basic soil processes such as mineralization and denitrification (Lavelle 1996). Invertebrates are critical to maintaining soil structure (Lavelle 1996, Salmon et al. 2008).

Communities and populations of mutualist species such as pollinators can be simplified, reduced or lost to disturbances (Goulson et al. 2002, Quintero et al. 2010). A loss of pollinators can negatively affect seed production for herbs that require longer pollinator visits to increase seed set (Ohara et al. 1994).

Dominant tree species can affect herbaceous composition by influencing light availability, litter depth and soil properties (Brewer 1980, Turner and Franz 1986; Newell and Peet 1998). In coniferous forests, late-successional herbs show a significant association with overstory variables such as canopy cover, stand density and tree-size distributions (McKenzie et al. 2000). However, large-scale disturbances such as logging destroy the predictable relationship between species composition and environmental factors (Motzkin et al. 1999, Wyatt 2009).

Herbaceous competition is an important driver of community composition. In some communities, competition can moderate some species advantages caused by environmental changes (Dunnett and Grime 1999). Competition decreases early reproductive investment of *Epilobium dodonaei* (marsh willowherb) but this leads to an increase in the seed to ovule ratio (Stöcklin 1997). Some species negatively affect survival and seedling recruitment of other species (Smith 1975). Therefore, where disturbance has altered environmental characteristics, superior competitors may exclude some species and allow habitat invasion by others (Smith 1975, Mooney and Cleland 2001, Brooker 2006).

Finally, exotic species are of particular concern because of their ability to exclude native species, whether through competition or their effects on the environment. Researchers have shown positive correlations among disturbance and the distribution and density of exotic species (Lake and Leishman 2004, Dorrough et al. 2006, Dodson et al. 2008). Exotic plants may have a greater fitness potential due to structural characteristics or a lack of predators (Lake and Leishman 2004). Exotic herbaceous species can be direct competitors for resources or pollinators (Mooney and Cleland 2001; Brooker 2006; Totland et al. 2006). Exotic pollinators can be parasitic on some native plants, or their foraging strategies may reduce the seed set of native species that are self-infertile (Goulson 2003). Exotic earthworms increase leaching of soil N and P near the soil surface. This nutrient loss leads to reduced abundances of many shallowly-rooted herbaceous genera in temperate and boreal forests (Frelich et al. 2006).

Dispersal factors

The proximity of secondary forests to less-disturbed, species-rich forests is positively correlated with diversity, richness, density and native composition of recovering herbaceous layers in secondary forest (Peterken and Game 1984, Matlack 1994, Singleton et al. 2001). Presumably, this is because proximity of degraded sites to sources of propagules facilitates dispersal in a shorter amount of time (Robinson and Handel 1993, Matlack 1994). Forest herbaceous perennials that disperse slowly commonly share one or a combination of life history traits including slow growth, small seed set, large seed size, low germination and recruitment and range-limiting dispersal vectors.

Many forest perennial herbs are long-lived but slow-growing. Most temperate species must undergo a cold season to germinate, and some require at least two years either to germinate or produce above-ground parts (Bierzychudek 1982, Cullina 2000, Davis and Greenfield 2002). In the field, low seed germination rates ranging from 1% - 20% plague the recruitment success of some herbs (Baeten et al. 2008). After germinating and surviving beyond the first year, a number of forest herbs may take 3-5 years or even more to reach flowering size (Bierzychudek 1982; Bender et al. 2000). Kranczoch (1997) reported that at least several decades are needed for *Paris quadrifolia* (herb Paris) to reach sexual maturity (cited by Jacquemyn et al. 2005). However, even when they are sexually mature, flowering plants can revert to a vegetative state, abandon rhizomatous shoots or go dormant (Silvertown et al. 1993; Philipp and Petersen 2007).

Understory herbs may invest more in asexual rather than sexual reproduction (Whigham 2004). Asexual propagules may even germinate at a higher rate than a species' seeds (Wang and Cronk 2003). However, vegetative and clonal dispersal is very slow. For example, *Anemone nemorosa* (wood anemone) rhizomes elongate by an average of 2.5 $cm \cdot year^{-1}$ (Shirreffs and Bell 1984). Meier et al. (1995) found that mean vegetative growth distance for 11 species of Appalachian understory herbs was less than 2 $cm \cdot year^{-1}$. Vegetative dispersal distance can also vary according to site quality. Cain and Damman (1997) found that the annual mean rhizome length in *Asarum canadense* (wild ginger) clones was 2.6 cm in late successional forests and significantly less (2.1 cm) in early successional forests. In species rich sites and species poor sites, the average distance between shoots of the summer herb *Maianthemum bifolium* (false lily of the valley) was 13.8 cm and 16.8 cm respectively (D'Hertefeldt and Jónsdóttir 1994).

Mean vegetative dispersal distance of *Brachypodium pinnatum* (tor grass) in four different land use regimes ranged between 4.47-17.5 mm·year^{-1} (Schläpfer and Fischer 1998).

Once they become sexually mature, many forest herbs produce larger, heavier seeds than other herb groups. For example, the seed weight of 56 species of prairie forbs ranges from 0.006-21.47 mg (Havercamp and Whitney 1983), while the seed weight of 22 species of forest herbs ranges from 0.03 - 34.4 mg (Bierzychudek 1982). Although larger seeds tend to confer survival advantage, seed size is negatively correlated with distribution range (Venable and Brown 1988, Guo et al. 2000, McEuen and Curran 2006).

Forest herbaceous perennials also produce a small annual seed set. From a sample of 45 species of forest perennial herbs, half annually produce fewer than 25 seeds per plant, and only four species produce more than 100 (Bierzychudek 1982). Seed set is also correlated with plant size (Kozlowski and Uchmanski 1987). In some species, individuals that begin reproducing earlier in life have both a smaller overall size and a smaller per year reproductive output (Kozlowski and Wiegert 1987). Seed set size can also be correlated with competition (Stöcklin 1997), population density (Kolb and Lindhorst 2006, Widén 1993), pollinator activity (Ohara et al. 1994) and environmental conditions (De Frenne et al. 2010).

Finally, many woodland herbs disperse by gravity or have elaiosome-bearing seeds that attract ant dispersers. These dispersal modes generally result in an average dispersal distances of less than 1 m·year^{-1} (Matlack 1994, Singleton et al. 2001). For example, in the Appalachian forest, Meier et al. (1995) found that gravity-dispersed seeds

of *Panax trifolium* (dwarf ginseng) dispersed no further than 25 cm, and most seeds embedded within 15 cm of the mother plant. However, in some cases, elaiosome-bearing seeds disperse farther than the estimated 1 $m \cdot year^{-1}$. In populations of *Asarum canadense,* Cain et al. (1998) found that ants typically transported seeds 2-7 m. In recent decades, researchers have found that other invertebrate taxa occasionally disperse elaiosome-bearing seeds much farther than ants. Slugs in beech forests in Germany consume elaiosome-bearing seeds and have the potential to transport them up to 14.6 m (Türke et al. 2010). In eastern North America, yellow-jackets can disperse three different *Trillium* species beyond 20 m (Zettler et al. 2001). However, reports of mutualisms between myrmechochores and species other than ants are uncommon in the literature. Therefore, the potential for regular long-distance dispersal via these vectors is unclear.

Assessing disturbance and recovery

There are very few long-term studies of herbaceous recovery. In studies of the forest herbaceous layer, many researchers quantify immediate effects of disturbance (< 10 yrs) (Elliott and Knoepp 2005, Zenner et al. 2006, Macdonald and Fenniak 2007, Dodson et al. 2008, Kembel et al. 2008), or compare the effects of different disturbance regimes (Frederickson et al. 1999, Griffis et al. 2001, Rapp et al. 2001, Dech et al. 2008). These types of studies are inherently problematic for conservation and restoration protocols because either they do not establish baselines, or they do not assess long-term recovery beyond canopy closure.

Sometimes, researchers compare the herbaceous layer of younger forests with “mature” forests that are not older than 150 years (Reader 1987, Gilliam and Turrill 1993,

Gilliam et al. 1995). However, direct comparisons of mature and old-growth forests reveal significant differences in the composition of their herbaceous layers (Duffy and Meier 1992, D'Amato et al. 2009, Wyatt and Silman 2010). Therefore, studies that use mature forests as recovery baselines may be problematic because they make conclusions based on comparisons between degraded habitats.

Studies linking herbaceous diversity or population growth to particular life-history characteristics and environmental changes are largely correlative. Thus, it can be difficult to determine the factors that most limit herbaceous recovery. For example, Matlack (1994) investigated dispersal distances by quantifying the migration distance of herbs from older to younger forests. However, he did not also test whether environmental limitations inhibited the further progression of these herbs into old-field forests. De Keersmaeker et al. (2004) showed that diversity of woodland flora was correlated with site characteristics influenced by disturbance but did not investigate life history characteristics that might influence dispersal of present or absent species.

Transplant studies come closer to identifying driving mechanisms of herbaceous composition because they eliminate long-distance dispersal issues and allow environmental factors to influence recolonization. Transplanting can even reveal species-specific differences in dispersal and environmental limitations at the same site (Ash et al. 1994).

Transplant studies and population establishment

Artificial dispersal can shed light on environmental limitations in disturbed habitats. However, the success or failure of introduced species may not arise until more

than a year after transplanting. For example, Ash et al. (1994) found that in two experimental sites, all introduced species germinated after the first year of introduction. However, because of high seedling mortality, only half of the species in each site had permanently established after six years. This study demonstrated the importance of an environment that can support germination, seedling recruitment, adult recruitment and self-propagation. Clearly, those species that established were dispersal-limited. Unfortunately, there are only a few forest studies that have used artificial dispersal to compare environmental and dispersal limitations.

Some researchers have investigated forest herbaceous recovery by sowing seed and monitoring germination and survival into adulthood. Rey et al. (2006) used both seed introduction (where the annual seed rain was zero) and seed augmentation (where there was some limited seed rain) to demonstrate that an ant-dispersed herb, *Helleborus foetidus* (dungwort), was dispersal-limited in two mountain pine forests. Some forest herbs require many years to mature, and factors limiting recovery are occasionally studied with a combination of seed introduction and adult transplantation. Ehrlén and Eriksson (2000) sowed seeds or bulbils of seven species and transplanted juveniles of one of the seven species into 48 plots in mixed deciduous and coniferous forest sites to investigate dispersal limitation and patch occupancy. Six of the seven species had recruited to adulthood by the fourth year in both forest types. The researchers also had control plots where no natural seedling recruitment occurred, and they concluded that experimental establishment indicated true recruitment and thus, dispersal limitation.

Environments must support flowering, germination and adult recruitment, but because of the long lifespan of many herbaceous perennials, it can be difficult to

investigate permanent population establishment. However, researchers can quantify habitat influences on adults, seedlings and seeds by sowing seeds and transplanting adults of the same species. Verheyen and Hermy (2004) transplanted both adults and propagules of two geophytic and two hemicryptophytic species into recent and ancient Belgian forests. Because adults survived, seeds germinated and seedlings recruited, all four study species showed evidence of being dispersal-limited in all forest habitats by the second full year after transplanting. Although these researchers had positive controls for seed germination, they did not have negative controls to test for natural seedling recruitment and the potential effects of site disturbance.

Objective

I investigated the hypothesis that spring-flowering species are dispersal-limited in mesic forests of south-central Kentucky. To test this hypothesis, I used a combination of transplanted adults and sown propagules of the same species. The experimental design included a negative field control. Experimental species had various life history characteristics common to dispersal-limited species, including delayed sexual maturation, ant- or gravity-dispersal vectors and the degree of sexual versus asexual reproductive investment. In the first year after transplanting, I looked for evidence of dispersal and environmental limitation by investigating adult survival, adult reproduction, seed germination and natural seedling recruitment of self-sown propagules.

Justification

In addition to their value as foods and medicines (Belew 1999, Miller 2005), herbaceous plants are critical to the health of entire forest ecosystems. The herbaceous layer provides microhabitats and food to invertebrates and vertebrates and microhabitats to vascular and non-vascular plants (Simonetti 1989, Dover et al. 1997, Grime 1998, Brooker 2006). A meta-analysis of the literature by Ricketts et al. (1999) shows that overall richness of avian, lepidopteran and mammalian taxa are better correlated with non-tree vascular plant richness than with tree richness. Also, a diverse herbaceous community may experience less herbivory and thereby have greater productivity than a community of fewer species (Ellison 1987, Matson et al. 1997). Finally, in some regions, spring herbs recycle critical nutrients that may otherwise be lost to runoff (Blank et al. 1980, Zak et al. 1990, Tessier and Raynal 2003).

A priori hypotheses

1) The presence of many ant- and gravity-dispersed species in disturbed forests is negatively correlated with distance of the disturbed forest to undisturbed forest where there are populations of source propagules (Peterken and Game 1984, Matlack 1994, Singleton et al. 2001). Because four of my chosen species were myrmechochores and one was a barochore, I believed the experimental species were dispersal-limited on selected mesic sites. Therefore, I expected that introduced seeds would germinate and that transplanted adults would survive, flower, fruit and produce seeds that would germinate.

2) Environmental factors can significantly influence growth and reproduction of herbaceous species. For example, severe soil compaction can negatively affect root growth (Bassett et al. 2005). The experimental forests were different ages and had different disturbance histories. Therefore, I expected that site characteristics would cause differences in survival rates, flowering and fruit production of transplants and differences in germination of introduced seeds.

3) Propagules of spring-flowering herbs become easily desiccated and must be kept moist to maintain viability (Cullina 2000). Therefore, I expected that a later planting date would have a negative effect on germination of introduced seeds and asexual propagules.

4) Water stress during a plant's reproductive cycle can cause early senescence (Brevedan and Egli 2003). I expected that root disturbance during transplantation would cause water stress, and that early senescence would decrease the likelihood of survival. Therefore, I expected both *Dicentra* species to have better survival rates in those sites

where dormant individuals were transplanted rather than those sites where flowering individuals were transplanted.

5) Deeper seed burial may result in reduced seedling emergence (Christian and Stanton 2004). Therefore, I expected that a higher percentage of more shallowly planted seeds would germinate.

Materials and Methods

I transplanted five herbaceous species thought sensitive to disturbance because of their absence from highly impacted forests. Transplanted species were *Dicentra canadensis* (squirrel corn), *Dicentra cucullaria* (Dutchman's breeches), *Jeffersonia diphylla* (twinleaf), *Polemonium reptans* (Jacob's ladder) and *Stylophorum diphyllum* (wood poppy). With replicate treatments and negative control quadrats in four different sites, I directly contrasted the effects of artificial dispersal and environmental factors on survival, reproduction, germination and natural seedling recruitment for transplanted species.

Sites

In February of 2009, I erected two sets of paired sites in mesic hardwood forests. These forests were younger than 100 years, and they were chosen based on the likelihood that they could support experimental species. The first pair of sites (Upper Green River Biological Preserve) was erected in Hart County, KY, on the edge of a limestone sinkhole plain at the intersection of the Crawford-Mammoth Cave Uplands and the Western Pennyroyal Karst Plain ecoregions (McGrain and Currens 1978, Woods et al. 2002). The second pair of sites (Marrowbone State Forest Wildlife Management Area) straddled the borders of Metcalfe and Cumberland counties on a rolling upland plateau at the intersection of the Eastern Highland Rim and the Outer Nashville Basin ecoregions (McGrain and Currens 1978, Woods et al. 2002). Paired sites were within six kilometers of each other and had similar overstory compositions and soil types. Experimental species emerged and flowered from March through May. In 2009, the average temperature for these months was 12.8˚C with a range of 1.2˚C to 28.8˚C, and the

total rainfall received for this period was 37.3 cm (Kentucky Mesonet). Historically, the mean temperature from March through May is 14.7˚C, with a range of 3.05˚C to 26.5˚C, and the average amount of rainfall is 37.6 cm (Kentucky Climate Center).

Upper Green River Biological Preserve paired experimental sites: UGRBP-Bush and UGRBP-Gardner

Both of these sites were located on the Upper Green River Biological Preserve (UGRBP) in Hart County, KY. Currently, this property consists of more than 400 ha of land which encompasses a variety of grass and woodland habitats that were once farmed, grazed and logged. Both experimental sites were on slopes that bordered the south-southwestern side of the Green River. The elevation at both sites was approximately 152 m above sea level. The dominant herbaceous flora for both sites (considered as that which was present in more than 75% of site quadrats) included *Erigenia bulbosa* (harbinger of spring), *Claytonia virginica* (spring beauty), *Dentaria laciniata* (cutleaf toothwort) and *Erythronium americanum* (yellow trout lily).

Site UGRBP-Bush: The map datum for this site was NAD 83, and the coordinates were N37 14.863 W86 00.576. This was a slim NE facing slope with a 20-30% grade (Soil Survey Staff) that encompassed 60m x 13m (780 m^2) along the Green River. Previous landowners logged the site and much of the plateau above the slope was cleared. The canopy consisted mainly of sugar maple (*Acer saccharum*) and hickory (*Carya* sp), but also included red elm (*Ulmus rubra*) and buckeye (*Aesculus* sp). The soils were rocky, Caneyville silt loam soils with a surface cation exchange capacity (CEC-7) of 13.9 milliequivalents per 100 g and a surface organic matter content (OM) of 3% (Soil Survey

Staff). The dominant herbaceous flora not also dominant at its paired site, UGRBP-Gardner, included *Stellaria pubera* (star chickweed). Roughly 10 m beyond the site, the slope abruptly dropped 2 m into the Green River.

Site UGRBP-Gardner: The map datum for this site was NAD 83, and the coordinates were N37 14.506 W86 00.094. This was an E-SE facing slope with a 20-30% grade (Soil Survey Staff) that encompassed roughly 22m x 30m (660 m^2). Previous landowners logged the slope and used it as a grazing site. The canopy consisted mainly of sugar maple (*Acer saccharum*), but also included bitternut hickory (*Carya cordiformis*), black walnut (*Juglans nigra*) and hackberry (*Celtis* sp). The soils were Caneyville silt loam soils with a CEC-7 of 13.9 milliequivalents per 100 g and 3% surface OM (Soil Survey Staff). The dominant herbaceous flora not also dominant at its paired site, UGRBP-Bush, included *Viola sororia* (wood violet) and *Viola pubescens* (downy yellow violet). At the bottom of the slope, the forest opened onto an alluvial flood plain that stretched 30 m and dropped 5 m to the Green River.

Marrowbone State Forest Wildlife Management Area paired experimental sites: MSF-Slate and MSF-Pitman

Both of these sites were located at Marrowbone State Forest Wildlife Management Area (MSF), a property which straddled the borders of Kentucky's Metcalfe and Cumberland Counties. This property included 626 ha of land that encompassed a variety of riparian zones, fields and woodland habitats in various successional stages. From the 1970s, the land was extensively logged and served as an active stewardship forest. The elevation at both sites was approximately 244 m above sea level. Both

experimental sites were on slopes in small valleys with ephemeral shale-bottomed creeks. The dominant herbaceous flora for both sites included *Claytonia virginica* and *Dentaria laciniata.*

Site MSF-Slate: The map datum for this site was NAD 83, and the coordinates were N36 51.820 W85 35.982. This was an E-SE facing slope with a 20-50% grade (Soil Survey Staff) that encompassed roughly 36m x 22m (792 m^2) along a tributary of Slate Creek. The canopy consisted mainly of beech (*Fagus grandifolia*), white oak (*Quercus alba*) and sugar maple but also included black walnut and basswood (*Tilia* sp.). The soils were Dandridge and Westmoreland shaly silt loams with a surface CEC-7 of 13.9 milliequivalents per 100 g and 1.75% surface OM (Soil Survey Staff). All dominant herbaceous flora were also dominant at its paired site, MSF-Pitman. Roughly 1-3 m beyond the site, the slope dropped 1 m into Slate Creek.

Site MSF-Pitman: The map datum for this site was NAD 83, and the coordinates were N36 52.136 W85 35.867. This was an E-NE facing slope with a 30-65% grade (Soil Survey Staff) that encompassed 30m x 22m (660 m^2) along Pitman Creek. The canopy consisted mainly of yellow poplar (*Liriodendron tulipifera*) and beech but also included basswood, sugar maple, red elm and northern red oak (*Quercus rubra*). The soils were rocky Garmon-Carpenter-Newbern complex soils with a surface CEC-7 of 6.9 milliequivalents per 100 g and 1.45% OM (Soil Survey Staff). The dominant herbaceous flora not also dominant at its paired site, MSF-Slate, included *Erigenia bulbosa, Hydrophyllum canadense* (bluntleaf waterleaf) and *Laportea canadensis* (stinging nettle). Roughly 1-3 m beyond the site the slope leveled off into Pitman Creek.

Species

I chose five perennial, spring-flowering herbaceous species that are often found in rich mesic forests. These species were chosen because there were large local source populations, and they had a variety of dispersal-limiting life-history traits that included 1) potential for asexual reproduction, 2) ability to persist in a vegetative state from year to year, 3) delayed sexual maturity, 4) small annual seed set and 5) seeds that were dispersed by gravity or ants (Table 1). Probably none of these species persist in the soil seed bank (Baskin and Baskin 1984, 1989, 1992; Leckie et al. 2000), and at least three species, *Dicentra cucullaria*, *Polemonium reptans* and *Stylophorum diphyllum*, are sensitive to ungulate grazing (Mabry 2002, *pers. obs.*).

Dicentra cucullaria (Dutchman's breeches) is a spring ephemeral that flowers for 2-3 weeks in March then drops its seed and becomes dormant by the end of April. This species grows from a base of 1-3 larger and dozens of smaller bulblets which fracture easily as a method of asexual reproduction. The scape typically supports 4-8 flowers with the potential to produce 3-7 seeds per pod. The flowers are pollinated by early bumblebees (*Bombus* spp.), as well as other long-tongued insects (Stern 1961). Ants disperse the small, elaiosome-bearing seed. Because the seed requires a cycle of moist warm and cold treatments to germinate, gardeners typically have more luck cultivating this plant by fracturing the bulblets (Cullina 2000).

Dicentra canadensis (squirrel corn) is a spring ephemeral that has a life cycle similar to *D. cucullaria* but is offset by approximately 1-2 weeks later in the season. It has an above-ground morphology similar to *D. cucullaria* but spreads vegetatively by

corms connected to rootstocks. Though each scape may support up to seven flowers, each fruit usually produces only 1-4 seeds. Similarly to *D. cucullaria*, *D. canadensis* is pollinated by long-tongued insects, and its elaiosome-bearing seed is dispersed by ants. However, its corms are also transplanted by mice and chipmunks (Wasowski and Wasowski 1994). The species is also more easily cultivated by corm than seed (Cullina 2000).

Polemonium reptans (Jacob's ladder, Greek valerian) is an evergreen which flowers for 4-6 weeks throughout April and May and drops its seed in June. Though some individuals may go through a short period of dormancy, *P. reptans* continually renews its leaves and larger individuals may persist through the winter. Individuals grow and propagate asexually from a rhizome. *Polemonium reptans* is the only species of this experimental group with gravity-dispersed seeds.

Jeffersonia diphylla (twinleaf, rheumatism-root) takes 4-5 years to reach sexual maturity (Phillips 1985 cited by Bender et al. 2000). Most individuals bloom for a couple of days in early April, drop seeds in late May and senesce in late June or early July. Some of the largest plants produce up to four fruits. However, most individuals produce 1-2 fruits which average 31 seeds per fruit (*pers. obs.*, n=20). Like *P. reptans*, *J. diphylla* can propagate asexually from a rhizome, but *J. diphylla* seeds appear to be more successful than *P. reptans* seeds (Cullina 2000). Of all species in this study group, *J. diphylla* appears most affected by invertebrate herbivory (*pers. obs.*).

Table 1. Reproductive characteristics of the five species transplanted in this study. "Dica" = *Dicentra canadensis*, "Dicu" = *Dicentra cucullaria*, "Jedi" = *Jeffersonia diphylla*, "Pore" = *Polemonium reptans*, "Stdi" = *Stylophorum diphyllum*.

				Reproductive strategy					
Species	**Flowers**	**Senescence**	**Asexual propagation**	**Asexual**	**Sexual**	**Seed dispersal**	**Seeds/ pod**	**Pods/ indiv**	**Earliest age of maturity**
Dica	Mar-Apr	May	corms	frequent	occasional	elaiosome	1-3	1 - 7	unknown; likely >1
Dicu	Mar-Apr	May	bulblets	frequent	occasional	elaiosome	3-7	1 - 8	>1 (Bender et al 2000)
Jedi	Apr	Jun-Jul	rhizome	frequent	occasional	elaiosome	10-60	1 - 4	4-5 (Bender et al 2000)
Pore	Apr-May	evergreen	rhizome	occasional	frequent	gravity	3	3 - 80+	unknown
Stdi	Mar-Apr	Sept-Nov	rhizome	possible	frequent	elaiosome	60-120	1 - 15+	2 (Bender et al 2000)

Stylophorum diphyllum (celandine poppy, yellow poppy, wood poppy) has a rhizome but does not propagate vegetatively (COSEWIC 2007). Cultivated plants are capable of flowering in their first year, but wild plants usually do not flower until the second year (COSEWIC 2007). *Stylophorum diphyllum* is capable of both outcrossing and selfing (COSEWIC 2007). In Kentucky, it flowers for 3-4 weeks in April, drops its seed by late May, and may retain its leaves into November. Flowering individuals in study populations support 1-10 flowering stems, and it is easily possible for a plant to produce more than 1000 seeds (*pers. obs.*). Seeds are quite successful after a long period of cold stratification (Baskin and Baskin 1984).

Design

I divided each of four forest sites into three plots which lie 3-15 m apart. Plots were separated by some geographic feature, such as a small drainage or abrupt change in slope. Each plot accommodated four randomly assigned 1-m^2 quadrats of each of four treatment groups (Fig. 1). Quadrats were spaced 1-1.5 m apart but offset in the case of masses of briars or woody stems greater than 2 m in height. Only quadrats for three of the four treatment groups were used in 2009.

Treatment 1. Transplanted adults: Each transplant quadrat was sectioned into a 5x5 grid. In three of the four treatment quadrats in each plot, I planted five individuals of each species into randomly assigned positions. The excluded quadrat was chosen randomly. I therefore planted 45 plants of each species at each site, and every quadrat had a different assortment of transplanted species (Fig. 2).

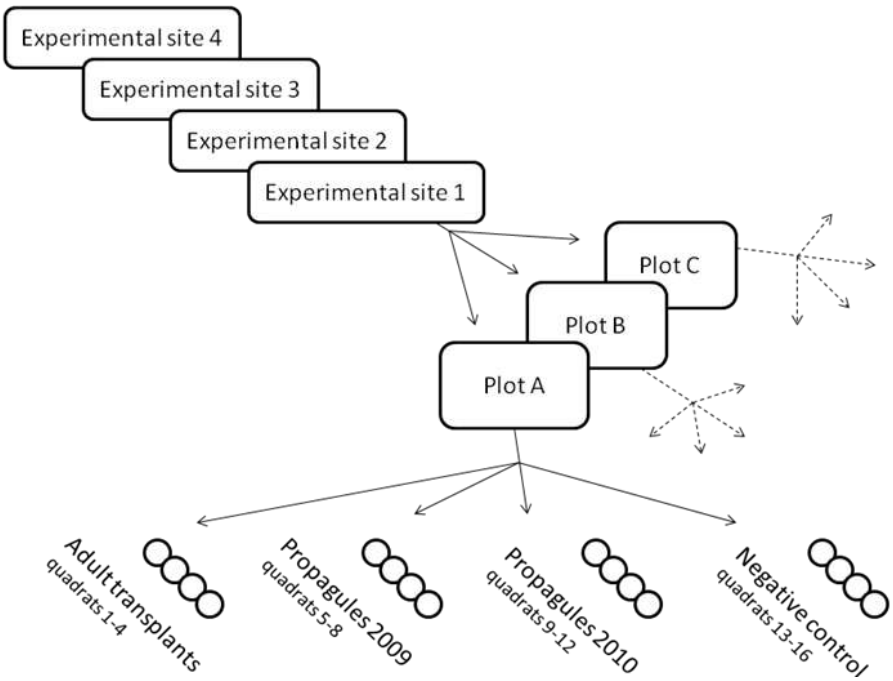

Fig. 1: In each of four experimental sites, three replicate plots were divided into four quadrats for each of four different treatment groups. In 2009, the "Propagules 2010" quadrats were not used.

All plants in this experiment were locally collected from robust populations in non-experimental forests. I layered wide, shallow plastic bins with 2-4 cm of the local soil. Then, harvested individuals were gently placed in the soil, lightly watered and covered with the bin's lid for protected transport to the lab. Most individuals were in a reproductive state when they were transplanted. This was so that I could be sure they were sexually mature. For each species, I collected all individuals for paired sites from the same population on the same day. All harvested individuals were transplanted 18-48 hours after harvesting.

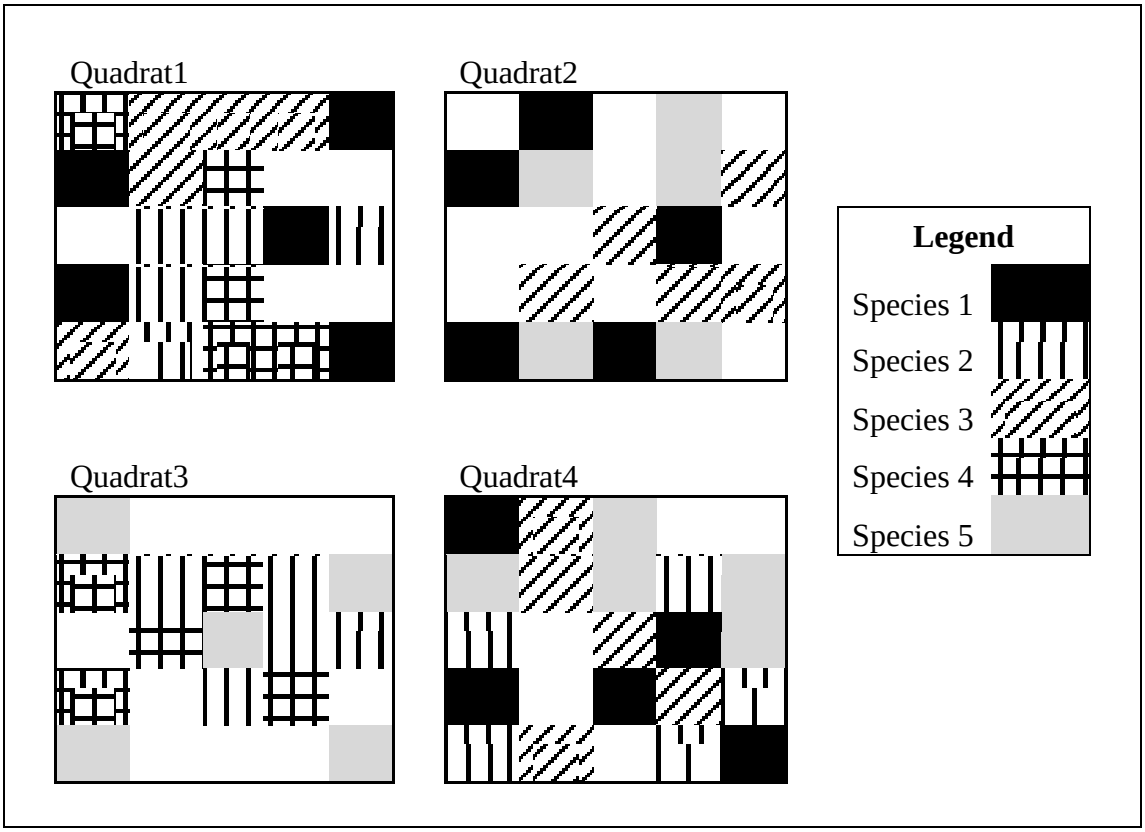

Fig. 2. Species layout of transplant quadrats in plot A of site MSF-Slate (four of 12 total quadrats in the site).

I transplanted *P. reptans* in late March before the reproductive status of most individuals was known; however, they were distributed between each set of paired sites according to the number of ramets each supported. I transplanted *J. diphylla* in mid-April and distributed them according to the number of fruits and ramets. All transplanted *J. diphylla* had at least one fruit. *Stylophorum diphyllum* were also transplanted in mid-April but were all in the early stages of flowering. I distributed *S.diphyllum* according to the number of ramets. For both *Dicentra* species, due to a shortage of flowering plants in source populations, only half of the plants were flowering when transplanted in early

March. The other half were senescing or already dormant when transplanted in early May. I transplanted flowering *D. canadensis* to UGRBP paired sites (UGRBP-Bush and UGRBP-Gardner) and distributed them according to the number of corms and flowers. I transplanted flowering *D. cucullaria* to MSF paired sites and distributed them according to the number of large bulblets and number of leaves. In early May, I transplanted dormant *D. canadensis* into paired MSF sites (MSF-Pitman and MSF-Slate) and distributed them according to the number of corms and corm groupings. I transplanted dormant *D. cucullaria* into paired UGRBP sites and distributed them according to the number of large bulblets. (Table 2).

Table 2. Life stage of transplanted species in paired sites.

Location	Species	Life stage
Marrowbone State Forest paired sites	*Polemonium reptans*	Flowering and vegetative
	Jeffersonia diphylla	Flowering
	Stylophorum diphyllum	Flowering
	Dicentra canadensis	Unknown
	Dicentra cucullaria	Flowering
Upper Green River Biological Preserve paired sites	*Polemonium reptans*	Flowering and vegetative
	Jeffersonia diphylla	Flowering
	Stylophorum diphyllum	Flowering
	Dicentra canadensis	Flowering
	Dicentra cucullaria	Unknown

Upon transplanting in 2009, I monitored plants once every 7-10 days until July, then once monthly until November. I resumed monitoring once every 7-10 days in March 2010 when all species had emerged from dormancy. Though data collection is ongoing, data collected after 27 May 2010 are not included in this thesis.

In 2009 and 2010, I monitored each transplant for the presence of green leaves, flowers, developing fruits and fruit dehiscence. With the exception of *P. reptans*, plants which were absent for two weeks in a row were considered dormant and not checked again until the following year. Because *P. reptans* continually renews its leaves, I examined every planting location during every visit. In 2010, I counted the number of flowers on all flowering individuals except *P. reptans*. I counted the number of fruits for *J. diphylla* and *S. diphyllum*.

I also searched for seedling recruits in a 3 m radius of all transplant quadrats. I investigated transplant quadrats for the presence of seedling recruits of all species. I investigated *Dicentra* dispersal in mid-April. I quantified seedling recruitment in *J. diphylla*, *P. reptans* and *S. diphyllum* in mid-May. I quantified minimum dispersal distance by measuring the distance from the base of the seedling to the base of the nearest conspecific adult. In cases of densely clustered seedlings, I made the measurement from the base of the farthest seedling in the group to the base of the nearest conspecific adult. I considered seedlings to be growing "independently" if they were farther than 6 cm from another conspecific seedling and "clustered" if two or more conspecific seedlings were within 6 cm of each other.

Finally, heavy rains from 01 to 03 May 2010 caused flooding throughout southern Kentucky and northern Tennessee. At the Munfordville, KY hydrologic station, about 16 km upstream of UGRBP sites, flooding of the Green River peaked on 04 May. The height of the river was 15.8 m, and peak discharge was 1611 $m^3 \cdot sec^{-1}$ (cms) (USGS 2010b). In the last 96 years, the river exceeded these levels only twice, once in 1984 and once in

1962 (USGS 2010a). Between 1970 and 2009, the mean annual discharge ranged from 35 cms to 150 cms (USGS 2010c).

Flood waters covered all quadrats at UGRBP-Bush for at least two days. Lower quadrats were covered for up to five days. Flooding at site UGRBP-Gardner affected only the four of 48 quadrats lowest on the hill. The precise amount of time that the quadrats were underwater is unknown; however, the amount of time was likely one day or less. Both sites at MSF were minimally affected by flooding.

Because of the extent of flood damage at UGRBP-Bush, after the initial visit, I visited this site only once every two weeks until June. I examined all plants for the presence of leaves, fruiting pods, fruit dehiscence and seed ripeness. I considered plants without green leaves to be dormant for the year. I did not quantify recruitment or dispersal distance at this site because heavy deposits of sand, silt and clay buried some seedlings.

Treatment 2. Propagules (seeds, bulblets or corms): Each treatment quadrat was sectioned into a 10x10 grid and each species was randomly assigned 10 positions in each quadrat. I hand collected all propagules from individuals remaining in previously harvested populations. I collected ripened seeds from *S. diphyllum* and *J. diphylla* individuals, and I split the bulblets and corms from dormant *D. canadensis* and *D. cucullaria* individuals. I did not sow propagules of *P. reptans*.

With the exception of *D. canadensis*, I sowed five seeds or two bulblets or corms from each species into 10 of the assigned positions in three of the four treatment quadrats of each plot. This means that a total of 450 seeds of *S. diphyllum* and *J. diphylla*, and 180 bulblets of *D. cucullaria* were planted in each site. Due to a shortage of *D. canadensis*

corms, UGRBP-Bush was the only site planted with 180 corms. One randomly chosen quadrat in each of the other sites was planted with only one corm per position, giving the three sites a total of 170 corms each.

Other researchers have had good germination rates of seeds with intact elaiosomes (Baskin and Baskin 1984 and 1989, Cullina 2000), so I did not remove elaiosomes from *J. diphylla* or *S. diphyllum* seeds. Heithaus (1981) indicated that buried seeds of *Jeffersonia diphylla, Sanguinaria canadensis* (bloodroot) and *Asarum canadense* (all elaiosome-bearing) are located less frequently by mice than unburied seeds. Seed burial of elaiosome-bearing seeds of *Leucospermum truncatulum* **(**pincushion protea) also enhanced survival of seeds from seed predators; however, deeper burial resulted in reduced seedling emergence (Christian and Stanton 2004). To discover if there was a similar trend for my experimental species, I planted half of the *J. diphylla* and *S. diphyllum* seeds in each quadrat 1 cm deep, and the other half 2-2.5 cm deep. I planted *D. cucullaria* bulblets near the soil surface by making a shallow scrape in the ground and then covering and pressing the bulblet into the ground. I planted *D. canadensis* corms about 1 cm deep. In early April 2010, I counted the number of *Dicentra* sprouts, and in late April I counted the number of *J. diphylla* and *S. diphyllum* seedlings.

Treatment 3. Negative control: I gently disturbed the soil and leaf litter in these quadrats but otherwise left them alone. In April 2009, late March 2010 and mid-May 2010, I censused these quadrats for herbaceous species composition and overall richness.

Analyses

I tested all hypotheses using an alpha level of 0.05. Adult transplants and seedlings were analyzed separately, and unless otherwise specifically indicated, each species was also analyzed separately. I performed an arcsine transformation on all percentages where these were used in analyses. To determine whether survival rates of transplants were different among sites, I performed chi-square tests for goodness of fit on the total number of individuals per site for all species. I calculated the expected values by dividing the total number of surviving individuals per species by the number of sites. To determine whether flowering rates of transplants were different among sites, I performed chi-square tests for goodness of fit on the total number of flowering individuals per site for all species. I calculated the expected value by totaling the number of flowering individuals per species and dividing by the number of sites. I also performed separate chi-square tests for the number of flowering *D. cucullaria* and *D. canadensis* between the paired sites where all these were transplanted when flowering in 2009. Finally, all active transplants of species other than *P. reptans* flowered in 2009. Therefore, because all sites had both vegetative and reproductive *P. reptans,* I created transition matrices for this species, but for this species only.

To determine whether sites similarly supported flowering, I performed chi-square tests on the total number of flowers or fruits produced for each species. Due to a timing miscalculation in collecting fruit data for *D. canadensis* and *D. cucullaria*, I only counted the number of flowers produced for these species. I calculated the number of fruits produced for *J. diphylla* and *S. diphyllum* as the largest number of fruits seen on the plant through the season. I performed ANOVAs to test whether site had an effect on the

number of flowers or fruits produced per individual for each species except *P. reptans*. Because of the difficulties of reliably assessing flower or fruit production in *P. reptans*, I did not quantify either of these parameters for this species.

I performed chi-square tests for goodness-of-fit to determine whether propagule emergence rates were different among sites. I calculated the expected value by dividing the total number of emerged seedlings by the total number of sites. Because a different number of propagules of *D. canadensis* were sown into UGRBP-Bush, this site was excluded in the chi-square test for this species. Due to the ease with which the seeds of many spring-flowering species become desiccated (Cullina 2000, *pers. obs.*), I performed unpaired t-tests to determine whether the differences between collection date and planting date of propagules had an effect on germination and emergence. I also performed unpaired t-tests to determine whether planting depth for *J. diphylla* had an effect on seedling emergence. For the calculation of minimum numbers of recruited individuals, I counted every independently growing seedling as one. I counted each cluster as two because every cluster had two or more individuals.

Results

Adult transplants of all species had at least 84% survival rates across all sites, and species did not significantly differ in their survival rates $\chi^2(4, N = 857) = 2.06$, $p = 0.725$ (Fig. 3). There were flowering individuals of every species at all sites, and the number of flowering individuals at each site varied greatly among species (Fig. 4). Sown asexual propagules of *Dicentra canadensis* and *Dicentra cucullaria* emerged at all sites, and sown seeds of *Jeffersonia diphylla* germinated at all sites (Fig. 5). One sown seed of *Stylophorum diphyllum* germinated. Transplanted individuals of every species except *Polemonium reptans* released propagules that sprouted. There were no experimental species in any of the control quadrats in any sites.

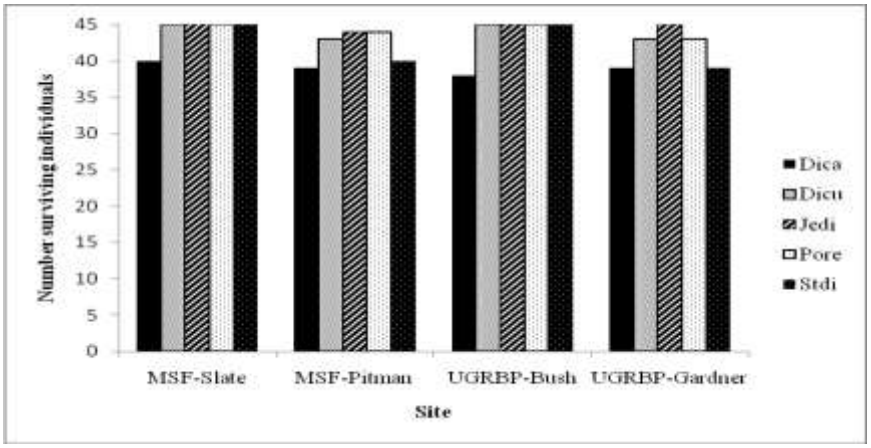

Fig. 3: Number of surviving transplants in 2010. In each site, the total possible number of survivors for each species was 45. "Dica" = *Dicentra canadensis*, "Dicu" = *Dicentra cucullaria*, "Jedi" = *Jeffersonia diphylla*, "Pore" = *Polemonium reptans*, "Stdi" = *Stylophorum diphyllum.*

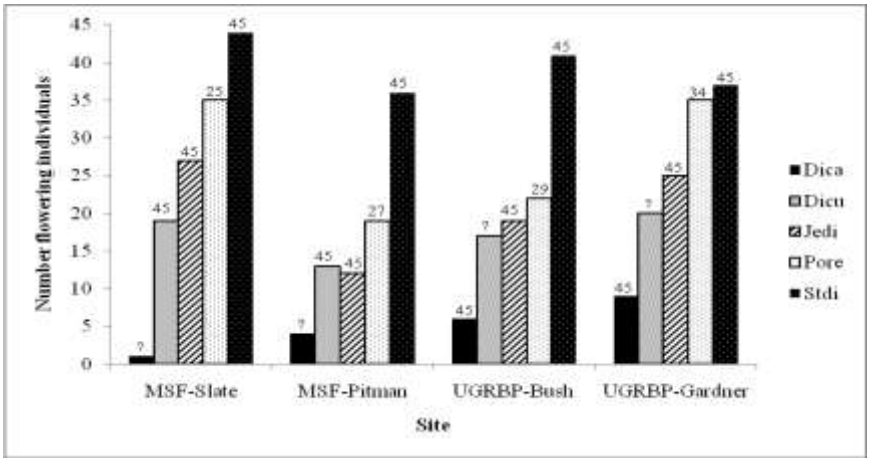

Fig. 4: Number of flowering transplants in 2010. Values above the bars indicate the number of transplanted individuals which flowered in 2009. "?" = unknown number of individuals that flowered, "Dica" = *Dicentra canadensis*, "Dicu" = *Dicentra cucullaria*, "Jedi" = *Jeffersonia diphylla*, "Pore" = *Polemonium reptans*, "Stdi" = *Stylophorum diphyllum*.

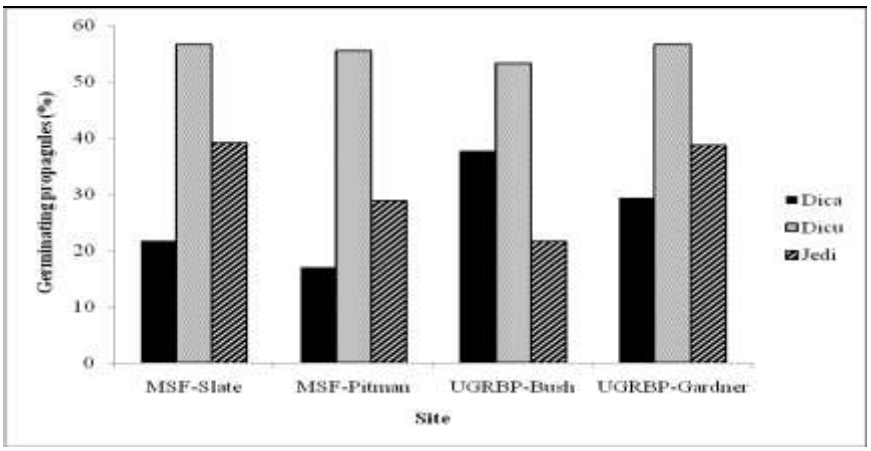

Fig. 5: Percentage of sown seeds that germinated in all four sites in 2010. "Dica" = *Dicentra canadensis*, "Dicu" = *Dicentra cucullaria*, "Jedi" = *Jeffersonia diphylla.*

Adult Survival

Dicentra canadensis had the lowest recorded survival rate while *J. diphylla* had the highest (Table 3). I found no experimental species growing in the control quadrats in April 2009, mid-March 2010 or mid-May 2010. This indicated that adults of these species were not previously present in any experimental sites.

Chi-square analyses showed that within species, there were no differences in survival rates across sites, *D. canadensis* $\chi^2(3, N = 156) = 0.05$, $p = 0.997$; *D. cucullaria* $\chi^2(3, N = 176) = 0.09$, p = 0.993; *J. diphylla* $\chi^2(3, N = 179) = 0.02$, $p = 0.999$; *P. reptans* $\chi^2(3, N = 177) = 0.06$, $p = 0.996$; *S. diphyllum* $\chi^2(3, N = 169) = 0.73$, p = 0.867.

Adult reproduction

No experimental species grew in the control plots; therefore, no flowering individuals of experimental species were in any control plots. However, transplants of each species flowered in all sites. Mean numbers of flowering individuals were lowest for *D. canadensis* ($M = 5$, $SD = 3.37$) and highest for *S. diphyllum* ($M = 39.5$, $SD = 3.70$). There was no difference in the number of flowering individuals among sites (Table 4).

There was a significant effect of site on the number of flowering *P. reptans* and *J. diphylla* within locations (Marrowbone State Forest, MSF, or Upper Green River Biological Preserve, UGRBP) (Table 4). In MSF, the number of flowering individuals for both species was lowest in the Pitman site. From column to row transition matrices for *P. reptans* showed that the probability of individuals remaining in or moving to a reproductive state in 2010 was much greater in the MSF-Slate (MSF) and UGRBP-

Gardner sites, while the probability of individuals remaining in or moving to a vegetative state was greater in the MSF-Pitman and UGRBP-Bush sites (Table 5).

Flower and fruit production

Given that there were no flowering individuals in control plots, flower and fruit production in control plots was zero in all sites. Only the presence or absence of flowers and fruits was recorded for *P. reptans*, so this species was excluded from flowering and fruiting analyses. For all other species, there was a significant effect of site on the total number of flowers or fruits produced (Table 6). Analysis of variance tests revealed that there was no effect of site on the number of flowers per flowering individual for *D. canadensis* or *D. cucullaria* (Table 7). There was no effect of site on number of fruits per fruiting *J. diphylla*. However, MSF-Slate and UGRBP-Gardner were the only sites with individuals bearing multiple fruits in 2010 (Table 8). There was a significant effect of site on the number of fruits per fruiting *S. diphyllum* (Table 7). A Tukey HSD post-hoc analysis revealed that there were significantly fewer fruits per individual at MSF-Pitman (M = 2.69, SD = 1.6) than any other site, MSF-Slate (M = 6.05, SD = 2.8), UGRBP-Bush (M = 4.15, SD = 2.4), UGRBP-Gardner (M = 5.08, SD = 2.6). In addition, UGRBP-Gardner supported fewer fruits per individual than MSF-Slate (Fig. 6).

Table 3: Percentage of individuals which survived to year two (2010), and the percentage of surviving individuals that flowered (*Dica, Dicu*) or fruited (*Jedi, Pore, Stdi*) in year two. "*Dica*" = *Dicentra canadensis*, "*Dicu*" = *Dicentra cucullaria*, "*Jedi*" = *Jeffersonia diphylla*, "*Stdi*" = *Stylophorum diphyllum*, "surv" = % surviving individuals, "flower" = % surviving individuals which flowered in 2010.

	Dicu		***Dica***		***Jedi***		***Pore***		***Stdi***	
Site	**surv**	flower	**surv**	flower	**surv**	flower	**surv**	flower	**surv**	flower
MSF-Slate	**100.0**	42.2	**88.9**	2.5	**100.0**	60.0	**100.0**	77.8	**100.0**	97.8
MSF-Pitman	**95.6**	30.2	**86.7**	10.3	**97.8**	27.3	**97.8**	43.2	**88.9**	90.0
UGRBP-Bush	**100.0**	37.8	**84.4**	15.8	**100.0**	42.2	**100.0**	48.9	**100.0**	91.1
UGRBP-Gardner	**95.6**	46.5	**86.7**	23.1	**100.0**	55.6	**95.6**	81.4	**86.7**	94.9
Average	**97.8**	39.2	**86.7**	12.8	**99.4**	**46.4**	**98.3**	**62.7**	**93.9**	93.5

Table 4: χ^2 statistics for number of flowering or fruiting individuals across all four sites "all" and within locations, MSF and UGRBP. "MSF" = Marrowbone State Forest, "UGRBP" = Upper Green River Biological Preserve, (rep) = all individuals flowered in 2009, "Dica" = *Dicentra canadensis*, "Dicu" = *Dicentra cucullaria*, "Jedi" = *Jeffersonia diphylla*, "Pore" = *Polemonium reptans*,"Stdi" = *Stylophorum diphyllum*.

	df	***N***	χ^2	***p***
all sites *Dicentra canadensis*	**3**	**20**	**6.80**	**0.080**
MSF	1	5	1.80	0.180
UGRBP (rep)	1	15	0.60	0.439
all sites *Dicentra cucullaria*	**3**	**69**	**1.66**	**0.644**
MSF (rep)	1	32	1.13	0.289
UGRBP	1	37	0.24	0.622
all sites *Jeffersonia diphylla*	**3**	**83**	**6.59**	**0.086**
MSF (rep)	1	39	5.77	0.016*
UGRBP (rep)	1	44	0.82	0.367
all sites *Polemonium reptans*	**3**	**111**	**7.74**	**0.052**
MSF	1	54	4.74	0.029*
UGRBP	1	57	2.96	0.085
all sites *Stylophorum diphyllum*	**3**	**158**	**1.04**	**0.792**
MSF (rep)	1	80	0.80	0.370
UGRBP (rep)	1	78	0.21	0.651

* Values are significant at $p \leq 0.05$

Table 5: From column to row transition matrices for *Polemonium reptans*.

	MSF-Slate			MSF-Pitman		
	Flowering 2009	Vegetative 2009	Dead 2009	Flowering 2009	Vegetative 2009	Dead 2009
Flowering 2010	0.88	0.65	0.00	0.44	0.28	0.00
Vegetative 2010	0.12	0.35	0.00	0.56	0.67	0.00
Dead 2010	0.00	0.00	1.00	0.00	0.05	1.00
	UGRBP-Bush			**UGRBP-Gardner**		
Flowering 2010	0.55	0.38	0.00	0.85	0.64	0.00
Vegetative 2010	0.45	0.63	0.00	0.15	0.18	0.00
Dead 2010	0.00	0.00	1.00	0.00	0.18	1.00

Table 6. χ^2 statistics for number of total flowers (*D. canadensis* or *D. canadensis*) or fruits (*J. diphylla* or *S. diphyllum*) per site.

Species	***df***	***N***	χ^2	***p****
Dicentra canadensis	3	99	29.36	< 0.001
Dicentra cucullaria	3	435	12.13	0.007
Jeffersonia diphylla	3	80	13.10	0.004
Stylophorum diphyllum	3	766	83.62	< 0.001

* Values are significant at $p \leq 0.05$

Table 7. ANOVA of number of flowers or fruits produced per individual across sites.

Reproductive paramater	Species	Mean	Std dev	*N*	*df*	*F*	*p*
Flower	***Dicentra canadensis***	4.95	± 1.76	20	3, 16	0.91	0.457
	Dicentra cucullaria	6.3	± 2.81	69	3, 65	1.33	0.274
Fruit	***Jeffersonia diphylla***	0.96	± 0.48	83	3, 79	2.19	0.096
	Stylophorum diphyllum	4.56	± 2.72	158	3, 154	13.39	< 0.001*

* Values are significant at $p \leq 0.05$

Table 8. Distribution of *Jeffersonia diphylla* which supported more than one fruit in 2009 and 2010.

Site	2009	2010	
	2 fruits	2 fruits	3 fruits
MSF-Slate	2	4	1
MSF-Pitman	3	0	0
UGRBP-Bush	2	0	0
UGRBP-Gardner	4	1	0

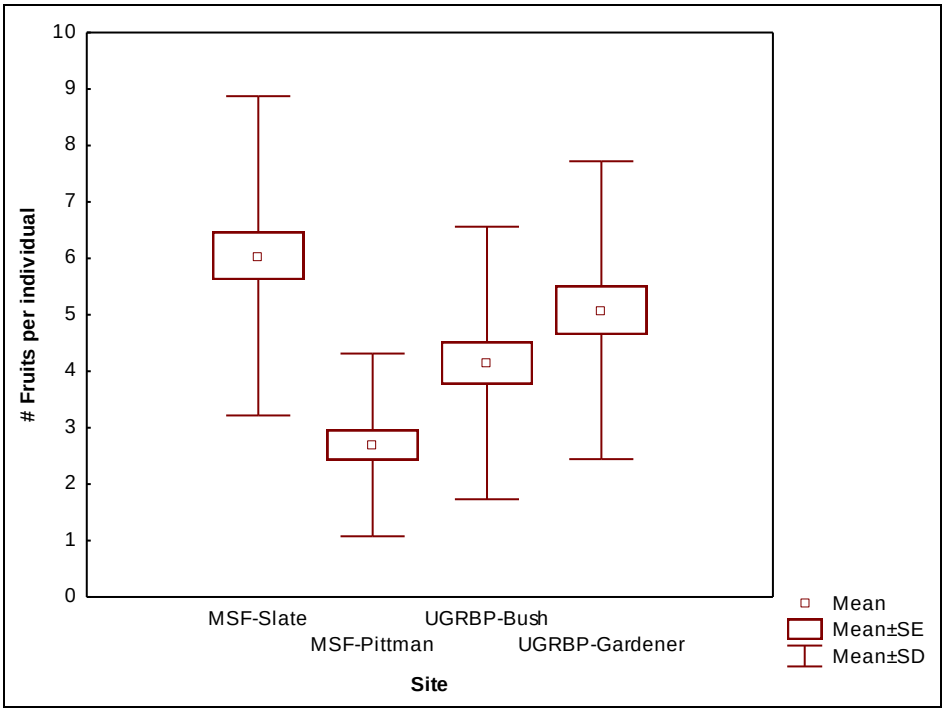

Fig. 6. Total number of fruits per reproducing *Stylophorum diphyllum* individual, $F(3, 154) = 13.3684$, $p < 0.001$.

Propagule emergence

There were no seedlings from experimental species growing in the control quadrats in late March or mid-May. Only one *S. diphyllum* seedling was found in UGRBP-Gardner, and I excluded this species from further analysis involving propagules. Overall, *D. cucullaria* bulblets germinated more successfully than those of other species (Table 9). Chi-square tests indicated the proportion of germinating *J. diphylla* seeds was different among sites, $\chi^2(3, N = 577) = 118.35$, $p < 0.001$. However, the proportion of

sprouting asexual propagules was not different for *D. cucullaria*, $\chi^2(3, N = 400) = 0.24$, $p = 0.971$, or *D. canadensis*, $\chi^2(2^*, N = 116) = 5.81$, $p = 0.055$ (*UGRBP-Bush was excluded from analysis because of a difference in number of introduced propagules).

Table 9. Percentage of propagules that produced seedlings or sprouts.

	Species		
SITE	***Dicentra canadensis***	***Dicentra cucullaria***	***Jeffersonia diphylla***
MSF-Slate	21.8	56.7	39.1
MSF-Pitman	17.1	55.6	28.9
UGRBP-Bush	38.3	53.3	21.6
UGRBP-Gardner	33.3	56.7	38.7
Grand Total	**27.3**	**55.6**	**32.1**

I used unpaired t-tests to determine whether numbers of sprouting propagules differed according to earlier or later planting date. The number of sprouting *D. canadensis* corms per quadrat was greater for those planted earlier ($M = 6.59$, $SD = 3.28$) than those planted five days later ($M = 3.94$, $SD = 2.77$), $t(34) = -2.50$, $p = 0.018$. There was no effect of day on the number of sprouting *D. cucullaria* bulblets, first planting day ($M = 11.2$, $SD = 5.4$), one day later ($M = 11.0$, $SD = 2.5$), $t(34) = 0.16$, $p = 0.876$, nor on the number of germinating *J. diphylla* seeds, first planting day ($M = 17$, $SD = 7.4$), one day later ($M = 15.1$, $SD = 6.7$), $t(34) = 0.83$, $p = 0.413$. The effect of planting depth on *J. diphylla* germination was also not significant, shallower ($M = 1.72$, $SD = 1.4$), deeper ($M = 1.45$, $SD = 1.3$), $t(361) = 1.91$, $p = 0.057$.

Natural seedling recruitment and dispersal

No species emerged in any of the control quadrats, which indicated that none of the experimental species dispersed into control quadrats. By mid-April, I found recruits of both *Dicentra* species in transplant quadrats of all sites. However, I did not quantify the extent of this dispersal because distinguishing between seedlings of the two species was difficult.

In MSF-Slate, I found *J.diphylla* seedlings in and around seven of nine transplant quadrats with *J. diphylla* transplants. In both MSF-Pitman and UGRBP-Gardner, I found *J. diphylla* seedlings in eight of nine transplant quadrats. Of 63 distance measurements, 49 were of independently growing seedlings, and 24 were of clustered seedlings. The average distance of all farthest seedlings from the nearest conspecific adult was 25.19 cm, while the average distance for independently growing individuals was 26.5 cm. The farthest documented seedling was 70.5 cm downhill of the closest adult. The farthest horizontal dispersal was 58.5 cm, and the farthest uphill dispersal was 45.5 cm. I found a minimum number of 31 individuals including five clusters in site UGRBP-Gardner, a minimum number of 23 individuals including five clusters in MSF-Slate, and a minimum number of 43 individuals including 14 clusters in MSF-Pitman. I found no *P. reptans* recruits. In site MSF-Pitman, I found a single *S. diphyllum* recruit 36.5 cm from the closest adult.

Flooding effects on adult transplants

In all sites, all *D. canadensis* and *D. cucullaria* were senesced by the time flood waters receded, so I was unable to quantify flooding effects for either species. By 12

May, all fruiting plants at UGRBP-Bush had aborted seed production. Fruits dehisced on 10 of 26 fruiting *J. diphylla*, but most seeds were not yet ripe. Fruits dehisced on nine of 44 *S. diphyllum*, and seeds were either unripe or black and shriveled. Indehisced fruits of both species molded or rotted without opening. Fruiting *P. reptans* stalks withered and aborted fruit production. By 27 May, only one *J. diphylla*, 17 *P. reptans* and eight *S. diphyllum* still had leaves. Nearly all other transplants in other sites still carried leaves at this time.

At UGRBP-Gardner, plants in the four flooded quadrats were only lightly covered in sediment. Of nine reproducing *J. diphylla*, two had dehisced fruits with ripe seed, two had dehisced with unripe seed, and one fruit was missing. Only one fruit from eight fruiting *S. diphyllum* plants dehisced with ripe seed. By 20 May, two additional *S. diphyllum* pods had molded without dehiscing. All remaining *S. diphyllum* fruits dehisced in the same time frame as those on unaffected plants. All four fruiting *P. reptans* continued with seed production.

At MSF- Pitman, heavy run-off from upper slopes removed all debris and plants from a 3 m wide path through the middle of the site. Most damage occurred between plots, and only two plants in one quadrat were negatively affected. One *J. diphylla* was obliterated by flood debris. The base of one *S. diphyllum* was covered with flood debris, but the leaves remained and the plant did not abort seed production. Transplant quadrats at MSF-Slate appeared unaffected by flooding.

Discussion

The absence of all experimental species from negative control plots confirmed that none of the experimental species were present before I introduced them. Therefore, if any experimental species establish self-sustaining populations, then their previous absence from experimental forests was due to dispersal limitations. After one year of experimental introduction, dispersal limitation would be strongly indicated by survival and flowering of adult transplants, seedling emergence of sown seeds and natural seedling recruitment. My first hypothesis stated that five herbaceous species were dispersal-limited in four mesic hardwood forests. Data supported this hypothesis for three species, *Dicentra canadensis, Dicentra cucullaria* and *Jeffersonia diphylla*. The data were less clear about whether *Polemonium reptans* and *Stylophorum diphyllum* were dispersal-limited. My hypothesis that transplanting flowering *Dicentra* individuals would negatively affect their survival was not supported. I also hypothesized that site characteristics would differently influence survival rates, reproductive parameters and germination rates. Site characteristics did not influence survival rates; however, they did influence the incidence of flowering for *P. reptans* and the number of fruits produced by *S. diphyllum*. Of all four sites, MSF-Slate and UGRBP-Gardner appeared to be most favorable for supporting reproductive individuals. Site characteristics appeared to influence the germination rate only for sown propagules of *J. diphylla*. My hypothesis that later planting date would have a negative effect on seedling emergence was only upheld for *D. canadensis* for which sowing dates differed by five days. Sowing dates for

all other propagules differed by only one day. Finally, my hypothesis that deeper burial would have a negative effect on seedling emergence was not supported for either *J. diphylla* or *S. diphyllum*.

Below, I discuss site differences in species survival, reproduction and seedling emergence. I then discuss the importance of these results to previously published hypotheses. Finally, I offer management suggestions for reestablishing these species.

Likely dispersal-limited herbs

Dicentra canadensis

Despite having the lowest re-emergence percentage of all species (> 84%), *Dicentra canadensis* had a high survival rate in all sites in the first year after transplanting.

Non-surviving individuals senesced during a natural time frame in 2009, and it is unlikely that they died during the transplant process. Though others have suggested that small mammals and birds readily transplant and feed upon *D. canadensis* corms (Wasowski and Wasowski 1994, David Nelson *pers. comm.*), there was no direct evidence of corm predation in the study sites. However, there were heavy storms during 2009 and 2010, and it is possible that some individuals were not planted deeply enough to allow them to withstand water and debris slides. These individuals may have been "washed away" and naturally transplanted to unknown locations. It is also possible that individuals succumbed to poor habitat quality or had reached the end of their life-spans.

Flowering and dormant transplants were not distributed among all sites, but were segregated to two sites for flowering transplants and two sites for dormant transplants.

Some site factors influencing survival may be obscured by this segregation. However, survival rates were similar between those individuals which were transplanted while flowering (Upper Green River Biological Preserve, UGRBP sites) and those transplanted while dormant (Marrowbone State Forest, MSF sites). It is probable that transplanting did not differently affect survival for plants moved during either stage.

Of all species, *D. canadensis* also had the lowest percentage of flowering individuals in 2010. The significant difference in the number of flowers produced per site was an artifact of the number of flowering plants in each site. Sites where dormant individuals were transplanted (MSF) supported fewer flowering individuals than sites where flowering individuals were transplanted (UGRBP). Although it is probable that all *D. canadensis* were at least three years old in 2010, the number of MSF transplants that were sexually mature in 2009 was unknown. I found no reference to indicate the age of *D. canadensis* at maturity. However, if the age of *D. canadensis* maturity is similar to that of *D. cucullaria*, which is 2-4 years, then it is probable that most, if not all *D. canadensis*, were sexually mature by 2010 (Sperka 1973 and Art 1986, cited by Bender et al. 2000). If all *D. canadensis* were sexually mature, then reproductive strategies in MSF were probably influenced by environmental variables. Flowering data in 2011 (when all individuals will be a minimum of 4 years old) should clarify this hypothesis.

Sown asexual propagules of *D. canadensis* sprouted at all sites. However, there was a significant effect of planting date on sprout emergence. This is probably because of the rapidity with which corms become desiccated. It is therefore unclear whether the lesser emergence rates seen at both MSF sites were due to habitat quality or propagule desiccation because of a delayed planting date.

Finally, *D. canadensis* naturally dispersed in all sites. Seedling recruits were found both in and outside transplant quadrats in all study sites in 2010. Also, some sown propagules were naturally transplanted between 2009 and 2010.

Without post-transplantation treatment, *D. canadensis* survived, flowered, sprouted from asexual propagules and naturally dispersed viable propagules. The results therefore strongly indicated dispersal-limitation at these four sites. Adult transplantation and sowing of asexual propagules were successful ways to introduce this species to all sites.

Dicentra cucullaria

Dicentra cucullaria had high survival rates across all sites (> 95%), and similar survival rates for individuals that were transplanted while flowering and dormant. The significant difference in the number of flowers produced per site was an artifact of the number of flowering individuals in each site in 2010. There was no difference in number of flowering individuals between sites where dormant (UGRBP) and flowering (MSF) *D. cucullaria* were transplanted. Like *D. canadensis*, it is unclear whether differences in rates of flowering were driven by environmental characteristics or individual plant factors. However, if *D. cucullaria* three years and older had equal probabilities of flowering, then all environments similarly supported flowering in this species.

Across sites, sprouting rates for sown *D. cucullaria* bulblets were greater than 53%. For some species, the probability of emergence from asexual propagules is greater than that from seeds (Wang and Cronk 2003). Because I did not deliberately plant seeds of this species, it is unknown whether there are similar trends in *D. cucullaria*.

Interestingly, quadrat emergence rates ranged from 0 to 90%. The range of quadrat germination rates in each site did not differ among sites. The average germination rate also did not differ among sites. The wide rage of germination rates within sites therefore suggested a strong degree of site heterogeneity.

Dicentra cucullaria also naturally dispersed in all sites. I found seedling recruits both in and outside transplant quadrats in all study sites in 2010. Some sown propagules were also naturally transplanted.

Results strongly indicated that *D. cucullaria* was dispersal-limited at all four sites. Without post-transplantation treatment, this species survived, flowered, sprouted from asexual propagules and naturally dispersed viable propagules. Adult transplantation and sowing of asexual propagules were successful ways to introduce this species to all sites.

Jeffersonia diphylla

Of all species, *J. diphylla* had the highest survival rates, with nearly 100% re-emergence across all sites. Individuals reproduced on all sites, and the number of fruiting individuals was not significantly different across sites. However, within MSF, site MSF-Slate supported a significantly larger number of reproducing individuals than MSF-Pitman.

The significant difference in the number of fruits produced per site was an artifact of total numbers of fruiting individuals. In 2009 and 2010, most reproducing *J. diphylla* supported only one fruit. Except for one individual in UGRBP-Gardner, all *J. diphylla* with multiple fruits were in MSF-Slate. Interestingly, none of the individuals supporting multiple fruits in 2009 did so in 2010. This may have been a result of stress experienced

because of the transplant process. However, this means that six “new” plants produced multiple fruits in only two sites. This suggested that flower and fruit production were strongly influenced by environmental characteristics. Sites which are able to support *J. diphylla* with multiple fruits will likely recover populations of *J. diphylla* more quickly because of the potential for increased seed rain.

By allowing elaiosome-bearing seeds of *J. diphylla* to experience normal temperature fluctuations in a pre-defined and regularly watered medium, Baskin and Baskin (1989) were able to obtain 51% germination rates; therefore, lower germination percentages in an uncontrolled environment were expected. Across sites, germination rates of sown seeds were significantly different, and within sites, germination rates varied as much as 0-90%. Although elaiosomes are often removed from seeds that are buried by ants, it is unlikely that the elaiosomes on sown seeds in this study had a significant negative effect on *J. diphylla* germination (Lobstein and Rockwood 1993). It is also unlikely that seeds were heavily predated. Heithaus (1981) found that experimentally buried *J. diphylla* seeds were less likely to be found by predators, and in this study, often at least one of five seeds germinated in each sown location. Therefore, because germination was not significantly affected by elaiosomes or predation, the variability of *J. diphylla* germination is likely influenced by site heterogeneity.

Most transplant quadrats with *J. diphylla* adults recruited seedlings from seed released by transplants. In this study, dispersal distances represented the minimum distance a seed traveled, because the mother of the seedling was assumed to be the nearest adult. The average dispersal distance was 25.19 cm, a range reachable by many *J. diphylla* scapes (Racke *unpublished data*). Seedlings beyond the range of scapes and

which were uphill of or horizontally aligned with adults probably germinated from seed that was dispersed by organisms. Despite some amount of organismal-dispersal, I calculated that no seed dispersed farther than 1 m, which supports data from previous studies (Matlack 1994). However, it is possible that seedlings growing beyond the 3 m search range were unnoticed and that future investigation will find adults which have recruited from these unknown seedlings.

Results strongly indicated that *J. diphylla* was dispersal-limited at all four sites. Without post-transplantation treatment, this species survived, flowered, germinated and naturally dispersed viable seed. Adult transplantation and seed sowing were successful ways to introduce this species to all sites. However, future re-colonization in all sites will be slow because of short dispersal distances. Also, future rates of population reestablishment may differ among sites because of environmental factors affecting fruit production and germination.

Potentially environmentally-limited herbs

Polemonium reptans

At all sites, *Polemonium reptans* survived well and flowered. Transition matrices showed that individuals were more likely to flower in MSF-Slate and UGRBP-Gardner, while individuals in MSF-Pitman and UGRBP-Bush were most likely to either stay in or revert to a vegetative state. In 2009, this species was transplanted before most individuals were flowering, and unlike other species, neither paired set of sites supported *P. reptans* that all flowered in 2009. I found no source to indicate the age of *P. reptans* at sexual maturity. However, based on size similarity, it is probable that sexually mature

individuals were evenly distributed between paired sites. Therefore, it is probable that environmental differences influenced the incidence of flowering for this species.

This is the only study species for which I did not deliberately sow seeds. The unknown number of viable seeds released from adults in 2009 made it difficult to determine site suitability for *P. reptans* germination. *Polemonium reptans* is also the only species for which no natural recruits were found in any sites.

Robust populations of *P. reptans* were found less than 50 m downstream of MSF-Slate and UGRBP-Bush. Therefore, it is probable that seeds were capable of germinating in these two sites at least. However, natural *P. reptans* populations in MSF and UGRBP were frequently found on gently sloping or level ground, and many study quadrats were erected on more steeply sloping ground. If *P. reptans* seeds are capable of germinating in any sites, natural recruits will likely first appear along level ground.

Without post-transplantation treatment, *P. reptans* survived and flowered in all four sites. However, habitat suitability for germination was less clear because of the absence of sown propagules and the lack of naturally recruited seedlings. Results suggested that this species is environmentally limited by factors affecting germination or the release of viable propagules. However, if this species is dispersal-limited in forest sites, adult transplantation is a successful way to introduce the species.

Stylophorum diphyllum

At all sites, *Stylophorum diphyllum* survived well, and more than 90% of transplants flowered. The high percentage of flowering individuals was expected, because in natural populations, *S. diphyllum* over two years old usually flower every year (Cullina

2000, COSEWIC 2007). Indicators of environmental suitability for *S. diphyllum* were expected to appear in productivity measures such as fruit or seed yield. Though most *S. diphyllum* flowered in 2010, plants at some sites produced significantly fewer fruits than plants at other sites. Larger individuals tend to yield more fruits (*pers. obs.*), and transplants were evenly distributed among sites according to the number of ramets. Therefore, it is likely that environmental factors significantly affected *S. diphyllum* fruit production.

Only one seedling was found in a propagule quadrat. It is possible that *S. diphyllum* seeds succumbed to a greenhouse effect induced by collection, transportation, and storage of seeds in a sealed plastic bag before sowing. In the lab, I was unable to induce germination in seeds with a protocol similar to Baskin and Baskin (1984) that stimulated 35% germination. It is therefore likely that the low germination rates in sown quadrats was due to the low viability of *S. diphyllum* seeds in 2009.

The only *S. diphyllum* seedling from naturally sown seed was in MSF-Pitman. With naturally fluctuating temperature and light levels, it was possible for Baskin and Baskin (1984) to induce up to 89% germination rates for this species. However, even in robust populations of *S. diphyllum*, it was often difficult to find first year individuals (*pers. obs.*). Though seeds are mostly viable, it is possible that field germination for this species is low in any site. Interestingly, although MSF-Pitman supported lower levels of fruiting than all other sites, it was also the only site where small *S. diphyllum* populations were found nearby. This suggested that *S. diphyllum* may be able to establish self-sustaining populations despite low fruiting levels. It may be that the species does not require a large annual number of seedlings to maintain population numbers.

Without post-transplantation treatment, *S. diphyllum* survived and flowered in all four sites. If this species is dispersal-limited in forest sites, adult transplantation is a successful way to introduce this species. Habitat suitability for germination was less clear because it was probable that most sown seeds were inviable. However, in most sites, the lack of seedlings recruited from naturally sown seeds suggested this species was environmentally-limited by factors affecting seedling recruitment.

Flooding effects

Extended duration of a spring flooding event negatively impacted *J. diphylla, P. reptans* and *S. diphyllum*. Stress during a plant's reproductive phase can lead to early maturation, fruit abortion, seed abortion and early senescence (Brevedan and Egli 2003; Adolf et al 2009; Zinn et al 2010). Fruit abortion and early senescence could be seen even in low-lying quadrats at UGRBP-Gardner where affected plants were covered by flood waters for likely no more than a day. Stress effects were much more pronounced in UGRBP-Bush where plants were covered between two to five days.

At UGRBP-Bush, both seedlings and adults survived, although some seedlings and adults were buried beneath 2-5 cm of sand, silt and clay. After flood waters receded, the leaves and fruits of most remaining adults were still covered in sediment. All transplants at this site aborted fruit production entirely or dehisced prematurely. Most individuals also senesced by two weeks after flooding, though fruits of less-affected individuals had not yet dehisced.

For species that do not persist in the seed bank, such as those in this study, environmental stresses that cause seed abortion will prevent seedling recruitment the

following year. It is currently unknown how early senescence of stressed plants will affect survival or reproduction in 2011. If early senescence increases mortality, then UGRBP-Bush will have higher mortality rates among *J. diphylla, P. reptans* and *S. diphyllum* than other sites. If stress during the reproductive stage affects survival, then at UGRBP-Bush, plants that were fruiting during the flood will have higher mortality than those which were vegetative.

In 2010, survival and reproductive parameters indicated that most experimental species are dispersal-limited in UGRBP-Bush. However, it is possible that repeated environmental stress, such as that experienced in 2010, has contributed to the loss of spring-flowering species in this site. If species can establish near areas at risk for similar types of disturbances, they should be able to periodically recolonize areas where populations become depleted by disturbances.

Site differences

It was interesting that favorable trends in reproductive parameters appeared in one site at MSF and one at UGRBP rather than at both sites in one of these locations. Given that overstory composition an soil type between two paired locations was similar, it is probable that factors such as nutrient levels, herbaceous competition, or faunal composition had more of an influencing effect on transplant survival and reproduction. Overall, experimental species at MSF-Slate and UGRBP-Gardner had greater flowering and germination rates than MSF-Pitman and UGRBP-Bush, respectively. Pre-experimental herbaceous composition and nutrient analyses will likely yield further

insight into the relative success of establishment for these species (Racke *unpublished data*).

Researchers have suggested that few myrmechochores disperse farther than 1 m per year (Matlack 1994; Meier et al. 1995). However, Türke et al. (2010) recently found that the elaiosomes on seeds of two ant-dispersed species, *Anemone nemorosa* (wood anemone) and *Asarum europaeum* (European wild ginger), were consumed by gastropods, and that gut passage of the seed did not negatively affect germination. They also found that if consumed, seeds had the potential to be dispersed at least 14.6 m. I did not see any seeds dispersed more than 1 m from potential parents. However, gastropod herbivory was evident in all sites, and seeds may have dispersed farther than current data document. An expanded investigation of the study areas in future years may reveal adult recruits that were unnoticed as seedlings. Because none of the experimental species persist in the seed bank (Baskin and Baskin 1984, 1989, 1992; Leckie et al. 2000), future dispersal distances will be attributable to the original introduction of these species.

Hypotheses by others

Researchers have shown that species with ant-, ejection- and gravity-dispersed seeds are absent or less common in post-agricultural or clearcut successional forests (Matlack 1994; Bossuyt et al. 1999; Singleton et al. 2001; Landenberger and McGraw 2004). Matlack (1994) and Meier et al. (1995) have suggested that this is because these dispersal strategies often restrict species' dispersal distances to less than 1 m annually. Also, some disturbed forests have fewer species of ground ants than less-disturbed sites (Graham et al. 2004, Sakchoowong et al. 2009). Ants are responsible for dispersing 20-

50% of herbaceous species in eastern deciduous forests (Zelikova et al. 2008). Therefore, a loss of ant species as a result of forest degradation may even further restrict a species' range (Heithaus and Humes 2003, Laughlin 2003). I physically dispersed species into potentially environmentally-limiting habitats and eliminated concerns of long-distance dispersal and absence of disperser species. Though environmental factors may yet show an effect on adult recruitment and dispersal distances, in this study, four ant-dispersed species were not previously present in forests where transplanted adults flowered and seedlings recruited. Therefore, my results supported the hypothesis that many ant-dispersed species are absent from forests because of range-limiting dispersal vectors.

In a list of possible hypotheses, Duffy and Meier (1992) suggested that rates of recovery in Appalachian forests may depend more on site characteristics rather than time. This hypothesis was not supported by the current study. The four experimental forests in this study differed in age, the extent of previous disturbance, nutrient levels and floral composition (Racke *unpublished data*). Despite this, artificially dispersed species survived, flowered, emerged and naturally recruited. In these forests, time rather than site characteristics more likely contributes to the absence of many spring-flowering species.

Finally, Duffy and Meier (1992) also suggested that logged Appalachian forests may never recover their primary compositions because climatic conditions have or will become unfavorable for establishment. Indeed, many studies have shown that high temperatures have negative direct and indirect effects on herbaceous plants (Parker and Borthwick 1939, Okagami 1979, Kamentsky et al. 2003). The current study showed that in forests of south-central Kentucky, climatic conditions are not yet factors limiting establishment in some herbaceous species. However, if temperature negatively affects

population growth rates of dispersal-limited species, it is conceivable that rising temperatures may subsequently prevent these species from ever reaching suitable microsites in depauperate forests. Therefore, reestablishing dispersal-limited species into forests before climatic shifts negatively affect establishment may allow species to persist and adapt to climate change in those sites.

Management suggestions

In this study, all transplanted species had high survival rates, and all except one species released propagules that germinated the following spring. Therefore, transplantation of spring-flowering herbs which do not persist in the seed bank will help restore diversity to depauperate forests. Also, transplantation of flowering individuals does allow some species to self-sow the year in which they are transplanted. Coincidentally, no transplanting event was preceded by more than one day of dry weather, and every transplanting event was followed by at least two days of rain beginning on the day of the transplant or the day following. It is possible that in this study the high rates of adult survival and release of viable propagules are a partial result of the wet climatic conditions surrounding each transplant event. Therefore, if transplanting during a dry spring, I recommend lightly watering transplants every 1-2 days for a few weeks following the transplant in order to minimize possible negative effects from drought stress. Also, for restoration projects involving these herbs, I recommend using transplants from local disjunct populations to decrease the potential for a genetic bottleneck in subsequent generations.

The large numbers of aborted flowers and fruits seen from *Dicentra canadensis* and *Dicentra cucullaria* (Racke *unpublished data*) are likely compensated by the successful emergence of dispersed asexual propagules. Because large populations of both species can be difficult to find, transplanting a greater number of bulblets and corms from fewer individuals is recommended. If these species are dispersal-limited in target forests, then evenly distributing propagules across a site may be more ecologically profitable than transplanting adults. Distributing propagules will require harvesting fewer adults and will therefore be less destructive to the source population. Also, even after division, the larger bulblets of *D. cucullaria* may still produce flowers the following year (*pers. obs.*). Because *D. cucullaria* and *D. canadensis* seem to produce few viable seeds annually, evenly spaced sowing regimes should decrease the amount of time it takes these species to recolonize an area via asexual strategies. As many gardening books suggest, the division of bulblets and corms should take place after the leaves senesce in order to minimize stress to the plant, but before the fall when root growth resumes. To avoid desiccation, asexual propagules of both species should be stored in moist soils until transplanted.

Jeffersonia diphylla seems to withstand root disturbance fairly well. Though individuals may change from reproductive to vegetative states from year to year, seedlings seem to recruit easily, and seeds readily disperse in most directions. Because this species takes 3-5 years to reach maturity, I recommend transplanting a few plots of 5-10 fruiting adults and allowing them to self-sow in the target forest. Distance between plots should be 10-20 m to allow this species to exploit environmental heterogeneity. Plots should be located at mid-elevations on a slope where the soil is still moist. This will

facilitate gravity dispersal. To speed recovery, additional seeds could be sown into the areas where adults are not transplanted.

In the four study forests, population reestablishment of *Stylophorum diphyllum* seemed to be more limited by seed germination and seedling recruitment rather than adult survival or reproduction. Therefore, if this species is dispersal-limited in the target site, establishing populations by transplanting flowering adults and allowing them to self-sow is likely more feasible than planting seed. Like *J. diphylla*, small, disjunct plots of reproducing adults should be transplanted at mid-elevations on a slope where the soil is still moist. High annual seed output should allow the species to exploit environmental heterogeneity.

Seed germination rates and the extent of environmental limitations of *Polemonium reptans* in these forests are currently unknown. However, if this species is dispersal-limited in the target forest, the easiest method of re-introduction will likely be by transplanting adults. They should be transplanted to the lowest levels of slopes where the ground is level and the soils are mesic though not hydric. Individuals can colonize an environment through clonal expansion via rhizomes as well as sexual reproduction. Therefore, transplanting flowering adults 1 to 2 m apart along the lower edges of a mesic slope should allow adults to exploit environmental heterogeneity through either sexual or asexual reproduction.

Conclusion

In many forests of south-central Kentucky, time and distance from propagule sources are the most likely causes for the absence of many ant-dispersed species in secondary forests. However, it is possible to successfully transplant flowering herbs into depauperate forests. Forest managers can rapidly enrich herbaceous diversity by transplanting ant-dispersed species or other species with range-limiting dispersal vectors. Forest managers can also enrich herbaceous diversity by transplanting or sowing species that do not have propagules that persist in the seed bank.

For species to be dispersal-limited, an environment must be able to support reproduction, germination and recruitment of new individuals. In south-central Kentucky, populations of *Dicentra canadensis, Dicentra cucullaria* and *Jeffersonia diphylla* showed strong evidence of being dispersal-limited in at least four mesic forests which differed in environmental characteristics. Populations of *Stylophorum diphyllum* appeared to be limited by factors affecting seedling recruitment in at least two forests. These four ant-dispersed species are likely dispersal-limited in many other mesic forests in the region. Populations of *Polemonium reptans* appeared to be environmentally limited by factors affecting seedling recruitment in all four sites. However, the species may have been limited by transplant locations.

For every studied species, differences in site characteristics had no significant effects on adult survival, though they did have an effect on reproductive parameters. The relationships among environmental parameters and reproductive parameters will assort

more clearly as populations become more firmly established. However, for many species with short-distance dispersal characteristics, environmental characteristics will more likely influence the speed of population establishment, rather than establishment itself.

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