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Long Term Population Dynamics For Rosa Multiflora In A Successional System

Stephen Eugene Banasiak

Eastern Illinois University

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LONG TERM POPULATION DYNAMICS OF
ROSA MULTIFLORA IN A SUCCESSIONAL SYSTEM

BANASIAK

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LONG TERM POPULATION DYNAMICS OF *ROSA MULTIFLORA* IN A
SUCCESSIONAL SYSTEM

BY

STEPHEN EUGENE BANASIAK

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF

MASTER OF SCIENCE NATURAL SCIENCES
BIOLOGICAL SCIENCE

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

2007

I HEREBY RECOMMEND THAT THIS THESIS BE ACCEPTED AS FULFILLING
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Arthur S. Motter
DEPARTMENT/SCHOOL HEAD

ABSTRACT

There is a real need for long term studies of invasions to develop a more complete understanding of the factors that influence species spread. *Rosa multiflora* was chosen to study to address this issue due to its pervasiveness throughout the study site's successional history. The study-site was composed of 10 abandoned agricultural fields near an old growth forest with fifty years of annual vegetation data collection. *R. multiflora* colonization and extinction rates were examined along with frequency and coefficient of variance since field abandonment. Environmental factors such as rainfall, tree cover, and common species and their effects on *R. multiflora* during its invasion and recession were also investigated. *R. multiflora* showed a 9 year lag when invading, followed by a 20 year period of expansion, stagnation, and eventually a decline as succession progresses. It was found that during all phases of *R. multiflora*'s invasion that there was constant colonization and extinction within plots. Rainfall was found to have a positive effect on *R. multiflora* during population expansion ($R=0.260$, $P<0.001$) while tree cover showed a negative effect, but only during population decline. Species richness was always positively associated with *R. multiflora* where various common species were positively or negatively correlated with *R. multiflora* growth. The final major influence on *R. multiflora*'s invasibility, growth, and survival appears to be canopy closure and the ensuing light reduction as established *R. multiflora* plants were much less likely to occur in tree dominated plots ($\chi^2=8.07$, $df=1$, $P=0.004$) during its declining period between a successional field age of 32 and 40. *R. multiflora* will decrease as forests age, but will most likely not disappear without management, seedlings consistently are produced in the forest understory.

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Introduction

Due to accidental, deliberate, or indirect introduction an estimated 4,500 non-native plant species have become established in the United States (Devine 1998). Estimated economic damage for these species is \$20 billion annually (US Department of Interior 2003). Non-native plants reduce the complexity and structure of invaded areas through the suppression of native species (Woods 1993; Luken and Thieret 1996; Wyckoff & Webb 1996; Hutchinson & Vankat 1997; Meiners *et al.* 2001). Non-native species are a major threat to biodiversity second only to habitat destruction (Wilcove *et al.* 1998) and also have detrimental effects on the reestablishment of native species (Bellemare *et al.* 2002). Despite these well-known threats, there is a real need for long term studies to fully understand the many factors that influence the spread and impact of non-native species in natural systems (Luken and Thieret 1996; Parker *et al.* 1999; Byers *et al.* 2002)

Most introductions of non-native species can be attributed to human actions (Sakai *et al.* 2007). Not only are most introductions due to human actions, but also some of the strongest promoters of invasion are anthropogenic habitat disturbances (Lundgren *et al.* 2004). However, not all promoters of invasions are human centered as general resource availability (Burke and Grime 1996; Davis *et al.* 2000) and propagule pressure (Drake and Lodge 2006) are key factors in an invasion. Colonizing species tend to have a limited window of expansion and growth based on the environment and successional stage (Gross 1980; Bartha *et al.* 2003; Yurkonis 2005) and the successional window for colonization may be different even among similar species (Rankin and Pickett 1989). An understanding of the factors that control the population dynamics of invaders in succession is important for both understanding overall community dynamics and for habitat management and restoration. In forest communities, non-native shrubs and trees have greater cover near edges (Hunter and

Mattice 2002; Lundgren *et al.* 2004). However, alien species often develop a vegetative wall at the edges, decreasing light and inhibiting their own establishment deeper into the forest (Brothers & Spingarn 1992). Other studies have also shown that closed canopy vegetation generally prevents the colonization of plant species (Bartha *et al.* 2003). This suggests that invasions into late-successional systems should be relatively limited.

Non-native species often alter species richness within invaded communities (Woods 1993; Wyckoff and Webb 1996; Hutchinson and Vankat 1997; Meiners *et al.* 2001). At the same time, areas of greater species richness are more often invaded than species poor areas (Robinson *et al.* 1995; Wiser *et al.* 1998; Levine and D'Antonio 1999; Lonsdale 1999; Huebner and Tobin 2006). While community-wide scales species richness and factors such as propagule supply make diverse communities more likely to be invaded, diversity may enhance community resistance at neighborhood scales (Levine 2000) acting as a regulator of invasibility (Knops *et al.* 1999; Levine and D'Antonio 1999; Kennedy *et al.* 2002). These seemingly contradictory results may be caused by variation in how individual invaders respond to species richness and how they impact communities. There are a plethora of individualistic controlling factors working together making generalizations about community invasibility impossible (Meiners *et al.* 2004) further emphasizing the need for detailed, long term studies on individual invaders to clarify these interactions.

Rosa multiflora

To better understand invasion dynamics, this study focused on the population dynamics of the invasive non-native, *Rosa multiflora* during secondary succession. *Rosa multiflora* is an erect branching shrub with prickles on the spreading branches and petioles. It is semi-evergreen, photosynthesizing during the winter when deciduous leaves have fallen

and more light can get through (Robertson *et. al* 1994). *Rosa multiflora* produces clusters of white flowers in May and June, after which they develop into fruits (Szafoni 1991). *Rosa multiflora* is pollinated by generalist insect pollinators (Jesse *et al.* 2006) and its seeds are bird-dispersed, however the species can also reproduce vegetatively (Szafoni 1991). *Rosa multiflora* germinates in the spring (USGS) and under controlled conditions requires only 30 days cold stratification at 4.4 °C to reach maximum germination (Stewart & Semeniuk 1965) and can remain viable in the soil for over 20 years (USDA Forest Service 2006).

Rosa multiflora is native to eastern Asia, and descriptions of it can be found in China dating back to Chi Han's *Nan-fang ts'ao-mu chuang* from 304 C.E. (Li 1979). It is also quite common in Japan where it is considered a mid-secondary succession species within disturbed grasslands (Numata 1974). *Rosa multiflora* was first introduced by a plant collector, Thomas Evans of the East India Company into England in 1804 (Cox 1961) and spread throughout Europe as cultivars by 1817, (Hill 1983). This invader was introduced into North America from Japan in 1866 (Wyman, 1949 cited in Evans 1983) but may have been introduced prior to 1833 (Eaton 1833 cited in Hill 1983). *Rosa multiflora* was actively promoted and spread throughout North America for several reasons. It was endorsed as a low cost, living-fence to contain livestock and to act as a general farm fence. As such it was promoted for the money it could save over wire and fence posts as well as its utility as a bird food source and ease of transplantation (Steavenson 1946). Government agencies actively promoted its use and distribution for soil conservation, ground cover for small game (Hill 1983) and it was used in large amounts in the horticultural trade as a rootstock for commercial roses (Steavenson 1946).

Rosa multiflora currently inhabits all but the Rocky Mountain region, the southeastern coastal plain and southwestern deserts (Plant conservation Alliance's Alien

Plant Working Group 2005) and has become a major issue in many states, with thirty-one states having it reported as invasive as of 2006 (USDA Forest Service 2006). *R. multiflora*'s success as an invader is partially due to a lack of its native seed predator. The large amount of seeds produced in its native habitat are kept in check by its seed predator, the multiflora rose seed chalcid, *Megastigmus aculeatus nigroflavus*, whose larvae eat and destroy the seeds from the inside after being deposited there as eggs. Since *R. multiflora* was distributed largely by cuttings and not by seeds, the predator was not originally spread with *R. multiflora* across North America, although it has now become established in some areas of North America (Amrine 2002). Native to North America, rose rosette disease has also begun to infect *R. multiflora* populations, and is even being investigated as a biological control to keep *R. multiflora* in check (Epstein *et al.* 1997).

Within invaded areas, it can have varying rates of success and effects on the native community. *Rosa multiflora* can be quite successful in invading riparian areas, thickets, and woodlands but is much less successful in mature forests where the amount of light is greatly reduced (Robertson *et al.* 1994). Yet *R. multiflora* has been found to be one of the more prominent alien species to extend deep into forests due to its broad seed dispersal (Brothers and Spingarn 2002). *Rosa multiflora*'s effects on tree regeneration appears to be two-fold. While seed predation is increased around shrubs generating an overall negative affect on forest regeneration at high densities (Meiners and LoGiudice 2003; Meiners *In press*) it also protects seedlings from larger herbivores and was associated with greater seedling height and decreased mortality if a seed could survive, germinate and establish itself at the seedling stage around *R. multiflora* (Meiners & Martinkovic 2002). Other invasive shrubs have also shown a negative effect on tree seedlings yet still offer protection from larger herbivores, such as deer, if a seedling becomes established (Gorchov and Trisel 2003).

To investigate long-term invasion dynamics, the non-native *Rosa multiflora* was examined in a permanent plot study of abandoned agricultural land in the New Jersey Piedmont as the fields developed into forests. *Rosa multiflora* was chosen as a focal species due to its pervasiveness throughout the study site's successional history and its status as a regionally problematic species. With continuous data collection extending back to field abandonment, the study site provides a unique opportunity to follow the activity of *Rosa multiflora* invasion over the succession of an abandoned agricultural field to forest. These data were used to: 1) document the fine-scale temporal dynamics of invader spread and decline, 2) determine community and population level controls on invasion, and 3) assess the influence of abiotic factors on population dynamics.

Methods

Study site and data collection

The data collected on the invasion and establishment of *R. multiflora* was taken from a long-term, experimental study of successional dynamics within abandoned agricultural land in the Piedmont region of New Jersey (40°30' N, 74° 34' W), the Buell-Small Succession Study (BSS). Initiated in 1958, the study consists of 10 agricultural fields abandoned in pairs over a period of 8 years (Buell *et al.* 1971; Pickett 1982). Fields are distributed across a fairly level site with uniform silt loam soils (Ugolini 1964). Fields experimentally differed in season of abandonment (autumn or spring), last crop (hay field or row crops) and final plowing regime (plowed or intact vegetation) to assess the impact of different disturbance legacies on succession (Myster & Pickett 1990). The sizes of fields range from 0.5 ha to 1 ha. Eight of the fields are directly adjacent to an old growth mixed-oak forest. The BSS site has a subcontinental temperate climate with 1180 mm of rain distributed evenly throughout the year. The mean annual temperature is 11.5°C with a mean January temperature of -1.3°C and a mean July temperature of 23.7°C as taken from the New Brunswick, New Jersey 3SE weather station (# 286055; 40°28' N, 74°26' W, elev. 26.2 m) located 12 km east of the BSS site (NCDC Annual Climatological Summary, NOAA).

Within each field, 48 permanently-marked 0.5 m x 2.0 m plots were established immediately after abandonment. The 48 plots are arranged in a regular pattern which varies somewhat with the shape of the fields. In each year (alternate years since 1979), the percent cover of all species present in each plot was recorded. As plants often have overlapping canopies, total plant cover may greatly exceed 100% within each plot. These data represent the longest continuous data set on post-agricultural successional change known. With continuous data collection extending back to field abandonment,

the BSS provides a unique opportunity to follow the activity of *Rosa multiflora*.

Nomenclature follows Gleason & Cronquist (1991).

Data analysis

Data analyses were restricted to years 0-40 as there was not complete replication across all fields past this period due to variation in abandonment time. Furthermore; it is around this age that rose rosette disease had begun to appear within the site (first observed in 1999, SJ Meiners, personal observation). As fields were abandoned over an 8-year period, data analyses involving time were conducted on field age rather than calendar year. All analyses were conducted using SPSS 13.0 (SPSS Inc., Chicago, IL).

Population dynamics

Gross population changes and the coefficient of variation were summarized across all 10 fields based on the average cover per plot and percent frequency within each field. To maintain even replication among fields, data collected in alternate years were condensed into two-year intervals (e.g. data from years 39 and 40 were condensed into one sample). To explore those temporal changes in more detail, plot colonization and extinction rates were also calculated for each field. Data collected in alternate years was adjusted to reflect annual colonization and extinction rates (e.g. 2 colonization events over two years was coded as one in each year). Net changes in plot occupancy (colonizations – extinctions) were also calculated. To assess spatial and temporal heterogeneity in the *R. multiflora* invasion, the coefficient of variation across the 10 fields was calculated for the total cover of *R. multiflora* for years 0 through 40. Temporal changes in these values were then quantified with a curve fitting procedure.

Limits to population growth

To understand biotic and abiotic limitations on the growth and decline of *R. multiflora*, two windows of the BSS data were examined. These windows were determined based on *R. multiflora* cover and to represent two nearly equal periods of population expansion (years 18-28) and decline (years 32-40) respectively. This generates roughly equivalent window lengths, comparable to similar analyses utilizing the BSS data (e.g. Yurkonis *et al.* 2005).

To determine the influence of canopy cover on *R. multiflora* spread and persistence, tree cover (summed across all species) was calculated for each plot over time. All plots with greater than 5% cover of *R. multiflora* were considered to have established *R. multiflora* for that period. This threshold avoids the influence of seedling plants in the analysis. Plots were separated into those with open and closed forest canopies based on total tree cover. Plots with a minimum of 95% tree cover were considered closed canopy plots, while those with less were considered open canopy plots. A Chi-square analysis relating canopy closure to established *R. multiflora* was run for data from years 18, 28 and 40.

Plant community controls on the spread of *R. multiflora* were assessed with multiple regression models for the change in *R. multiflora* cover for the windows 18-28 and 32-40. To assess the impacts of individual species on *R. multiflora*, the cover of the 10 most abundant resident species at the beginning of the period (years 18 and 32) were included in the model. Species richness, total tree cover and total plot cover were also included to assess community level controls on plant performance. All regression models were run forwards, backwards and stepwise, though all converged on the same final model for both periods. Multicollinearity was not an issue in this analysis as variance inflation ratios were consistently 1.236 or less. Besides the species directly tested, other less common species may have important positive or negative effects on *R.*

multiflora. However, these species did not appear in sufficient numbers for statistically valid tests.

The average rainfall during the summer (June through August) for years 1957 to 2005 was determined and the deviation of each growing season from that mean was calculated. Deviation from average rainfall was correlated with the number of plot colonization and extinction events within each field. This was done for years 9-28, when *R. multiflora* was expanding in the site. This analysis was repeated using the prior growing season's rainfall.

Results

Gross population trends

Two years after abandonment, the first of the fields showed *Rosa multiflora* coverage with the average field being invaded within six to seven years. Overall, *R. multiflora* had an extended lag period when invading a newly abandoned field, a rapid growth and invasion period, and an eventual decline as succession continued towards a forested system. During the initial lag period, no more than 4% of the average plot was covered by *R. multiflora* until the field reached an age of nine years where *R. multiflora* cover began to increase sharply in coverage until around age 28, when the mean plot cover was almost 30%. Even at the population peak, individual plot cover varied dramatically, ranging from 0 to 100%. After a brief four year plateau at this peak, *R. multiflora* coverage declined each consecutive year into the mid-twenties by year 40 (Figure 1a). Frequency showed largely the same temporal response as cover, with several differences. A lag period, with a smoother transition into the growth phase extended until a peak of nearly 75% frequency was reached at age 32 (Figure 1b). As with cover, a decrease followed year 32, but it was a more gradual decline. The percent of occupied plots followed a pattern similar to frequency with a lag and sharp increase until 76% of plots were occupied, followed by a steady decrease so that by year 40 only 64% of plots were occupied.

Heterogeneity among fields in *R. multiflora* cover was high early in the invasion and decreased rapidly as the species increased in abundance across the site. As *R. multiflora* cover declined after year 32, heterogeneity increased, with some fields experiencing rapid declines in cover while others persisted (Figure 2). The best fit equation was $\text{cover} = 558.98 \times \text{age}^{-0.7817}$, $R^2=0.9272$.

Colonization and extinction

Colonization rates started very low after abandonment but increased linearly until a maximum was reached in year 19 (Figure 3a). After this peak, plot colonization decreased dramatically, leveling off at around three colonization events per field, but with annual variation around that amount. Extinction events had a more consistent and gradual increase over time, but had a similar lag in the beginning, when the population was low (Figure 3b). The net annual change in the number of plots occupied (colonization - extinction) was positive and increasing until year 19, at which point net colonization decreased, although it remained positive. Extinction events exceeded colonization events in most years after age 32 (Figure 3c).

Trees and growth windows

Tree cover was very low for the first 10 years after abandonment and then experienced a sharp exponential increase in growth until age 30 when the rate of increase slowed down (Figure 4). When compared with the increases in *R. multiflora*, tree cover was remarkably similar for the first 18 years. After this tree cover continued to increase at a much greater rate than *R. multiflora* cover.

Tree dominated plots, those with $\geq 95\%$ tree cover, did not affect patterns of *R. multiflora* expansion, but they were related to population collapse. In years 18 and 28, plots with established *Rosa* plants ($\geq 5\%$ cover) were independent of canopy cover (year 18 - $\chi^2=1.77$, $df=1$, $P=0.674$; year 28 - $\chi^2=1.72$, $df=1$, $P=0.190$), but once *R. multiflora* cover began to decline, in year 40, established *R. multiflora* plants were much less likely to occur in tree dominated plots ($\chi^2=8.07$, $df=1$, $P=0.004$).

Constraints on *Rosa* growth and expansion

From years 18 to 28, change in *Rosa multiflora* cover was significantly associated with several factors (Table 1, $F_{5,474}=16.37$, $P<0.001$, $R^2=0.15$). *Acer rubrum* and *Juniperus virginiana* depressed rose cover, while *R. multiflora* cover was positively associated with *Lonicera japonica* and *Aster pilosus* (Table 1a). Interestingly, species richness was positively associated with increases in *R. multiflora* cover over this time period. The remaining species included in the regression model, *Hieracium caespitosum*, *Fragaria virginiana*, *Cornus florida*, *Toxicodendron radicans*, *Poa pratensis*, *Solidago juncea*, and *Euthamia graminifolia* did not show an association with *R. multiflora* growth. Surprisingly, during this stage of succession total cover was also not associated with *R. multiflora* growth.

For the regression model of the window 32-40, when the *R. multiflora* population was in decline, change in *R. multiflora* cover was significantly associated with several species and community metrics. Change in *Rosa multiflora* cover was positively associated with *Juniperus virginiana*, *Acer rubrum*, *Toxicodendron radicans*, *Cornus florida*, and *Solidago rugosa* (Table 1b). As when *R. multiflora* cover was increasing, species richness was positively associated with the change in *Rosa* cover. The only negative influence on *R. multiflora* cover was total cover of all species within each plot. *Lonicera japonica*, *Juglans nigra*, *Parthenocissus quinquefolia*, *Eupatorium perfoliatum*, and *Acer negundo* were the other species tested and were not associated with *Rosa multiflora* during this period of decline.

Rainfall

The strongest association between the population dynamics of *R. multiflora* was with summer rainfall (June-August) of the previous year (Figure 5). The number of colonization events during the period of expansion were correlated with the previous

summer's deviation from average rainfall for all fields ($R=0.162$, $P=0.022$). Extinction events were negatively correlated with the previous summer's deviation from average summer rainfall ($R=-0.176$, $P=0.013$). Net colonization rates (annual colonization – extinction) were also positively correlated with the previous summer's rainfall ($R=0.260$, $P<0.001$). Colonization, extinction, and net colonization were all not correlated with the current year's is rainfall (all $P > 0.33$).

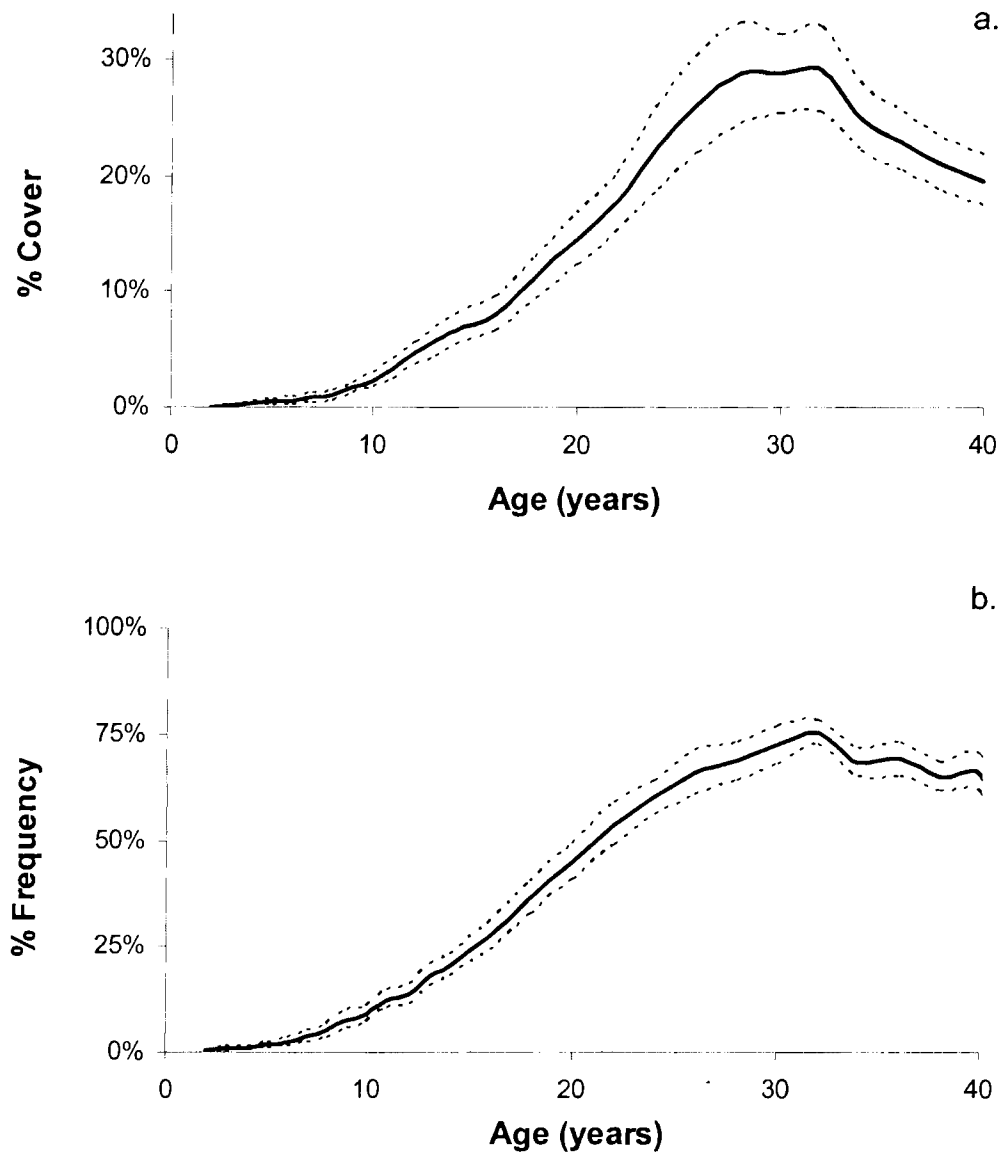


Figure 1 Average percent cover (a) and frequency (b) of *Rosa multiflora* over the forty years since abandonment. Dotted lines represent +/- SE.

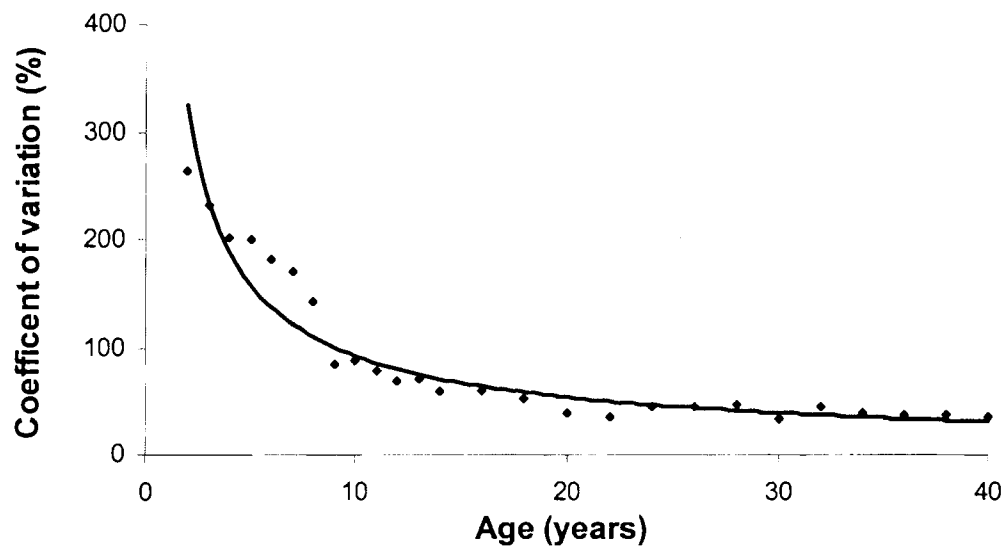
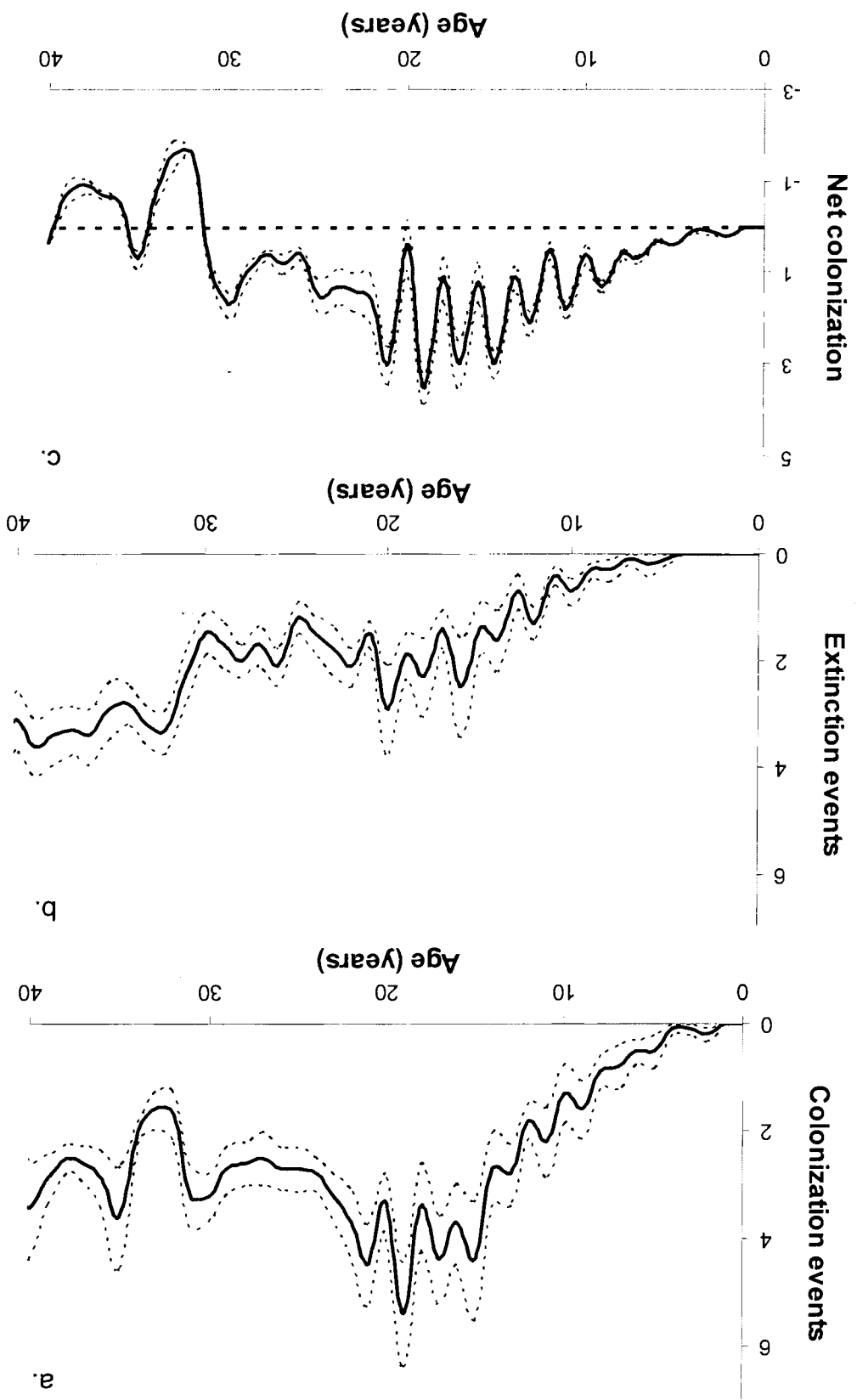


Figure 2 The coefficient of variance for ages 0-40 since abandonment. The first appearance of *R. multiflora* was in year 2 in two fields.

Figure 3 Mean colonization (a) and extinction (b) events for the ten study fields over the forty years since abandonment. The net colonization rate (c) where negative values are years where mean extinction events outnumber mean colonization events, resulting in a decline in plots occupied. There is a dashed reference line at zero for net colonization rate and dotted lines represent +/- SE for all graphs.



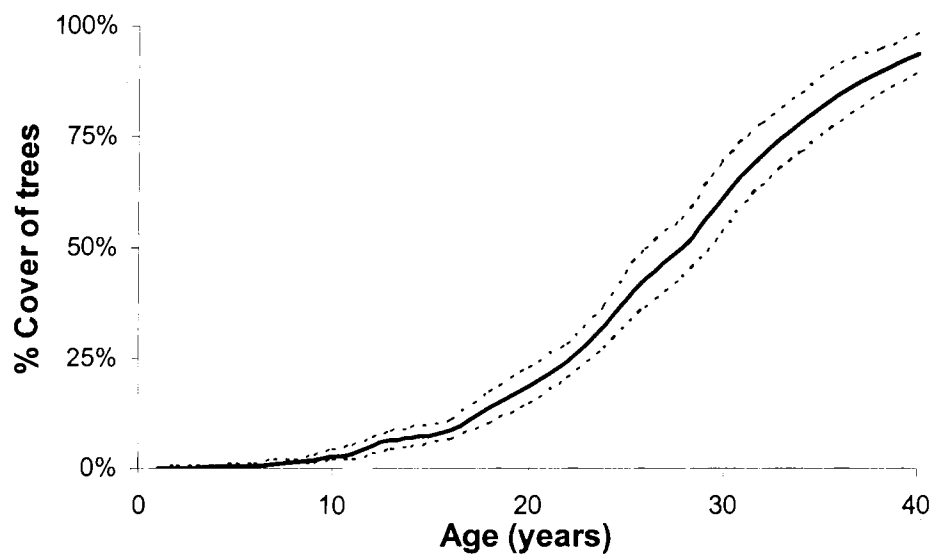


Figure 4 Percent cover of the average plot by trees over the 40 years since abandonment.

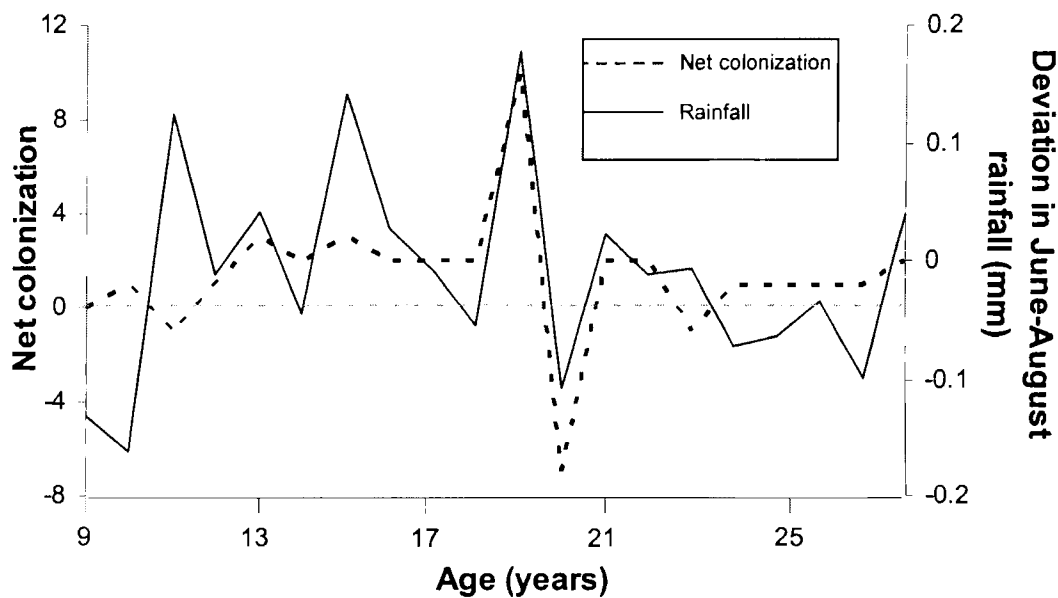


Figure 5 An example of previous summers (June-August) rainfall influences on net colonization during the population expansion in years on 9-28. This example is for field C3, net colonization is on the left y-axis and is the heavy-dashed line, the deviation from the average June-August rainfall for the previous year is on the right y-axis and represented with the thin line. A reference line for zero net colonization is shown.

Table 1 (a) Results for the growth window 18-28 on a regression model, run forward. $R^2 = 0.147$. Model investigates change in *R. multiflora* cover against the top 10 species at year 18, total cover, and species richness.

Model term	β	Std. error	P
Intercept	-7.623	6.105	0.212
Richness	1.451	0.388	0
<i>L. japonica</i>	0.164	0.057	0.004
<i>A. rubrum</i>	-0.262	0.098	0.008
<i>J. virginiana</i>	-0.696	0.177	0
<i>A. pilosus</i>	0.995	0.208	0

(b) Results for the growth window 32-40 on a regression model, run forward. $R^2 = 0.158$. Model investigates change in *R. multiflora* cover against the top 10 species at year 32, total cover, and species richness.

Model term	β	Std. error	P
Intercept	-3.702	6.416	0.564
Richness	1.031	0.25	0
Total cover	-0.191	0.027	0
<i>J. virginiana</i>	0.142	0.06	0.019
<i>A. rubrum</i>	0.194	0.047	0
<i>T. radicans</i>	0.223	0.073	0.002
<i>C. florida</i>	0.159	0.049	0.001
<i>S. juncea</i>	0.495	0.125	0

Discussion

The long-term population dynamics of *Rosa multiflora* revealed a variety of controls on fine-scale turnover that resulted in the overall population change. Though the species invaded the fields very early after abandonment, *Rosa multiflora* did not begin to increase explosively until the successional fields were older than ten years, reaching a peak by year 32. Beyond this peak, the cover and the net colonization rate declined. Details of the lag time, population expansion, and population decline are addressed individually below .

With the ability to follow colonization and extinctions events on a small temporal scale, the turnover of *Rosa multiflora* within plots could be documented. Even when fields were heavily invaded, local extinctions were constantly occurring. Likewise, and of more interest to *Rosa multiflora* management, during population decline, colonization events were constantly occurring. Even in decline, *R. multiflora* was becoming established in new plots allowing it to take advantage of disturbances to the community, especially within the tree canopy. This also suggests that as succession towards a closed-canopy forest proceeds, *R. multiflora* will persist. It will also most likely remain established at edges, where it has found to be successful regardless of successional stage due to the high light and seed availability (Ambler 1965; Robertson *et. al* 1994; Brothers and Spingarn 2002). While this study was conducted prior to its arrival at the site, rose rosette disease may accelerate the rate of decline of this species and shift it to occur earlier in succession.

Lag time, years 0-9

Rosa multiflora exhibited a lag time of nine to ten years before an explosion in frequency and cover occurred, even though the species appeared as early as year two in some fields. Competition from early successional plants as well as limited seed dispersal are

the two most likely factors generating this time lag. At the BSS study site, *R. multiflora* was found to be one of the top three bird-dispersed seeds (McDonnell 1986) suggesting seed production and bird dispersal would not be limiting factors for *R. multiflora* expansion at the site once established, however the behavior of bird dispersers may be limiting. Within early successional habitats, taller vegetation that act as perches recruit significantly more bird-dispersed seedlings around their base (McDonnell 1986), so the amount, location, and patterns of these perch sites would effect initial dispersal. As these perch sites would be limited early in succession, dispersal of *R. multiflora* may be limited despite its abundance in the surrounding landscape at the time of abandonment.

As the fields aged, propagule pressure would have increased as both as the number of perch sites increased and as *R. multiflora* shrubs within the fields became reproductive, leading to an explosion in the population. In addition, the change to a growth phase may be due to the microsite availability coupled with increasing propagule pressure (Huebner and Tobin 2006) as well as the high turnover of early successional plants. During this stage, tree cover had no effect on *R. multiflora* as the number and size of trees were very small. The initially small number of *R. multiflora* occupied plots did not allow for statistically strong evaluation of the relationship between *R. multiflora* and other species and rainfall during this stage.

Population expansion, years 9-28

Rosa multiflora rapidly increased in cover to become one of the most dominant plants in the study site, with the average plot having just under 30% cover (range 0-100%). As a shrub it is no surprise that *R. multiflora* took several years to become established as it takes years to grow and be able to produce a sizable number of seeds. It is during this population expansion that rainfall was found to have its most prevalent impact. Rainfall in the previous year had a large effect on the *R. multiflora* establishment and mortality

while current year's rainfall was not correlated with population dynamics. The previous summer's rainfall showed a strong positive correlation with net colonization. It appears that rainfall increased seed production, so that seed availability the following year would be greater, increasing colonization. This linkage with rainfall may be a time delayed example of the fluctuating resource availability theory of invasion (Davis *et al.* 2000) where greater water availability enhanced reproduction of the invader, increasing its propagule pressure in the following year. Greater rainfall also increased the over-winter survival of established plants during this period.

Several species and community metrics appear to be important to the population dynamics of *R. multiflora* during the second half of the growth phase (years 18-28). Most notably, *R. multiflora* grew better in plots with higher species richness and was inhibited by the trees *Acer rubrum* and *Juniperus virginiana* during its population expansion. During the same period it's growth was positively associated with cover of *Lonicera japonica* and *Aster pilosus*. It has been previously found that *Lonicera japonica* decreases *R. multiflora* colonization rates within heavily invaded plots (Yurkonis & Meiners 2004), yet during the period of 18-28 post-abandonment, there was a positive correlation with increase in cover, perhaps due to the climbing nature of both species. At this point tree cover did not show any correlation with *R. multiflora* performance, however canopy closure had not yet occurred during this stage. The study site seemed open to *R. multiflora* colonization and growth until canopy closure became a limiting factor.

Population decline, years 32-40

The balance between colonization and extinction events never shifted towards extinctions until year 32, which is also the year plot cover began to decrease. Most likely, shade associated with canopy-closure and was the dominant limiting factor later in

succession. As the average plot approached 90% tree cover, *R. multiflora* was well on the decline. During population decline, the increased number of plots available to *R. multiflora* did not lead to an increase in colonization, even temporarily, further suggesting that lack of light plays a large role in the decrease of *R. multiflora*. At this time, rainfall was no longer linked with population dynamics. In general, older forests tend to produce lower exotic plant abundance due to low light levels produced by the canopy and shade tolerant species in the understory (Robertson *et al.* 1994). *Rosa multiflora* appears to be under these light constraints, especially since the number of open plots had grown and propagule pressure would have remained high.

As trees became the main contributor to overall cover, it is no surprise that *R. multiflora* presence showed a negative association with tree dominated plots during population decline, yet surprisingly its cover was not associated with total tree cover. This is most likely due to differential influences of individual tree species. During population decline, several tree species had a positive correlation with *R. multiflora*, despite the overall negative influence of canopy cover. In plots with these species, *R. multiflora* was better able to persist than elsewhere. These species were associated with higher light levels or with the ability of *Rosa multiflora* to reach the canopy. *Juniperus virginiana* has a narrow, conical canopy, allowing light penetration down the sides of the tree. *Rosa multiflora* tends to climb on *Acer rubrum* and *Cornus florida*, allowing it to reach full sun in the canopy. Since *J. virginiana* and *A. rubrum* both inhibit *R. multiflora* during population expansion, it suggests that *R. multiflora* has difficulty establishing near these species, but can persist once established near them.

During both population growth and decline, *R. multiflora* abundance was positively associated with species richness. This positive correlation between invasive species and richness (Levine and D'Antonio 1999; Robinson *et al.* 1995; Wiser *et al.* 1998; Lonsdale 1999) and specifically with *R. multiflora* (Meiners *et al.* 2004) has been

noticed in previous studies. It appears that species rich areas are very susceptible to invasion, either due to resource abundance, openness, or other properties of species rich areas.

Persistence in forested habitats

Although *R. multiflora* is successful in invading established forests, it does not become dominant as it does in abandoned fields. Non-native shrubs, including *R. multiflora*, have greater % cover near the edges as edges tend to share characteristics with disturbed habitats (Brothers and Spingarn 1992; Hunter and Mattice 2002; Lundgren et al. 2004). *Rosa multiflora* success in invading established and older forests is poor compared to its invasiveness in riparian forests, edges and other open habitats. Mature forests may also possess shade tolerant understory species, further reducing light (Robertson et al. 1994). Within the study site, *R. multiflora* was present in older successional fields and neighboring woods as well as along thickets and roadsides at the beginning of the study. Despite this availability within the landscape, *R. multiflora* showed no signs of becoming aggressive within the old growth forest (Ambler 1965). More recent observations of the old-growth forest continue to show sporadic *R. multiflora* individuals, but never to the extent seen in abandoned fields (SJ Meiners, personal communication). It seems likely that this invader will persist indefinitely within these forests, periodically expanding to capitalize on openings within the forest canopy. *R. multiflora* may continue to impact the plant community indefinitely.

Conclusions and management implications

Detailed documentation of the population dynamics of *R. multiflora* at this site has yielded several interesting results. Despite the severity and apparent permanence of this invasion at its peak, there was constant turnover during all stages of the invasion.

This turnover should provide opportunities for resident species to persist during the invasion, but also shows the ability of *R. multiflora* populations to rebound following disturbances. The increased growth of *R. multiflora* in species rich plots suggests that beyond shading, there is little control of the recipient plant community to resist this invasion and that invasion impacts on the community may be strong (Meiners *et al.* 2001). In sites where succession proceeds unimpeded to a forested system, the invasion should be limited by shading. In older forests *R. multiflora* should remain at manageable numbers if disturbances to the canopy are kept to a minimum. However, canopy opening events, particularly those preceded by relatively wet years, may allow the population to expand again. If *R. multiflora* were to become abundant enough to reduce tree establishment, the species may arrest succession at the shrub stage.

Detailed, long term studies of pervasive invaders offer greater understanding of their role within communities as well as a greater comprehension of the biotic and abiotic factors that influence their populations. While not all studies can be as lengthy and detailed as the data presented here, any measures of population dynamics, however limited, can dramatically improve our understanding of invasion and should be incorporated into monitoring schemes. This information can be critical to tailoring management and containment strategies as well as to setting management priorities.

LITERATURE CITED

- Ambler MA (1965) Seven alien plant species. William L. Hutcheson Memorial Forest Bulletin 2: 1-8
- Amrine Jr JA (2002) Multiflora Rose In: Van Driesche R *et al.* Biological Control of Invasive Plants in the Eastern United States, USDA Forest Service Publication FHTET-2002-04 p. 413-434
- Bartha S, Meiners SJ, Pickett STA and Cadenasso ML (2003) Plant colonization windows in a mesic old field succession. *Applied Vegetation Science* 6: 205-212
- Bellemare J, Motzkin G and Foster, DR (2002) Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *Journal of Biogeography* 29: 1401-1420
- Brothers TS and Spingarn A (1992) Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conservation Biology* 6: 91-100
- Buell MF, Buell HF, Small JA and Siccama TG (1971) Invasion of trees and secondary succession on the New Jersey Piedmont. *Bulletin of the Torrey Botanical Club* 98; 67-74
- Burke MJW and Grime JP (1996) An experimental study of plant community invasibility. *Ecology* 77: 776-790
- Byers JE, Reichard S, Randall JM, Parker IM, Smith CS, Lonsdale WM, Atkinson IAE, Seastedt TR, Williamson M, Chornesky E and Hayes D (2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* 16: 630-640
- Cox EHM (1961) Chapter II The honourable east India Company and China. In *Plant Hunting in China*, pp 46-48. Oldbourne Press, London, England

- Davis MA, Grime JP and Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *The Journal of Ecology* 88; 528-534
- Devine RS (1998) Alien Invasion: America's Battle with non-native animals and plants. National Geographic Society, Washington DC. p. 6
- Drake JM and Lodge Dm (2006) Allee effects, propagule pressure and the probability of establishment: risk analysis for biological invasions. *Biological Invasions* 8: 365-375
- Eaton A (1833) Manual of botany, plants of North America. Oliver Steele, Albany. p. 401
- Epstein AH, Hill JH and Nutter FW Jr (1997) Augmentation of rose rosette disease for biocontrol of multiflora rose (*Rosa multiflora*). *Weed Science* 45; 172-178
- Evans JE (1983) A literature review of management practices for multiflora rose (*Rosa multiflora*). *Natural Areas Journal* 3: 6-15
- Gleason HA and Cronquist A (1991) Manual of vascular plants of northeastern United States and adjacent Canada. New York Botanical Garden, Bronx.
- Gorchov DL and Trisel DE (2003) Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. *Plant Ecology* 166: 13-24
- Gross KL (1980) Colonization by *Verbascum Thapsus* (Mullein) of an old-field in Michigan: experiments on the effects of vegetation. *The Journal of Ecology* 68: 919-927
- Hill RJ (1983) Multiflora rose, *Rosa multiflora* Thunb. Regulatory Horticulture Weed Circular No 6. Pennsylvania Department of Agriculture, Bureau of Plant Industry
- Huebner CD and Tobin PC (2006) Invasibility of mature and 15-year-old deciduous forests by exotic plants. *Plant Ecology* 186: 57-68

- Hunter JC and Mattice JA (2002) The spread of woody exotics into the forests of a northeastern landscape, 1939-1999. *Journal of the Torrey Botanical Society* 129: 220-227
- Hutchinson TF and Vankat JL (1997) Invasibility and effects of amur honeysuckle in southwestern Ohio forests. *Conservation Biology* 11; 1117-1124
- Jesse LC, Moloney KA and Obrycki JJ (2006) Insect pollinators of the invasive plant, *Rosa multiflora* (Rosaceae), in Iowa, USA. *Weed Biology and Management* 6: 235-240
- Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D and Reich P (2002) Biodiversity as a barrier to ecological invasion. *Nature* 417; 636-638
- Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E and Groth J (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundance and diversity. *Ecology Letters* 2; 286-293
- Levine JM (2000) Species diversity and biological invasions: relating local process to community pattern. *Science* 288: 852-854
- Levine JM and D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87: 15-26
- Li, Hui-Lin. 1979. In: Nan-fang ts'ao-mu chang; A forth Century Flora of Southeast Asia p. 36. The Chinese University Press, Shatin, N.T., Hong Kong
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invisibility. *Ecology* 80: 1522-1536
- Luken JO and Thieret JW (1996) Amur honeysuckle, its fall from grace. *BioScience* 46: 18-24

- Lundgren MR, Small CJ and Dreyer GD (2004) Influence of land use and site characteristics on invasive plant abundance in the quinebaug highlands of southern New England. *Northeastern Naturalist* 11: 313-332
- McDonnell MJ (1986) Old field vegetation height and the dispersal pattern of bird-disseminated woody plants. *Bulletin of the Torrey Botanical Club* 113: 6-11
- Meiner SJ, Pickett STA and Cadenasso ML (2001) Effects of plant invasions on the species richness of abandoned agricultural land. *Ecography* 24: 633-644
- Meiners (*In Press*) Apparent competition: an impact of exotic shrub invasion on tree invasion. *Biological Invasions*
- Meiners SJ and LoGiudice K (2003) Temporal consistency in the spatial pattern of seed predation across a forest – old field edge. *Plant Ecology* 168: 45-55
- Meiners SJ and Martinkovic MJ (2002) Survival of and herbivore damage to a cohort of *Quercus rubra* planted across a forest-old-field edge. *American Midland Naturalist* 147: 247-255
- Meiners, S.J., Cadenasso, M.,L. & Pickett, S.T.A. (2004) Beyond biodiversity: individualistic controls of invasion in a self-assembled community. *Ecology Letters*, 7, 121-126
- Myster RW and Pickett STA (1990) Initial conditions, history and successional pathways in ten contrasting old fields. *American Midland Naturalist* 124; 231-238
- NCDC Annual Climatological Summary, NOAA
- Numata EM (1974) Chapter 2 Origin and characteristics of Japan's flora and Chapter 4 Grassland vegetation. In: *The Flora and Vegetation of Japan*, pp. 65, 131. American Elsevier Publishing Company, Inc., New York
- Parker IM, Simberloff D, Lonsdale WM, Goodall K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE and Goldwasser L (1999) Impact: towards

- a framework for understanding the ecological effects of invaders. *Biological Invasions* 1:3-19
- Pickett STA (1982) Population patterns through twenty years of oldfield succession. *Vegetatio* 49: 45-59
- Plant conservation Alliance's Alien Plant Working Group 2005 , *Weeds Gone Wild: Alien Plant Invaders of Natural Areas* <http://www.nps.gov/plants/alien> Accessed on 18 June 2007
- Rankin WT and Pickett STA (1989) Time establishment of red maple (*Acer rubrum*) in early oldfield succession. *Bulletin of the Torrey Botanical Club* 116: 182-186
- Robertson DJ, Robertson MC and Tague T (1994) Colonization dynamics of four exotic plants in a northern piedmont natural area. *Bulletin of the Torrey Botanical Club* 121: 107-118
- Robinson GR, Quinn JF and Stanton ML (1995) Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* 76: 786-794
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, and Weller SG (2007) The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305-332
- Stevenson HA (1946) Multiflora rose for farm hedges. *The Journal of Wildlife Management* 10: 227-234
- Stewart RN and Semeniuk P (1965) The effect of the interaction of temperature with after-ripening requirement and compensation temperature on germination of seed of five species of *Rosa*. *American Journal of Botany* 52: 755-760
- Szafoni RE (1991) Vegetation management guideline: multiflora rose. *Natural Areas Journal* 11: 215-216

- Ugolini FC (1964) Soil development on the red beds of New Jersey. William L. Hutchenson Memorial Forest Bulletin 2; 1-34
- United States Department of Interior (2003) Interior secretary's science advisor calls for new actions to combat invasive species
- USDA Forest Service, Forest Health Staff (2006) Weed of the week: Multiflora rose
Rosa multiflora Thunb. Ex Murr. Newtown Square, PA
- USGS, Northern Prairie Wildlife Research Center. Species abstracts of highly disruptive exotic plants at Effigy Mounds National Monument, *Rosa multiflora*.
<http://www.npwrc.usgs.gov/resource/plants/exoticab/effirosa.htm> Accessed on 18 June 2007
- Wilcove DS, Rothstein D, Dubow J, Phillips A and Losos E (1998) Quantifying threats to imperiled species in the United States: assessing the relative importance of habitat destruction, alien species, pollution, overexploitation, and disease. *BioScience* 48: 607-615
- Wiser SK, Allen RB, Clinton PW and Platt KH (1998) Community structure and forest invasion by an exotic herb over 23 years. *Ecology* 79: 2071-2081
- Woods KD (1993) Effects of invasion by *Lonicera tartarica* L. on herbs and tree seedlings in four New England forests. *American Midland Naturalist* 130; 62-74
- Wyckoff PH and Webb SL (1996) Understory influence of the invasive Norway maple (*Acer platanoides*). *Bulletin of the Torrey Botanical Club* 123; 197-205
- Wyman D (1949) Shrubs and Vines for American Gardens. MacMillan Co. New York p. 613
- Yurkonis KA and Meiners SJ (2004) Invasion impacts local species turnover in a successional system. *Ecology Letters* 7: 764-769
- Yurkonis KA, Meiners SJ and Wachholder BE (2005) Invasion impacts diversity through altered community dynamics. *Journal of Ecology* 93: 1053-1061