

Spring 2008

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BreAnne M. Nott
Eastern Illinois University

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Edge Influence on Reproductive Success of *Symphoricarpos orbiculatus*

by

BreAnne M. Nott

HONORS THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

BACHELOR OF SCIENCE IN BIOLOGICAL SCIENCES WITH HONORS

AT EASTERN ILLINOIS UNIVERSITY

CHARLESTON, ILLINOIS

April, 2008

I hereby recommend that this Honors Thesis be accepted as fulfilling this part of the undergraduate degree cited above:

Thesis Director

Date

Honors Program Director

Date

EDGE INFLUENCE ON REPRODUCTIVE SUCCESS OF *SYMPHORICARPOS*
ORBICULATUS

By BreAnne M. Nott

Eastern Illinois University, Department of Biological Sciences, Charleston, IL

Abstract

With continued forest fragmentation, edge effects play an important role in shaping the structure and composition of plant communities. Some forest plant species exhibit increased abundance at forest edges, while other species have a negative edge response. Despite well-documented edge effects, there are few studies that document the underlying effects on population dynamics of individual species that result in edge responses. Two mechanisms may generate differential distribution of a species across an edge. Edges may 1) alter population demographics by influencing the plant's uptake and allocation of resources, or may 2) influence the spatial pattern of seed dispersal. Coral berry (*Symphoricarpos orbiculatus*) is a fleshy-fruited native shrub present at both forest edge and interior habitats. In order to assess spatial demographic responses of *S. orbiculatus*, reproductive success was determined for individuals occurring along transects perpendicular to the forest edge. Following light gradients, population density of *S. orbiculatus* declined with distance into the forest, with few individuals occurring eight meters into the forest. Similarly, total fruit production by each individual was positively correlated with light intensity and negatively correlated with distance from the edge. The quality of offspring produced was unaffected by the edge as the weight of individual seeds and fruits did not change significantly with distance from the edge. Seeds produced were ~99% viable across the entire population with no edge effects. For this species, increased growth and reproductive

performance at forest edges appears sufficient to generate the observed spatial pattern of the species. With increasing forest fragmentation, these data suggest that populations of this understory shrub could see rapid growth at edges and that the high seed production of edge plants may increase seed availability even beyond edges.

Introduction

An edge is a landscape element often described as a boundary or transition zone between different habitat types (Wales 1972; Chen et al 1992). The increased diversity often associated with these transition zones has been called the edge effect principle (Harris 1988). Changes in vegetation at edges are a well-documented phenomenon where many plant species exhibit either positive or negative spatial associations with the edge (Matlack 1994; Jules 1998; Jules and Rathcke 1999; Meiners and Pickett 1999). This spatial heterogeneity in plant abundance can be attributed to two general mechanisms functioning at the population scale: differential plant performance and differential dispersal.

Edges generate abiotic heterogeneity in forests which may generate subsequent heterogeneity within the vegetation. Forest edges have been shown to affect the plant community by altering the availability of resources, changing the overall microclimate, and shifting competitive outcomes between plant species (Matlack 1993; Jules 1998; Jules and Rathcke 1999; Bach et al. 2004). Edges generate complex gradients of changing abiotic conditions, such as light intensity, air temperature, wind speed, humidity, and soil moisture (Wales 1972; Williams-Linera 1990; Brothers and Spingarn 1992; Matlack 1994; Cadenasso and Pickett 2001). The greater density of trees at edges further alters the environment by affecting shrub cover, sapling growth, and increasing variability in canopy cover. These characteristics

lead to variability in light and rainfall penetration that can influence community composition (Matlack 1993,1994; Chen et al. 1992; Goldblum and Beatty 1999; Meiners and Pickett 1999). Other factors influenced by edges include the steady transition of climatic factors from the forest edge to interior. Forest interiors more homogeneous light intensity than edges (Chen et al 1992). The consistently low light levels of forest interiors restricts many species to regenerate only in the forest gaps, a natural source of environmental heterogeneity within a forest (Matlack 1994; Cadenasso and Pickett 2001). Gap regenerating species are opportunistic species by nature, and would be expected to rapidly colonize and spread within locations with increased light availability. These opportunistic, gap-regenerating species would also be expected to proliferate in edge systems.

Alteration of plant performance is one mechanism that can lead to large changes in vegetation associated with edges. Generally the forest edge consists of a dense wall of understory vegetation followed by a relatively homogenous interior community (Williams-Linera 1990, Cadenasso and Pickett 2001). Selective assortment of individuals can be due, at least in part, to climate conditions in each microhabitat. Variation in climatic conditions across the edge gradient can lead to allocation and demographic variation within populations including effects on seed set, leaf area, and survivorship of seeds that can produce spatial variation in population density (Jules 1998). Some species reach peak densities at the edge, while others peak in the interior indicating that climatic conditions differentially influence distribution of individual species along the gradient (Wales 1972, Harris 1988, Williams-Linera 1990, Chen et al. 1992, Goldblum and Beatty 1999, Matlack 1994).

Edge vegetation, while influencing climatic conditions, can limit dispersal to the forest edge and become an effective barrier to seed dispersal affecting spatial distribution of plant

communities. Edge vegetation may likewise function as a buffer or refuge for many dispersers as well as a collector of seeds leading to heterogeneity in individual spatial distributions (Cadenasso and Pickett 2001). High densities of animal dispersers in the transition zone increase the amount of seeds deposited at edges leading to an increase in plant density. Plant-animal interactions also increase due to the abundance of plant species deposited at the edge (Chen et al. 1992; Weathers et al. 2001; Meiners and LoGiudice 2003).

Most forest edge studies focus on changes across the entire plant community to document edge responses, often resulting in a structural edge response. However, individual plant species might exhibit individualistic edge responses that can be explained by population-level responses. By examining static community patterns across an edge, detailed mechanisms for population demographics are often missed.

The purpose of this research was to assess the population-level characteristics of a native forest shrub to explain the species' edge response. *Symphoricarpos orbiculatus* (Coral berry) is often abundant at forest edge throughout Midwestern oak-hickory forests. In this study, *S. orbiculatus* was examined to address three main objectives: 1) document the spatial response of a native forest species in relation to forest edges, 2) assess the response of plant size and population density along the forest edge gradient, 3) evaluate the potential for reproductive variation to generate spatial patterns associated with the edges.

Methods

Study site-This study was conducted at Warbler Woods Nature Preserve Coles County, Illinois. The site is a heavily dissected upland which contains 18.6 ha of former pasture (last mown in 1996) on the level ridge tops surrounded by mature oak-hickory forests on the steeper slopes.

Due to the irregular nature of the forest field border, this site contained over 4500 m of forest edge. In October of 2005 through 2008, the pasture land was still dominated by remaining pasture grasses.

Study Species-*Symphoricarpos orbiculatus* is a native, understory shrub that spreads clonally through a series of rhizomes. This small shrub (typically less than 1m in height) is slender with arching branches containing clusters of purple drupes on the abaxial surface. Seeds of *S. orbiculatus* have underdeveloped embryos which require a stratification treatment in order to germinate (Hidayati et al. 2001). *S. orbiculatus* abundant along forest edges and in open forest understory.

Sampling design-Twelve 10m transects were spread at least 60 m apart and throughout the site. For each transect, the position of the forest edge was defined as the base of the first trees with ≥ 10 cm DBH. Individuals were census along each meter of the transect to document growth and reproduction. Because *S. orbiculatus* plants are strongly clonal, it was not possible to identify separate individuals. For this reason, data analysis are conducted on a per stem basis. Along transects a subsample of individual plants were marked until the collection of the ripened fruits. Light data (PAR) were collected every two meters into the forest interior and in the open pasture between 1200 and 1400hours on a cloudless day.

For each individual stem, the number of branches, and fruits were recorded. After ripening in November 2005, fruits were collected and average seed and fruit mass was determined for each individual. A subset of the seeds collected from across all transects and distance from the edge (n=132) were tested for viability using 1% tetrazolium.

Morphological analysis-Mature leaves of 25 individuals collected across all 12 transects at the edge (0-1m) from the forest interior (7-10m) were collected in October 2007. Each leaf was

measured longitudinally from the base of the leaf to the apex, and horizontally at the widest part of the leaf. Anatomical characteristics of a subset of leaves were also recorded. Mesophyll thickness was compared for leaves at the edge and interior.

Statistical analyses-Transect data were divided into 1m increments to calculate the density of stems, branches and fruit across the edge gradient. These data were analyzed with ANOVA followed by Duncan's post-hoc tests. Density data were analyzed using distance from edge as a categorical variable to allow detection of non-linear edge responses. Light data were treated similarly to examine the response of individual plants to the edge gradient. Pearson correlations were calculated between distance from the edge and number of branches, total number of fruit produced, fruit produced per branch, and seed mass. To control for multiple comparisons, significance criteria were Bonferonni adjusted. To improve normality of the response variables, seed mass was analyzed as $\ln(\text{seed mass})$; total number of fruit and fruit produced per branch were analyzed as $\ln(\text{count} + 1)$. Density and fruit mass data did not require transformation. All analyses were conducted using SPSS 13.0 (SPSS Inc, Chicago, Illinois).

Results

A total of 154 *S. orbiculatus* plants were monitored for reproduction across the 10 transects.

Symphoricarpus orbiculatus populations were denser near the forest edge and declined dramatically with distance into the forest interior (Fig. 1). Stem density ($F_{9,110} = 9.32$; $P < 0.001$; $R^2 = 0.43$) and branch density ($F_{9,110} = 3.44$; $P < 0.01$; $R^2 = 0.22$) were both associated with distance from the edge, with very few stems located >8 m into the forest. Similarly, fruit production was greatest 1-2 m into the forest, but dropped off dramatically past that ($F_{9,110} = 3.27$; $P = 0.001$; $R^2 = 0.211$).

Performance of individual plants also varied across the edge gradient. Bigger plants, those with more branches, produced more fruit ($R=0.640$; $P<0.001$). However, plant size did not change across the edge as the number of branches produced by each stem was not correlated with distance ($R=0.069$, $P=0.394$). Reproductive output changed dramatically with both the total number of fruit produced by a plant ($R=-0.290$; $p<0.001$) and the number produced per branch ($R=-0.465$; $P<0.001$) were negatively correlated with distance (Fig. 2). Despite the changes in number of fruit produced, average fruit and seed mass did not change with edge position. Viability testing revealed that 99% (131/132) of seeds tested for germination were viable at the end of stratification treatment.

Leaf size also varied with position relative to the edge. Plants located near the edge (0-1m) had leaves that were 37% shorter ($F_{1,48}=78.07$; $P<0.001$; $R^2=0.62$) and 41% narrower ($F_{1,48}=67.26$; $P<0.001$; $R^2=0.58$) when compared to leaves for plants in the forest interior (7-10m). Light also significantly differed in relation to the edge; percent light transmittance decreased going into the interior (Fig. 3).

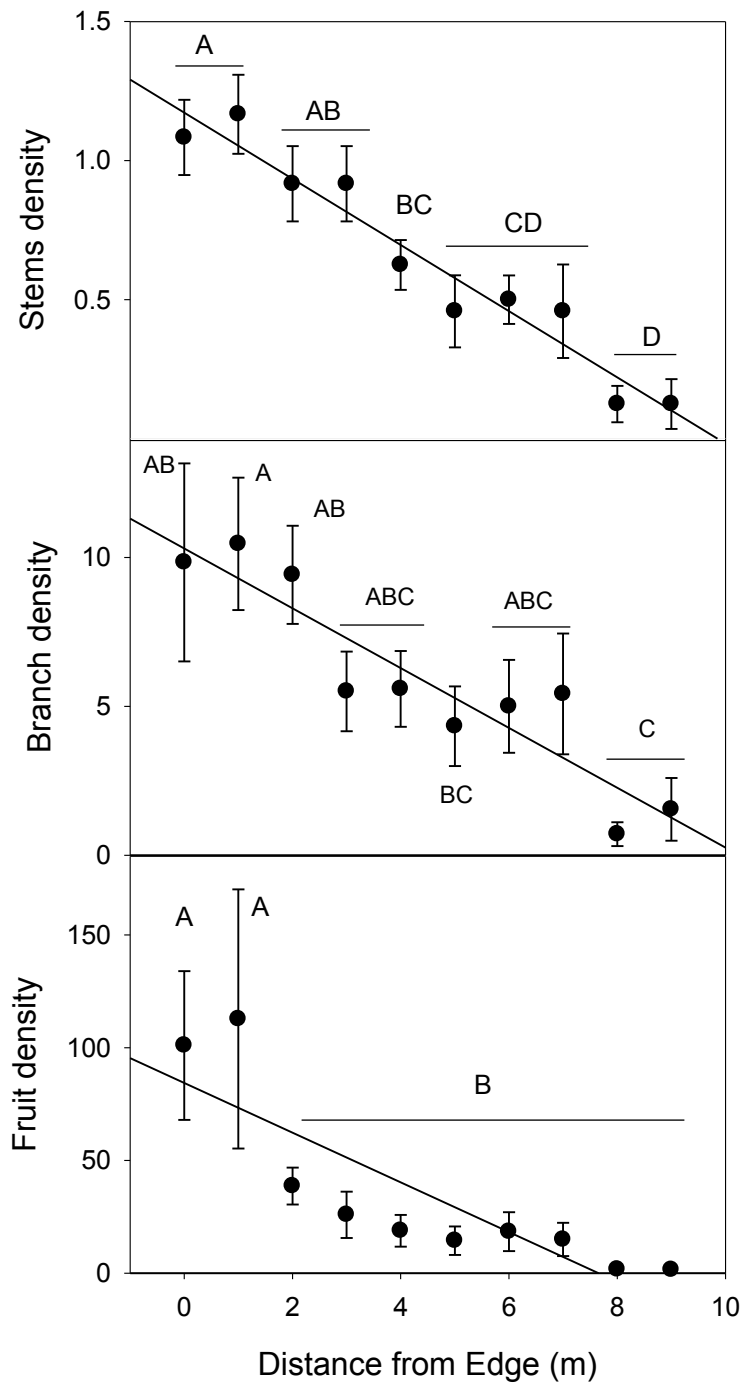


Figure 1. Population density and fruit production of *Symphoricarpos orbicularis* across a forest edge gradient in October 2005. Data plotted are means \pm 1 SE. Line is a best-fit line through the

means at each distance class. Means sharing the same letter are not statistically different at $P < 0.05$.

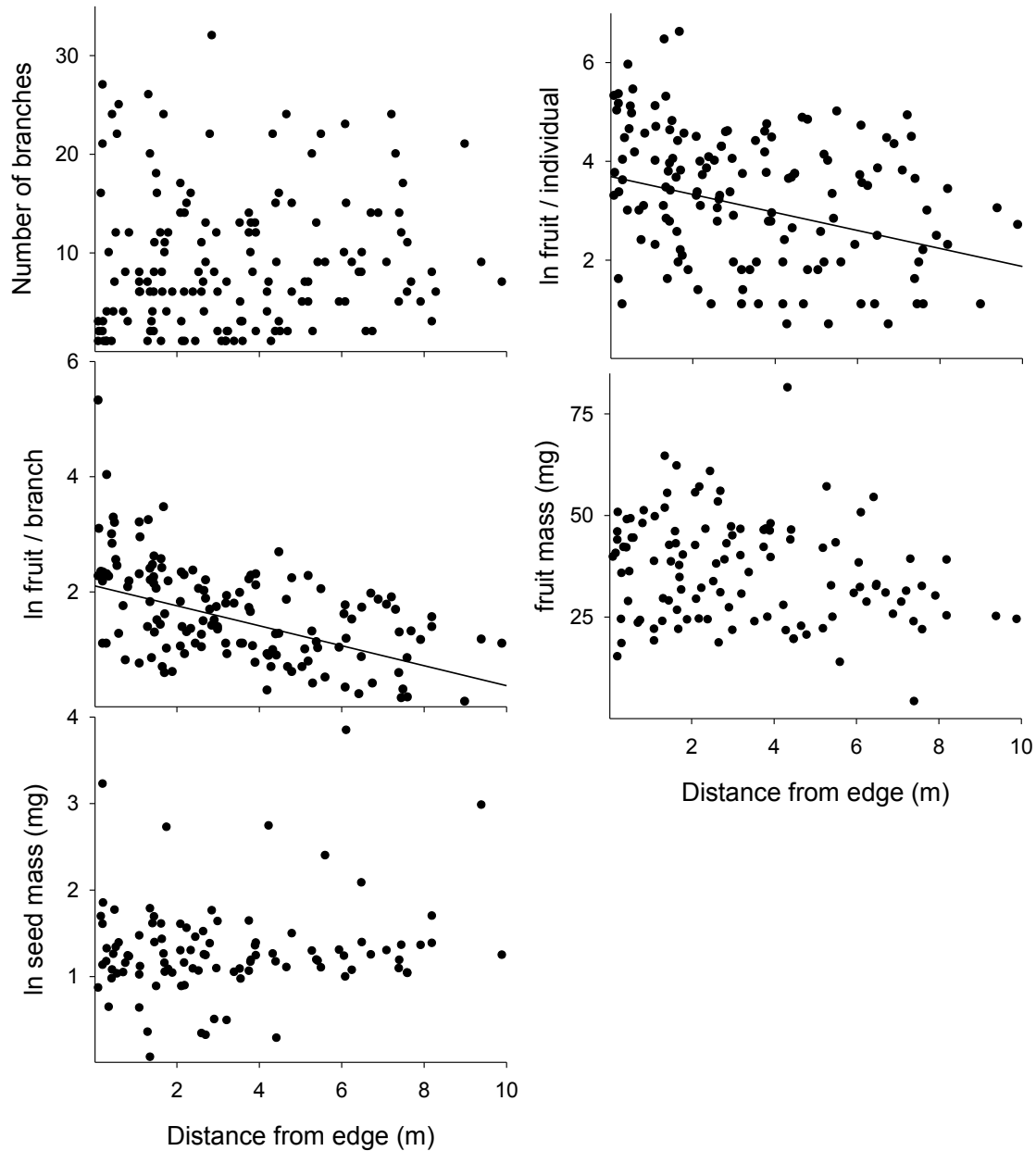


Figure 2. Response of individual plant performance to the edge gradient in October 2005. Best-fit lines are plotted on those graphs with significant correlations.

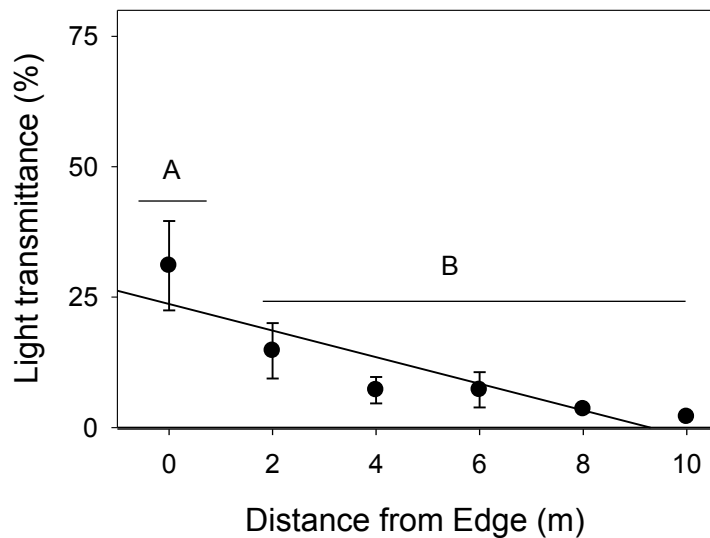


Figure 3. Percent light transmittance correlated with distance among transects in October 2005.

Discussion

Forest edges contain greater biodiversity of both plant and animal species than the forest interior (Wales 1972; Harris 1988; Matlack 1994). Populations of *S. orbiculatus* responded positively with a higher density at forest edge. However, total fruit and seed mass did not change across the forest-edge gradient. Due to similarities in the quality of offspring between the interior and forest edge, *S. orbiculatus* should not show differences in the distribution of individuals in a forest population; however variability in light and *S. orbiculatus* in relation to the edge does occur. Two mechanisms can be used to explain the observed demographics of *S. orbiculatus* in forested systems.

Edges have been well documented to contain high activity of seed dispersal. Mammals and ant dispersal lead to unequal distribution of seeds. At locations with greater numbers of

dispersers and dispersal activity there is a higher density of plant species (Thompson and Willson 1978; Jules 1996; Harris 1998; Tallmon et al. 2003). Differences in the rate of dispersal, due to the number of dispersers in a region, can thus lead to spatial responses in plant communities. Field mice, common seed predators throughout North America, are found in high abundance at edge sites, and are significantly less abundant in the forest interior and by reducing seed abundance can influence *S. orbiculatus* spatial distribution (Meiners and LoGiudice 2003; Tallmon et al. 2003). *Symphoricarpos orbiculatus*, is clearly bird dispersed and is a preferred cover species for birds (Johnsgard and Rickard 1957). Due to dense barrier-like qualities of the forest edge bird dispersers are often concentrated at the edge. As fruit size and seed mass did not change across the edge, the quality of individual fruits to dispersers was unchanged. Herbaceous species with fleshy fruits are often more abundant along edges and appear to be correlated with an increase of dispersal in the edge transition zone (Williams-Linera 1990). Changes in plant-animal interactions can be used to explain densities of plant species associated with edges.

Another plant-animal interaction that can explain spatial distributions of *S. orbiculatus* include pollination rates. In the forest herb *Trillium ovatum*, differences in pollination rates between interior and edge individuals led to higher rates of viable seedlings and higher densities of individuals along the edge (Jules and Rathcke 1999). *Trillium ovatum* and *S. orbiculatus* both display similar spatial heterogeneity in relation to the edge, giving credence to pollination rates as a mechanism for explaining spatial variability in edge systems.

Differences in structure of vegetation also play a significant role in the distribution of individuals. Forest edges provide an effective barrier against wind dispersed seeds and may contribute to plant density at the edge as well as increase competition intensity at the edge (Johnsgard and Rickard 1957; Didham and Lawton 1999; Cadenasso and Pickett 2001).

Dispersal can therefore be a contributing mechanism that can lead indirectly to variable plant densities in a forest community. While we cannot directly assess the role of dispersal and pollination in *S. orbiculatus* we can postulate on the role that they play in the distribution of plant populations.

While we cannot rule out dispersal as a mechanism for edge effects, variation in plant performance appears sufficient to drive spatial pattern seen in *Symphoricarpos orbiculatus*. The spatial patterns likely relate to the ability of an individual to compete for and capture essential resources. One essential resource that plays an important role in the composition of vegetation and presumably *S. orbiculatus* is light. Light is especially important in forested systems with a closed canopy that allows only small concentrations of light in the interior (Williams-Linera 1990; Matlack 1993, 1994; Didham and Lawton 1999).

Reflecting the ability of *S. orbiculatus* to capitalize on light gradients leaves exhibit differential morphological characteristics between edge and interior habitats. Individuals at the forest edge had smaller leaves with thicker palisade layers and would be more efficient at capturing light while minimizing heat gain in a high light environment. Individuals of *S. orbiculatus* were responding strongly to light gradients and indicate that light may drive edge effects observed in *S. orbiculatus*. Branching is another strategy to capitalize on low light environments. Individuals that are highly branched are better able to capture sunlight and may have better survival than less branched individuals (Grime 1979).

Demographic effects of increased branch and stem density at the edge involve the production of more fruits and seeds. With greater availability of resources, individuals of *S. orbiculatus* were able to allocate more resources towards fruit production at the edge. In our study, *S. orbiculatus* produced more fruits per square meter and fruits per branch at the forest

edge. However, fruit size and seed size did not vary across the edge. Thus, it appears that plants in low light of the forest interior reduced the quantity but not the quality of offspring produced.

My results indicate a reduction in the density of individual stems of *S. orbiculatus* into the forest interior. While the size of individuals and the number of fruits produced was greater at the edge, viability of offspring and fruit size did not change. One explanation for this occurrence lies in the morphological form of *S. orbiculatus*. Individual plants of *S. orbiculatus* are connected through a series of rhizomes and translocate nutrients and carbohydrates. This also appears to be the main method of local expansion of *S. orbiculatus*. Further research needs to be conducted to determine whether essential resources are being translocated to individuals in the forest interior.

Overall, although edge effects of *S. orbiculatus* can be explained using plant performance alone, it is probable that both dispersal and plant performance contribute to differences in population structure. While the establishment of a new seedling may be a low-probability event, once established, plants near an edge may grow larger and expand clonally. Further studies should be conducted in order to determine the effects of dispersal and nutrient exchange between individuals of *S. orbiculatus*. It is our goal to be able to use *S. orbiculatus* as a model to determine edge response of gap regenerating species. By knowing population mechanisms behind spatial patterns of *Symphoricarpos orbiculatus*, we are better able to understand how to conserve biodiversity as the natural environment of these species is being decimated by continued forest fragmentation in the world today.

Acknowledgements

I would like to thank Garden Clubs of America for funding this research as well as my reviewers for their comments and helpful suggestions. I would also like to thank Scott Meiners, Meghan Horn, and family for their help in the collection of fruits and seeds and Elise Tulloss for introducing me to the dynamics of forest edges.

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