A Resource Induced Shift in Growth Strategy and Rhizome Morphology in a Non-native Clonal Plant Species

By

JOSHUA D. ECHOLS

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ABSTRACT OF THE THESIS

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Thesis Director:

Steven Handel, PhD

In recent years, a non-native plant, *Aralia elata,* has emerged as an invasive plant species

in the eastern United States. Introduced in New York in the 1830s, *A. elata* has since

spread, via avian dispersal, across much of the mid-Atlantic region. The large scale

windthrow and resulting canopy gaps created by the storms of 2011 and 2012 produced

the disturbed habitat preferred by *A. elata*. Clonal growth is a life history trait common

among invasive plant species, including *A. elata*, affording the genet the benefit of

improving its fitness through the production of an exploratory rhizome system capable of

foraging to acquire limited resources. I hypothesized that the amount of canopy cover

will affect rhizome growth dynamics and main stem size over the first three years of

invasion. Rhizome dimension data of 150 individual genets were collected and plotted

against the percent open canopy. Results indicate that rhizome size and structure are

significantly affected by the percent of open canopy. Plants occupying higher light

locations had larger main stems, more rhizomes with more branching points, and were

shorter in total length than plants growing in low light, indicating investment by the genet

into its current location. Unexpectedly, plant growing in low light conditions possessed

the longer, less branching rhizome morphology often observed in foraging plants,

suggesting that they were attempting to escape the lower light location.

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Introduction

The introduction of non-native plant species in habitats can produce negative consequences for native communities (Reichard and Hamilton 1997, Pimentel et al. 2000 and 2005, Mooney 2001, Vila 2004). The non-native's ability to change the abiotic and biotic composition and function of ecosystems represents a threat to native diversity (Levine et al. 2003, Chacón et al. 2009, Novoa et al. 2012). If a non-native plant naturalizes and spreads unchecked, that invader can dominate the local community and potentially drive some native populations to extirpation (Rejmanek and Richardson 1996, Reichard and Hamilton 1997, Kolar and Lodge 2001). There are numerous examples of alien species dominating and endangering native populations. *Phragmites australis* (Chambers et. al 1999, Meyerson et al. 2000) and *Lythrum salicaria* (Malecki et al. 1993, Blossey et al. 2001) are both well-documented invaders of wetland ecosystems. Woody shrub species such as *Elaeagnus angustifolia* (Lesica 1999, Katz and Shafroth 2003) and *Lonicera maackii* (Gould and Gorchov 2000, Hartman and Brian 2008) are each dominant invaders of riparian and upland habitats. However, the understanding of why some introduced species become invasive and others do not is not well understood and continues to be the subject of much ecological research. To determine the invasive potential of an introduced species, it is important to understand the underlying mechanisms that permit it survive and persist and whether it possesses traits that will enable it to adversely affect its new habitat (Martínez and García-Franco 2004).

Invasive plants tend to share common traits that enhance their invasive ability. They often are adaptable, aggressive, capable of thriving outside of their natural ranges, and have high reproductive outputs (Goodwin 1999, Martínez and García-Franco 2004). They usually have small short-lived seeds that germinate easily, a short period of time to

reach sexual maturity, frequent large seed crops, long flowering times, large size and in some invasive species, asexual reproduction (Rejmanek and Richardson 1996, Goodwin, 1999). Combine these advantageous traits with an absence of natural predators and disease, and the potential for invasion increases as the invader is free to increase its growth and reproduction (Crawley 1986, Keane and Crawley 2002, van Kleunen et al. 2010, USDA 2012),

Even though clonal growth is one of the most commonly shared traits among successful invaders (Pyšeket 1995), there has been little research in this area (Yu et al. 2009, Roiloa et al. 2010, 2013). Only recently has clonal growth received attention as a trait contributing to invasion (Liu et al. 2006, Song et al. 2013). The production of clonal ramets is advantageous to the genet as it creates a larger, super-organism like structure, thereby increasing access to resources. The physiological integration of all ramets creates a division of labor (Slade and Hutchings 1987a and 1987b, Saitoh et al. 2002, Roiloa et al. 2013, Song et al. 2013) between the different ramets of the superstructure. The transfer of carbohydrates, water, and minerals among ramets (Alpert and Mooney 1986, Alpert 1996) allows the plant to exploit patchy, heterogeneous resources (de Kroon and Knops 1990).

Much of the published and often cited evidence for clonal invaders comes from the study of herbaceous species; however, the success of invasive, woody species can also be attributed to clonal reproduction (Herron et al. 2007). In the eastern United States, an introduced woody species possessing many of the traits attributed to invaders has mostly gone unnoticed for decades. Originally native to northeastern Asia (e.g., China, Russia, Korea and Japan), *Aralia elata* has spread throughout the Northeastern, Mid-

Atlantic, and Midwestern regions of the United States since its introduction into the New York metropolitan area in the 1830s (Moore 2009). Subsequent introductions have also led to established populations in the Pacific Northwest. Though it has been present in the mid-Atlantic region for nearly 200 years, it has only recently been recognized as a nuisance species when, in 2010, the New Jersey Invasive Species Strike Team (NJIST) declared it an emerging stage three invasive (common or regionally abundant; highly threatening to natural communities) (NJIST 2011).

Aralia elata is a deciduous, shade intolerant shrub capable of growing 10 – 15 meters tall and commonly occupies disturbed, high light habitats such as canopy gaps, roadsides, stream banks, and abandoned agricultural fields (Sarver et al. 2008, USDA 2012). Like many invasive species, A. elata takes advantage of both asexual and sexual reproduction strategies (Douhovnikoff 2004, NJIST 2011). It reproduces sexually through the production of thousands of avian dispersed seeds and asexually through the production of new ramets via rhizomes and root suckering (Missouri Botanical Gardens 2016). The typical growth form of the plant is of a single stemmed tree; however, it can take on a shrub morphology consisting of closely spaced stems when the main meristem receives damage (Moore 2009). That clonal response to damage can lead to the formation of dense clumps capable of dominating disturbed areas (Figures 1 and 2) (USDA 2012, NJIST 2011).

Clonal growth dynamics are known for other early successional species and invaders, such as: Rhus spp. (Gilbert 1966, Werner 1982); and Robina spp. (Zhang et al. 2006), but little quantitative data is available for A. elata. Other than its potential pharmacological benefits (Mingming et al. 2015), little is known of the basic life history

strategies or role that *A. elata* plays in local community dynamics. Government agencies and nonprofits, such as the US Forest Service or NJIST provide what little information we know. The need to better understand its early invasion dynamics and habitat preferences/tolerances is vital for early detection and rapid response management of this species before it becomes a much larger problem regionally.

In 2011 and 2012, New Jersey experienced two weather events that will have lasting effects on its forest communities. Hurricane Irene in 2011 and Superstorm Sandy in 2012 created a mosaic of new canopy gaps throughout the region's forests. In the ensuing years, invasion into these gaps by the area's typical invasive plant species, including *A. elata* (pers. obs.), has been ongoing. These new gaps have allowed new populations of *A. elata* to emerge affording the opportunity to study the dynamics of early invasion in a non-native, clonal woody species (Figures 3 and 4). The goal of this project is to explore the relationship between forest canopy cover and the clonal growth response of a non-native, invasive woody species. I tested the hypothesis that the amount of canopy cover will change rhizome growth dynamics and main stem size over the first three years of invasion. The alternate hypothesis is that rhizome length and main stem size are not correlated to light.

Methodology

Study Sites

The two research sites were located in central New Jersey and selected based upon proximity and similarity in forest age, community composition, and previous land use. Site One was located in Franklin Township, NJ, at The Hutcheson Memorial Forest (HMF) (40°29'51'' N; 74°33'52" W). Site Two was located in Piscataway, NJ, at the Rutgers University Ecological Preserve (RUEP) (40°30'56'' N; 74°26'16" W). Native tree species (*Quercus alba, Q. rubra, Q. velutina, Carya spp.,* and *Fagus grandifolia*) dominate the forest canopy; however, non-native tree species also have a significant presence (*Acer platanoides and Ailanthus altissima*). Non-native invasive plant species, in conjunction with high deer populations, have created a forest low in native diversity at each site. High levels of white-tailed deer herbivory have resulted in a thin forest understory and shrub layer lacking the younger, native cohorts needed to replace the aging canopy layer. *Lonicera maackii, Rosa multiflora, Rubus phoenicolasius,* and *R. allegheniensis* occupy much of the shrub layer and canopy gaps, while *Lonicera japonica* and *Microstegium vimineum* dominate the forest floor (Figure 5). At both locations, populations of *A. elata* established in several large canopy gaps during the previous decades. The age of the older gaps and populations is unknown; however, multiple individuals with heights approaching the recognized size limit of the species (10 – 12 m) were located at each site. Aside from these older populations, no other large populations have been located on or around the remainder of either property (pers. obs.).

Genet Verification and Specimen Aging

The height of the first year's growth scar above the soil was used as the primary method of differentiating unique genets from clonal ramets. A unique genet's first growth scar is located just a few centimeters above the soil, but a ramet's first growth scar will occur much higher on the stem (pers. obs.). Secondary verification occurred during rhizome excavation when a definite determination of uniqueness was made based upon the presence or absence of a rhizome connection to an older, larger genet. Any plant with obvious damage to the main stem was rejected from this study so as to avoid confounding the data with results from any unknown compensatory growth response due to damage to the main meristem.

Age was determined by matching the number of growth scars with the growth rings counted at a height of 2 cm of the main stem. The height of 2 cm places the count below the average height of 1-yr individuals. Based on pilot observations, this method of age calculation is accurate during the first 3 – 4 years, after which the growth scars and growth rings become more difficult to discern as the bark becomes rougher and the wood pithier. See Table 1 for the total number of individuals per age and canopy classification.

Densiometer Measurements

The average percent canopy cover for each specimen was determined by summing the canopy readings taken from each of the four cardinal directions at the location of each plant using a handheld analog spherical densitometer (Spherical Densiometer Model-C, Forestry Suppliers, Inc., Jackson, MS) Study specimens were located in conditions of almost complete closure (97%) to gaps as large as 40%. 43, 39, 32, and 35 individuals were examined in each of the 10, 20, 30, and 40% open canopy classes respectively.

Above-ground Measurements

The height of the main stem was determined with a measuring tape. The main stem diameter was measured at a height of 2 cm above the soil using a digital caliper. (General Ultratech® Digital Calipers, General Tools and Instruments, New York, NY)

Rhizome Excavation

Excavation was timed so as to occur when *A. elata* was dormant. To measure total growth per growing season, all excavation was performed during the late-winter/early-spring and late-fall/early-winter of each year in 2014 and 2015, prior to and after that year's growing season. During the winter of 2014, prior to the first field season, individual *A. elata* specimens, between the ages of one and three, were identified and flagged at each site.

Each plant's rhizome system was excavated using a trowel and 5 cm wide nylon paintbrush. The top few centimeters of soil was removed from the base of the main stem until all rhizomes were identified. Each individual rhizome was carefully uncovered until the entire rhizomatous structure of the plant laid exposed (Figure 6). I recorded the following for each rhizome: the total number of rhizome per specimen (Figure 7), total length of each rhizome, number of branching points per rhizome (Figure 8), the distance between each branching point, the rhizome diameter at 2.5 and at 25 cm from the main stem, and the presence or absence of reproduction. The act of excavation killed many of the smaller plants; therefore no repeated measures of any individual specimens were collected for this project.

Soil Analysis

Five sub-sites at each of the two research locations were sampled the first week of May 2015. Topsoil samples collected at the surface to a depth of 12 cm and subsoil samples collected between the depths of 25 – 35 cm were combined and thoroughly mixed into a single representative sample for each layer at each of the five sub-sites. All samples were tested for pH, macronutrients (P, K, Mg and Ca), micronutrients (Zn, Cu, B, Mn and Fe), and texture (sand %, silt % and clay %). The Rutgers University Soil Testing Laboratory performed the soil analysis in May 2015.

Weather Analysis

All temperature and precipitation data for this study was collected from the Office of the New Jersey State Climatologist website (accessed June 9, 2016). Plants excavated in the spring of 2014 experienced the growing conditions of the previous year; therefore, data for the 2013 growing season has been included, even though there were no excavations performed during 2013.

Statistical Analysis

Data from 2014 and 2015 were combined based on the lack of difference in weather among the growing seasons. Using generalized regression analysis, I tested the relationship between percent open canopy and the following variables: main stem height and diameter, the total number of rhizomes per plant, total and mean rhizome length per plant, the total number of rhizome branching points per plant, the mean rhizome length

per branching point, and the mean rhizome diameter measured at 2.5 and 25 cm of rhizome length per plant. I nested specimens with site to determine if the observed results were a function of between site differences. I also analyzed the relationship between percent open canopy and the above variables using linear regression. Both sites (HMF and RUEP) were combined due to a lack of significant difference between sites. T-tests determined similarity in soil conditions for pH, macronutrients, micronutrients, and soil texture between sites. The significance for all tests was $\alpha = 0.05$. All statistical analyses were performed using JMP®, Version 11 PRO, (SAS Institute Inc., Cary, NC, 1989-2007).

Results

Age Distribution

A total of 150 unique genets with an age distribution of 53 1-year, 50 2-year, and 47 3-year old specimens were excavated between April 2014 and November 2015 (Table 1).

Reproduction

No flowering occurred for any specimen during the course of this project; however, clonal reproduction did occur. There was no clonal reproduction or flowering for individuals in either the one or two-year old age classes. Three-year old specimens produced twelve clonal ramets by eight different individuals. All twelve clonal ramets were determined to be one year of age.

Soil Analysis

Topsoil and subsoil analysis determined texture and nutrient levels for both sites (HMF and RUEP). T-tests ($\alpha = 0.05$) of the topsoil identified a significant difference in the levels of Mn ($p = 0.0094$) between the two sites. Subsoil analysis showed significant differences between sites for only Mn ($p = 0.0249$) and K ($p = 0.0426$). Mechanical analysis identified no significant difference in topsoil and subsoil texture (Table 2).

Weather Analysis

An ANOVA comparing the inter-annual monthly average temperatures ($F_{2,33} = 0.144$, $p = 0.8667$) and precipitation ($F_{2,33} = 0.512$, $p = 0.6043$) provided no significant difference in weather conditions between growing seasons.

Above-ground

Above-ground stem height and diameter increased significantly in response to increased open canopy for 1-yr, 2-yr, and 3-yr plants. Plants in the 40% open canopy class were, on average, larger than those plants growing in the 10% open canopy class (Figures 9 and 10). One year specimens displayed increases in mean stem height of 2.6 cm $\pm$ 0.53 and mean stem diameter of 1.81 $\pm$ 0.53 mm as open canopy increased. Two year specimens exhibited an increase in mean stem height of 34.76 $\pm$ 8.98 cm and mean stem diameter of 4.32 $\pm$ 1.71 mm. Three year specimens also displayed increases in mean stem height of 66.90 $\pm$ 26.09 cm and mean stem diameter of 12.07 $\pm$ 4.34 mm (Table 3). Linear and general regression analysis provided evidence of significant differences in these variables. All three ages were significantly affected by increases in open canopy for height and diameter (Tables 5 and 6). Site was not found to be a significant influence on either height or diameter (Table 6). Variance increased with age for both height and diameter (Table 5).

Below-ground

Plants under a higher percent open canopy have more rhizomes with more branching points than plants in lower light conditions. One-year specimens displayed an increase in the mean number of rhizomes per plant of 1.48 $\pm$ 0.92 and an increase in the mean number of branching points per plant of 1.84 $\pm$ 1.13 as open canopy increased. Two-year old specimens also had an increase of 2.09 $\pm$ 0.85 for the mean number of rhizomes per plant and 6.73 $\pm$ 2.07 for mean number of branching points. Three-year specimens

exhibited increases in the mean number of rhizomes per plant of 1.62 ± 0.95 and mean number of branching points per plant of 10.12 ± 4.57 as open canopy increased (Table 4). Both simple linear and generalized regression analysis indicate the significant changes in mean number of rhizomes per plant and mean number of branching points are a function of open canopy (Tables 5 and 6, Figures 11 and 12) . Neither the mean number of rhizomes nor the mean number of branching points was influenced by between site differences (Table 6). Variance increased with age for both the mean number of rhizomes and mean number of branching points per plant (Table 5).

Fewer individuals occupying higher light locations possessed rhizomes reaching a length ≥ 50 cm than those in lower light conditions. Only three 1-yr individuals possessed a rhizome that grew to a length ≥ 50 cm from the main stem: 1 individual from the 20% canopy class and 2 from the 10% canopy class. A total of 24 2-yr specimens had rhizomes that reached a distance ≥ 50 cm: 15 individuals from the 10%; 8 from the 20%; 1 from the 30%; and 0 from the 40% canopy classes. Forty-two 3-yr specimens possessed rhizomes that reached a distance ≥ 50 cm: 13 individuals from the 10%; 13 from the 20%; 5 from the 30%; and 8 from the 40% canopy classes.

During the first two growing seasons, data indicate that increased open canopy enabled plants to not only out-grow lower light specimens above-ground, but below-ground as well. One year specimens in the 40% canopy class had a mean total rhizome length increase of 27.88 ± 11.53 cm over the 10% canopy class, while mean average rhizome length decreased 15.99 ± 19.47 cm as open canopy increased (Table 4). Second year plants also displayed a mean total rhizome length increase of 16.43 ± 17.96 cm but a mean average rhizome length per plant decrease of 42.06 ± 22.13 cm as open canopy

increased (Table 4). The decrease in mean average rhizome length per plant results from plants growing under higher percent open canopy having, on average, more rhizomes per plant (Table 4, Figure 11). The pattern observed for the first two years for the total and mean rhizome length per plant flips in year three, when longer overall rhizomatous growth occurs in plants growing under lower light conditions. The mean total rhizome length of 3-yr individuals decreased 266.44 ± 62.53 cm, while the mean average rhizome length decreased 108.65 ± 36.96 cm as open canopy increased (Table 4). Linear and generalized regression analysis indicates that the significant increases in total rhizome length per plant and mean rhizome length per plant are a function of open canopy (Tables 5, Figures 13 and 14). No significant effect for between site differences was identified for total rhizome length per plant or mean rhizome length per plant (Table 6). Overall variance increased with age for both mean total rhizome length per plant and mean rhizome length per plant (Table 5).

The mean length of rhizome per branching point and the mean length of the longest rhizome per plant significantly decreased with increased open canopy. One-year specimens decreased by an average of 20.88 ± 21.56 cm for mean length of rhizome per point and 16.39 ± 12.24 for the mean length of the longest rhizome as open canopy increased. The mean length of rhizome per branching point of two- and three-year specimens decreased by an average of 61.14 ± 20.69 cm and 127.56 ± 35.64 cm respectively. The mean length of the longest rhizome per plant also decreased 42.37 ± 15.11 for two-year and 93.54 ± 31.03 for three-year specimens as open canopy increased (Table 4, Figure 18). This decrease in mean length of rhizome per branching point and the longest rhizome per plant was supported statistically with linear and generalized

regression analysis (Tables 5 and 6, Figures 13 and 14). Site was not found to be a significant influence on mean length of rhizome per branching point (Table 6). Variance increased with age for mean length of rhizome per branching point and mean longest rhizome per plant (Table 5).

Rhizome diameter measurements taken at 2.5 and 25 cm from the main stem of each rhizome displayed a weak, yet significant linear increase in diameter as open canopy increases (Figures 16 and 17). The mean rhizome diameter for each plant measured 2.5 cm from the main stem increased with age and open canopy. The 25 cm measurements also increased in mean rhizome diameter for 2-yr, but a decrease in mean rhizome diameter for 1-yr and 3-yr plants. One-year specimens displayed an increase in rhizome diameter at 2.5 cm of 1.65 ± 2.10 mm and a decrease of 1.18 ± 1.14 mm at 25 cm as open canopy increased. The rhizome diameter of two-year old specimens increased by 0.85 ± 2.17 mm and at 2.5 cm and increased by 2.06 ± 2.80 mm at 25 cm. Rhizome diameter increased by 1.59 ± 3.26 mm at 2.5 cm and 0.27 ± 3.11 mm at 25 cm in three-year specimens (Table 7). Simple linear regression indicates that a significant effect of open canopy cover exists during the first two years on rhizome diameter for measurements 2.5 and 25 cm from the main stem. However, during the third year, the 25 cm rhizome diameter was not significantly different (Table 5). Generalized regression analysis indicated a significant effect of open canopy on the rhizome diameter measurements at 2.5 cm from the main stem during years two and three. Year three analyses of rhizome diameter measurements at 2.5 cm from the main stem were not significantly affected by open canopy increased (Tables 6). Between site effects were shown to significantly affect root diameter at 2.5 cm from the main stem during year one but not for years two or

three. Rhizome diameter measurements at 25 cm from the main stem indicated a significantly effect by open canopy during year one and two, but not in year three. Between site effects were shown to significantly affect root diameter at 25 cm from the main stem during year three but not for years one or two (Table 6). Variances for the mean rhizome diameter increased with age at 2.5 and 25 cm from the main stem as open canopy increased (Table 5).

Discussion

This project has provided previously unknown insight into the early invasion dynamics of the invasive woody species, *Aralia elata*. As a species most often associated with the higher light environments of disturbed habitats (Sarver et al. 2008, USDA 2012), *A. elata* was well suited to invade and dominate the mosaic of forest canopy gaps created in the Mid-Atlantic States during the storms of 2011 and 2012. The timing of these storms provided the opportunity to follow the early invasion of *A. elata* into several new, unoccupied canopy gaps at HMF and RUEP.

Initial introduction of *A. elata* into novel habitats primarily occurs via avian seed dispersal (Moore 2009), however, there are no reports in the literature on the clonal dynamics of small, localized populations. Many invasive, clonal plant species possess the capacity to spread horizontally potentially dominating large areas (Stocklin 1992, de Kroon and Hutchings 1995, Hutchings and Wijesinghe 1997) and upon visiting a population of *A. elata,* it becomes evident that this species does spread along the horizontal plane; often forming dense clusters of above-ground stems capable of shading out native plant species (pers. obs.)

Aralia elata spreads locally through the creation of new, sexually reproduced genets and asexually from the production of new clonal ramets (Douhovnikoff et al. 2004). Sexual maturity usually occurs around year 4 or 5, once the main stem reaches a height of 2 to 3 meters (pers. obs.). Currently there are no published data for an age specific trigger inducing clonal growth in an undisturbed individual; however, this project identified a total of 12 clonal ramets belonging to eight different 3-yr individuals. All eight clones were associated with individuals growing under canopies that were 20% to

40% open. I identified no clonal ramets for 1-yr or 2-yr specimens or for specimens growing beneath denser canopy conditions.

The evidence from this study supports the previously observed behavior in some clonal plants growing in higher resource locations producing a rhizomatous system that is shorter, thicker, and more branching than individuals growing in lower resource locations, whose rhizomes tend to be longer, thinner, and less branching (Cain 1994). Plants can detect changes in nutrient concentrations as they grow through the heterogeneously distributed nutrients bands in the soil (Robinson 1999, Giehl and von Wirén 2014). Once the plant encounters a desirable resource patch, the plant can produce a new clonal ramet to take advantage of that resource (de Kroon and Hutchings 1997).

In essence, the plants growing in the optimal resource locations invest in a root structure that maximize resource acquisition at their present locale, while the lower resource plants invest in longer more exploratory rhizomes enabling them to explore the local environment (Cain 1994). This reallocation of resources into longer rhizomes in resource stressed environments is evidence of a foraging behavior often observed in clonal plant species (Ming 1996, Tian and Doerner 2013). The modular structure and integrated connections of clonal ramets provide a means to not only share resources, but to improve a genet's location on the landscape that non-clonal species do not possess (Zhang et al. 2006, Lechuga-Lago et al. 2016). The ability to escape from a less than desirable location is valuable, as it enables the genet to access resources not otherwise available (Slade and Hutchings 1987a and 1987b, Roiloa et al. 2013, Song et al. 2013).

Much of the published literature on plant foraging concerns the exploration of the soil by root structures in relation to nutrient concentrations (López-Bucio et al. 2003) or

the above-ground stem elongation and leaf orientation in response to sunlight (Collins and Wein 2000, Smith 2000). The literature is lacking in the study of rhizomatous morphological changes in response to differential light exposure; however, the results of this project indicate that light exposure significantly affects the rhizomatous morphology of *A. elata* during the first three years of invasion.

The main stem height and diameter significantly increased linearly with increasing open canopy, regardless of age. Plants in the 40% open canopy class (high light) were, on average, larger than those plants growing in the 10% open canopy class (low light). There was no evidence of main stem elongation, as observed in previous studies, by plants exposed to this level of reduced sunlight (Collins and Wein 2000).

The mean number of rhizomes and the mean number of branching points per plant mirrored the observed above-ground growth patterns. Regardless of the age, increases in open canopy resulted in an increase in the number of rhizomes and rhizome branching points per plant. This coincides with observations of plants growing in high resource locations solidifying their hold on a particular site by investing in more rhizomes with more branching points; allowing the individual increased resource acquisition (Cain 1994, de Kroon and Hutchings 1995).

The significant results for the mean total rhizome length per plant provide evidence of a shift in the clonal growth strategy of *A. elata.* During the first year, plants occupying higher light locations possessed longer rhizomes than plants growing in lower light locations; paralleling the results observed for the main stem dimensions, the mean number of rhizomes, and the mean number of branching points per plant. During year two, the first evidence of a shift in clonal strategy appears. The difference in mean total

rhizome growth between light extremes for year one and two was small, but did increase illustrating that the total rhizomatous growth increased at a higher rate from year one to year two in plants occupying lower light locations; and indicating that the advantage of higher light begins to disappear in relation to rhizome length in the second year. The rate of total rhizome growth decreased significantly as open canopy increased during year three. This finding was unexpected as the published literature indicates that a reduction in light negatively effects root growth (Wahl et al. 2001). There was a similar significant linear pattern observed for the longest rhizome per plant which showed that plants exposed to higher light conditions produced shorter rhizomes than those growing in lower light.

The mean rhizome length per plant and the mean rhizome length per branching point per plant each decreased as open canopy increased, across all years. This finding is reasonable considering that the number of rhizomes and the number of branching points per plant each increased with open canopy, and are divided into the total rhizome length per plant reducing the mean length of the rhizome and length between branching points as compared with plants in lower light conditions. The resulting rhizomatous structure consists of a higher number of shorter rhizomes with more branching points that do not extend far from the main stem.

Rhizome diameters provided mixed results that did not precisely fit with previous observations that foraging plants have thinner rhizomes (Cain 1994). The mean 2.5 cm diameters increased with age as open canopy increased. This matches the expected results that higher light plants would have thicker rhizomes needed to store the additional carbohydrates produced from increased photosynthesis (Loescher et al. 1990, Klimeš et

al. 1999). The mean diameters at 25 cm increased linearly with age, but not necessarily with open canopy cover. During year one, higher light plants had thinner rhizome than lower light plants, likely a result of additional rhizome branching in the higher light specimens. In year two, there was little difference in the mean diameter of plants growing in the 10, 20, and 30% open canopy classes, but the 40% canopy class diameter increased 30% as open canopy increased. There was not a significant linear effect of canopy cover on rhizome diameters at 25 cm during year three which is likely a result of the combination of: 1) the additional branching points in higher light plants reducing the diameter of the rhizome; and 2) the plants reaching an age-related maximum diameter at 25 cm, with the new growth occurring at the terminal end of the rhizome. Site was shown to have a significant effect on rhizome diameter at 2.5 cm from the main stem during year one, but that effect disappeared in years two and three.

Variance increased with age for all variables except the mean rhizome diameter at 25 cm from the main stem, which was shown not to be significantly affected by open canopy during the third year. The increased variance may be driven by the selective stress imposed on the individual phenotypes by differential light conditions. During the first year, seeds expressing varying phenotypes germinate across a wide range of light levels, and the genotypic diversity of the cohort is at its highest and variance is low. As the cohort ages, variance increase as the less fit phenotypes die out leaving behind the individuals most fit to grow and survive at their germination location.

Soil analysis provided significant between-site concentration differences for only Mn and K concentration. The Rutgers Soil Testing Laboratory scored the mean Mn concentrations in the topsoil and subsoils of both sites as high, meaning that Mn is likely

not a limiting nutrient to *A. elata* at either site. Manganese is toxic at $\leq$ pH 5.5 when

solubility and root absorption increases (Foy et al. 1988, Marschner 1995). The mean pH

for both sites was below the pH 5.5 toxicity threshold, but because Mn tolerances are

highly dependent upon the species and genotypes within the population (Foy et al., 1988,

Horst, 1988), it is unclear how affected *A. elata* was by the high Mn concentrations.

Potassium concentrations scored as optimal at RUEP and slightly below optimal at HMF.

Potassium is important as a catalyst in many biochemical reactions involved in

photosynthesis and protein synthesis (Zhao et al. 2001, Ashley et al. 2005), but because

the K requirement of *A. elata* is unknown, it is difficult to determine if the difference in K

effected growth between the two sites. The similarity in soil texture is of particular

importance, because soil texture plays an important role in the difficulty of rhizome

exploration (Laycock 1967, Jones 1983). Both sites had the same average soil texture

(sandy-loam/loam), meaning that all plants encountered the same soil texture regardless

of site; therefore, soil texture was not an important influence on differential rhizome

growth.

Conclusion

The findings of this project, in part, supported the hypothesis that the amount of canopy cover will change rhizome growth dynamics and main stem size over the first three years of invasion, however, not every variable responded as expected. The results did provide evidence of a significant linear response by *A. elata* to canopy conditions. Main stem height, main stem diameter, the number of rhizomes per plant, and the number of branching points per plant all showed a significant, positive linear response to increased open canopy, which indicates that the *A. elata* plants growing under higher light conditions invested more resources into growth of the main stem and a shorter, highly branching rhizomatous structure best suited to dominate their current location. In contrast, plants growing in less than optimal light locations shifted their resource investment into under-ground rhizomatous development at the expense of main stem growth. The longer, less branching rhizomatous structures of these plants affords the opportunity to forage for limiting light resources, essentially, allowing the plant to escape a less than desirable germination location through clonal reproduction. The unexpected findings of this project concern the observed patterns of the total rhizome length, the mean rhizome length per plant, and the longest rhizome per plant, which failed to support the original hypothesis; that rhizome growth would be greater in plants occupying higher light environments. Instead, overall rhizome size decreased with increased light exposure.

Future research projects into the early invasion dynamics of *A. elata* include investigating if the observations of rhizomatous morphological shifts in response to light continue beyond the first three years of invasion and, if so, how does it affect the distribution of ramets across the landscape? How does that behavior contribute to

invasion success? Will the individuals at the lower light extremes eventually migrate and produce a clonal ramet that can provide the much need photosynthetic resources, or will the genet eventually exhaust itself and die? Is there an age specific trigger that induces clonal reproduction or is it resource or damaged induced? And finally, does soil temperature play a role in the detection of the differential light cues by the rhizome? As a land manager, this information provides knowledge into the early invasion timeline of *A. elata* allowing for a more economical use of resources. The results indicated that eradication efforts should focus on higher light locations, which supports the reported gap dependent (disturbance related) nature of the species, even though this work shows that the species can overcome an unfortunate germination location. The mechanical removal of invading genets should occur within the first three years in high light locations to prevent new ramet establishment; as low light plants are not as likely to reproduce during the first three years of invasion. Individuals located far from the gap still need removal because the foraging behavior of the genet may eventually allow it to reach a higher light environment; however, this management action can take a lower priority.

Like other non-native clonal woody shrubs (*Rhus* spp., Ortmann et al. 1997; *Elaeagnus angustifolia*, Patterson and Worwood 2010), herbicides can control genets too large for mechanical removal. Because *Aralia's* compensatory response to cutting results in the production of many clonal ramets, the timing of herbicide treatment is important. Current best practice techniques recommend late season foliar application of a systemic herbicide, such as glyphosate, or application of triclopyr to cut stumps to best control *A. elata* (National Park Service 2012, Pennsylvania DCNR 2012). Cutting too early in the growing season can create an explosion of ramets that will only exacerbate management

issues. The recommended late season cutting and herbicide application will not give the plants enough time to recover to respond clonally before the end of the growing season. To exterminate larger genets, repeated herbicide application may be needed for several growing seasons.

Appendices

Tables and Figures

Table 1. Age distribution by site and percent open canopy class.

Age	Site	Percent Open Canopy				Specimen Totals
		10%	20%	30%	40%	
1	HMF	6	5	7	8	26
	RUEP	9	8	6	4	27
	Total	15	13	13	12	**53**
2	HMF	9	7	5	8	29
	RUEP	6	6	5	4	21
	Total	15	13	10	12	**50**
3	HMF	8	8	5	6	27
	RUEP	5	5	4	6	20
	Total	13	13	9	12	**47**
Percent Open Canopy Class Totals		**43**	**39**	**32**	**36**	**150**

Table 2. T-test results for between site soil analyses. ($\alpha = 0.05$)

Test	Site	Mean	SD	t	df	*p*
Topsoil						
pH	HMF	4.84	0.27	-0.307	8	0.767
	REUP	4.78	0.27			
P	HMF	24.40	7.197	2.432	4	0.067
	REUP	62.20	33.97			
K	HMF	175.80	22.58	2.109	4	0.098
	REUP	295.60	124.98			
Mg	HMF	90.00	35.52	1.574	4	0.181
	REUP	182.60	126.63			
Ca	HMF	565.00	211.85	1.265	4	0.264
	REUP	966.80	677.70			
Zn	HMF	3.69	1.05	0.094	7	0.928
	REUP	3.76	1.17			
Cu	HMF	7.87	6.57	0.170	5	0.871
	REUP	8.41	2.75			
B	HMF	0.37	0.11	0.139	7	0.893
	REUP	0.38	0.12			
Mn	HMF	122.54	34.33	-4.476	4	**0.009[a]**
	REUP	52.57	6.57			
Fe	HMF	132.38	34.06	0.326	6	0.755

	REUP	138.04	18.55			
Sand %	HMF	53.40	7.99	0.259	5	0.805
	REUP	54.40	3.29			
Silt %	HMF	33.20	7.46	-1.037	6	0.337
	REUP	29.20	4.32			
Clay %	HMF	13.40	1.34	1.853	5	0.120
	REUP	16.40	3.36			

Subsoil

pH	HMF	4.72	0.19	0.560	7	0.592
	REUP	4.78	0.14			
P	HMF	19.20	14.79	1.592	5	0.165
	REUP	30.75	31.57			
K	HMF	96.60	7.02	2.890	4	**0.043**[a]
	REUP	162.80	50.74			
Mg	HMF	53.80	10.09	1.756	4	0.152
	REUP	122.40	86.79			
Ca	HMF	270.00	90.70	1.388	4	0.235
	REUP	665.80	631.22			
Zn	HMF	2.27	0.36	0.550	6	0.601
	REUP	2.44	0.60			
Cu	HMF	4.12	4.97	-0.270	4	0.800
	REUP	3.52	0.81			
B	HMF	0.26	0.07	0.453	7	0.663

	REUP	0.28	0.07			
Mn	HMF	96.48	37.11	-3.431	4	**0.025[a]**
	REUP	38.97	5.28			
Fe	HMF	117.78	18.54	-0.320	7	0.758
	REUP	114.28	15.98			
Sand %	HMF	48.80	10.16	0.525	6	0.616
	REUP	51.60	6.23			
Silt %	HMF	31.00	7.68	-0.785	5	0.463
	REUP	28.00	3.74			
Clay %	HMF	20.20	2.68	0.120	7	0.908
	REUP	20.40	2.61			

Table 3. Above-ground mean height and diameter combined for both sites (HMF and RUEP).

	% Open canopy class	Mean height (cm)	SD	Mean diameter (mm)	SD
1-yr	10	3.78	0.39	6.78	0.37
	20	5.21	0.47	7.62	0.51
	30	6.15	0.43	8.20	0.37
	40	6.38	0.36	8.59	0.38
2-yr	10	52.05	5.77	8.35	1.03
	20	61.67	7.99	9.24	1.08
	30	80.95	6.35	11.33	1.24
	40	86.81	6.88	12.67	1.37
3-yr	10	117.04	10.74	11.71	1.71
	20	138.81	14.44	13.40	2.76
	30	174.69	18.01	19.12	4.14
	40	183.94	17.54	23.78	3.99

Table 4. Below-ground means combined for both sites (HMF and RUEP).

Age	% Open canopy class	Mean # of rhizome	SD	Mean total rhizome length per plant (cm)	SD	Mean rhizome length per plant (cm)	SD	Mean # of branching points per plant	SD	Mean rhizome length per branching point (cm)	SD	Mean Longest Rhizome per Plant (cm)	SD
1-yr	10	1.60	0.63	68.50	9.27	48.69	17.90	1.33	0.62	53.90	19.09	44.52	9.50
	20	2.38	0.51	78.83	7.96	34.18	6.56	2.00	0.91	41.54	18.22	33.21	8.84
	30	2.77	0.60	90.12	7.58	34.30	9.46	3.15	0.80	30.24	7.66	27.52	5.07
	40	3.08	0.67	96.38	6.86	32.70	7.66	3.17	0.94	33.02	10.01	28.13	7.72
2-yr	10	2.33	0.49	215.45	13.79	95.95	19.46	2.60	0.64	87.10	19.78	78.20	14.42
	20	3.00	0.58	206.62	17.69	71.31	15.47	4.62	1.45	48.00	12.24	55.27	12.74
	30	4.20	0.63	228.23	19.11	55.42	8.88	6.40	1.17	36.50	5.62	45.03	5.76
	40	4.42	0.69	231.88	11.51	53.89	10.54	9.33	1.97	25.96	6.06	35.83	4.50
3-yr	10	3.46	0.52	685.15	55.08	201.57	31.31	4.46	0.78	158.94	34.79	152.75	27.94

20	4.38	0.87	557.38	47.80	133.39	35.76	6.23	2.31	100.92	39.69	109.94	30.54
30	4.67	0.87	481.03	28.97	107.29	26.51	13.00	5.22	44.15	23.12	69.22	22.38
40	5.08	0.79	458.71	29.61	92.92	19.64	15.58	4.50	31.38	7.73	59.21	13.50

Table 5. Results from linear regression testing the relationship between each variable and percent open canopy.

	R^2	F	p	B	Int	DF	Error	σ^2
Main stem height of stem (cm)								
1-yr	0.810	216.89	< 0.0001	0.088	3.56	1	51	1.28
2-yr	0.755	147.56	< 0.0001	1.164	46.12	1	48	252.13
3-yr	0.773	153.09	< 0.0001	2.322	105.75	1	45	975.27
Main stem diameter of stem (mm)								
1-yr	0.747	150.57	< 0.0001	0.060	6.55	1	51	0.65
2-yr	0.732	131.43	< 0.0001	0.150	7.30	1	48	4.34
3-yr	0.760	142.83	< 0.0001	0.439	7.94	1	45	35.43
Number of rhizomes per plant								
1-yr	0.458	43.06	< 0.0001	0.048	1.46	1	51	0.67
2-yr	0.671	97.73	< 0.0001	0.072	1.98	1	48	1.10
3-yr	0.403	30.41	< 0.0001	0.052	3.35	1	45	0.93
Mean total rhizome length per plant								
1-yr	0.680	108.24	< 0.0001	0.965	63.65	1	51	179.75
2-yr	0.186	10.99	0.0017	0.662	206.82	1	48	329.83

3-yr	0.761	142.93	< 0.0001	-7.383	697.34	1	45	10599.00

Mean rhizome length per plant

1-yr	0.180	36.60	< 0.0015	-0.487	47.65	1	51	175.75
2-yr	0.543	56.99	< 0.0001	-1.415	98.77	1	48	518.04
3-yr	0.619	73.17	> 0.0001	-3.436	204.14	1	45	2665.22

Number of branching points per plant

1-yr	0.428	36.60	< 0.0001	0.060	1.23	1	49	1.27
2-yr	0.715	120.33	< 0.0001	0.206	1.51	1	48	8.30
3-yr	0.620	73.37	< 0.0001	0.385	1.89	1	45	20.63

Mean rhizome length per branching point

1-yr	0.226	14.28	0.0004	-0.713	54.60	1	49	294.98
2-yr	0.625	79.86	< 0.0001	-1.838	87.75	1	48	759.03
3-yr	0.702	105.87	< 0.0001	-4.201	170.53	1	45	3722.25

Mean longest rhizome per plant

1-yr	0.358	28.43	< 0.0001	-0.552	44.83	1	51	117.63
2-yr	0.670	97.33	< 0.0001	-1.355	81.69	1	48	384.68
3-yr	0.661	90.76	< 0.0001	-3.101	161.69	1	45	2010.26

Mean rhizome diameter (mm) at 2.5 cm

1-yr	0.156	8.48	0.0055	0.063	2.84	1	46	0.82
2-yr	0.197	11.77	0.0012	0.030	7.30	1	48	0.57
3-yr	0.401	30.09	< 0.0001	0.088	7.23	1	45	1.32
Mean rhizome diameter (mm) at 25 cm								
1-yr	0.257	13.47	0.0007	-0.056	2.79	1	39	1.17
2-yr	0.224	13.83	0.0005	-0.043	4.44	1	48	0.74
3-yr	0.007	0.31	0.5775	-0.009	5.31	1	45	1.11

Table 6. Results from generalized regression testing the relationship between each variable and percent open canopy and site.

	% Open Canopy		Site	
	Wald X^2	p	Wald X^2	p
Main stem height of stem (cm)				
1-yr	192.923	< 0.0001	2.593	0.1073
2-yr	140.472	< 0.0001	0.473	0.4916
3-yr	152.542	< 0.0001	0.001	0.9760
Main stem diameter of stem (mm)				
1-yr	127.227	< 0.0001	0.176	0.6745
2-yr	131.861	< 0.0001	1.407	0.2356
3-yr	157.512	< 0.0001	3.205	0.0734
Number of rhizomes per plant				
1-yr	39.311	< 0.0001	1.674	0.1958
2-yr	88.087	< 0.0001	0.095	0.7579
3-yr	32.496	< 0.0001	1.623	0.2026
Total rhizome length per plant				
1-yr	94.747	< 0.0001	0.004	0.9522
2-yr	7.957	0.0048	0.020	0.8881
3-yr	150.996	< 0.0001	0.908	0.3405
Mean rhizome length per plant				
1-yr	9.968	0.0016	1.888	0.1694
2-yr	51.717	< 0.0001	0.037	0.8277
3-yr	79.564	< 0.0001	2.357	0.1247
Number of branching points per plant				
1-yr	28.451	< 0.0001	1.485	0.2230

2-yr	118.418	< 0.0001	3.529	0.0603
3-yr	83.772	< 0.0001	1.393	0.2379
Mean rhizome length per branching point				
1-yr	11.031	0.0009	2.377	0.1232
2-yr	91.389	< 0.0001	0.971	0.3244
3-yr	104.538	< 0.0001	0.157	0.6920
Mean longest rhizome per plant				
1-yr	21.678	< 0.0001	2.646	0.1038
2-yr	100.739	< 0.0001	0.112	0.7378
3-yr	85.990	< 0.0001	0.577	0.4473
Mean rhizome diameter (mm) at 2.5 cm				
1-yr	2.362	0.1243	8.730	0.0031
2-yr	14.110	0.0002	1.833	0.1758
3-yr	38.073	< 0.0001	3.433	0.0639
Mean rhizome diameter (mm) at 25 cm				
1-yr	13.339	0.0003	0.075	0.7837
2-yr	14.029	0.0002	0.111	0.7395
3-yr	0.0431	0.8355	0.354	0.5518

Table 7. Mean rhizome diameter (mm) measured at 2.5 and at 25 cm from the main stem.

	% Open canopy class	2.5 (mm)	SD	25 (mm)	SD
1-yr	10	4.83	1.43	3.46	1.05
	20	4.76	1.03	5.81	1.27
	30	7.90	1.63	1.87	0.55
	40	6.48	1.54	2.28	0.45
2-yr	10	7.32	1.08	4.10	1.25
	20	7.98	1.48	4.11	1.15
	30	7.69	1.79	4.22	1.54
	40	8.17	1.88	6.14	2.51
3-yr	10	7.76	1.55	5.25	1.55
	20	7.98	1.74	5.40	1.79
	30	10.03	2.21	5.43	1.93
	40	9.35	2.87	5.51	2.70

Figure 1. A dense clup of *Aralia elata* ramets growing in a canopy gap formed in 2012 by Superstorm Sandy at the RUEP. Photo: Joshua D. Echols

Figure 2. An example of clonal ramets forming a thicket of *Aralia elata* at the RUEP. Photo: Joshua D. Echols.

Figure 3. An example of a new canopy gap under invasion by *Aralia elata*. Photo: Joshua D. Echols

Figure 4. *Aralia elata* invasion into a canopy gap formed by Superstorm Sandy. Photo: Joshua D. Echols

Figure 5. An example of invasive species, including *Aralia elata*, invading a canopy gap. Photo: Joshua D. Echols

 Figure 6. The excavated rhizome system of an *Aralia elata* genet. Photo: Joshua D. Echols

Figure 7. An excavated 2-year old plant with three main rhizomes. Photo: Joshua D. Echols

Figure 8. An example of rhizome branching points. Photo: Joshua D. Echols

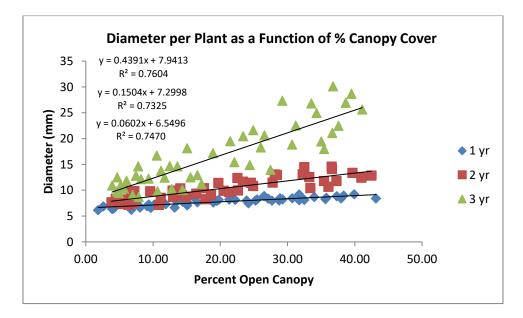Figure 9. Main stem height plotted against percent open canopy.

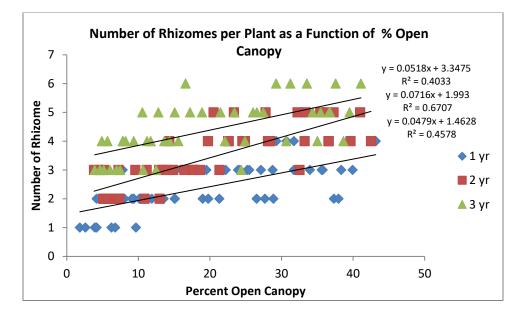Figure 10. Main stem diameter plotted against percent open canopy.

Figure 11. Total number of rhizomes of each plant plotted against percent open canopy.
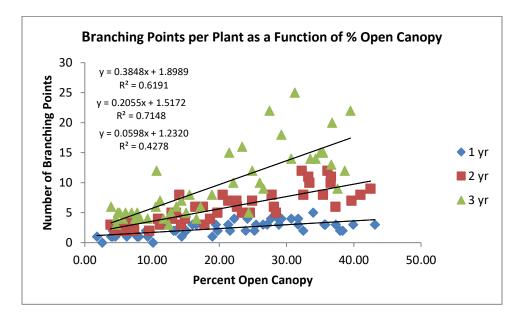

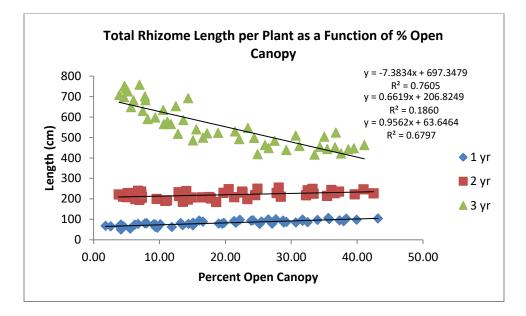Figure 12. Total number of rhizome branching points of each plant plotted against percent open canopy.

Figure 13. Total rhizome length of each plant plotted against percent open canopy.
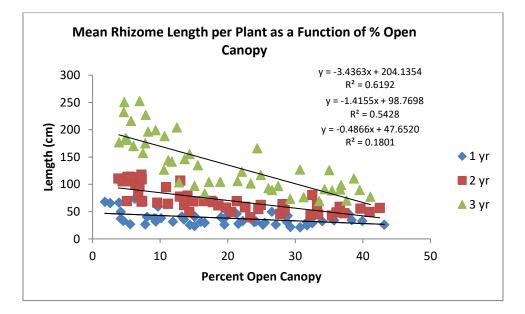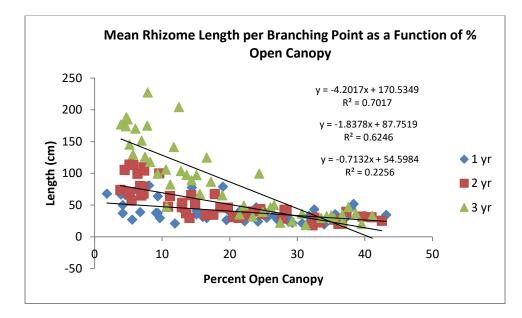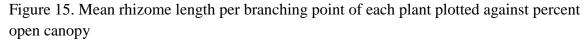

Figure 14. Mean rhizome length of each plant plotted against percent open canopy.

Figure 15. Mean rhizome length per branching point of each plant plotted against percent open canopy
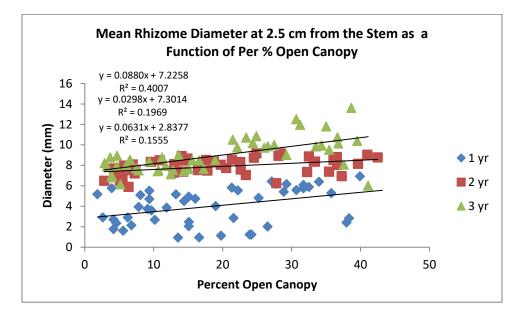

Figure 16. Mean rhizome diameter at 2.5 cm from the main stem of each plant plotted against percent open canopy
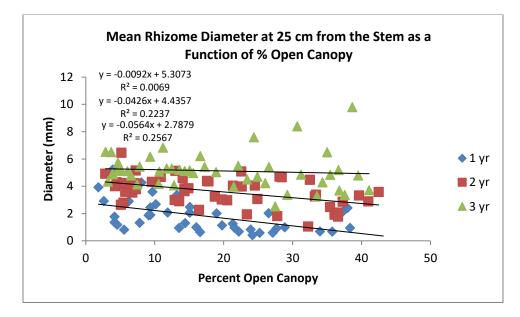
Figure 17. Mean rhizome diameter at 25 cm from the main stem of each plant plotted against percent open canopy
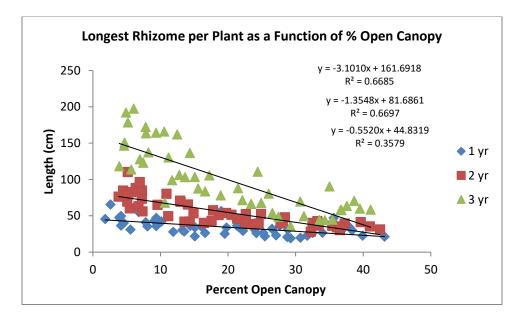

Figure 18. The length of the longest rhizome per plant plotted against percent open canopy.

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