

**A Life History Analysis of Invasive Behavior in Native and Naturalized Species:  
*Rubus odoratus* and *Rubus allegheniensis* in the Nichols Arboretum, Ann Arbor, MI**

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**Abstract:**

Invasive species are defined broadly as “non-indigenous species or strains that become established in natural plant communities and wild areas and replace native vegetation” (Czarapata, 2005). Based on my own recent research as well as the data reviewed in this paper, I argue that this definition is limiting in the context of climate change and globalization. Human disturbances have already changed ecosystem composition to such an extent that the original location of plant origin, although still extremely important, plays less of a deciding factor in the invasive capacity of the species. The native and naturalized species in this study (*Rubus odoratus* and *Rubus allegheniensis*) display many of the same life history characteristics often attributed to non-native species. Research was carried out through two field studies in the University of Michigan’s Nichols Arboretum in Ann Arbor. The study used life history theory as a framework to assess the role environmental factors can play in shaping an organism’s traits. Tradeoffs between seed quantity and seed size, as well as cane growth and fruit production were carefully examined. Lastly, a test was done to replicate the effect of increased atmospheric nitrogen, removing the limiting effect of nitrogen on plant growth. Results from the study reveal that the two species use two different life history strategies that nonetheless provide them with a similar potential for invasive behavior. Understanding the tradeoffs present in these species informs management decisions on how to keep population numbers in check most effectively.

## Introduction

The effective management of wildlands has become increasingly important as urban development continues to fragment critical habitats into small patches. The integrity of these ecological areas is further threatened by the spread of non-native species and opportunistic native species that are able to colonize habitats very quickly. By outcompeting and appropriating resources from other organisms, non-native species have a negative effect on both the lifecycles of native organisms and the biodiversity of the ecosystem as a whole.

Past research (McDowell 2002; Bazzaz 1986; Rejmanek 1996) has shown that there are several characteristics common to invasive species that allow them to have such dramatic impacts: for example, high reproductive allocation, rapid vegetative growth, and a high potential for acclimation. Little research has been done on the interconnection of these three characteristics within the framework of life history theory.

Before categorizing any species as “invasive” one must first address the meaning of this term. Some sources define invasive plants as “non-indigenous species or strains that become established in natural plant communities and wild areas and replace native vegetation” (Czarapata 2005). The definition used by the International Union for the Conservation of Nature (IUCN) is: “an alien species which becomes established in natural or semi-natural ecosystems or habitats, is an agent of change, and threatens native biological diversity” (Global Invasive Species Database, 2012). These definitions are limiting in that they excludes native species that display some of the same extreme colonizing behaviors as many exotic plants. Reichard and White (2001) give a slightly more inclusive definition of invasive plants as organisms that can be either native or non-native, but are able to “spread into native flora and managed systems, develop self-sustaining populations and become dominant or disruptive.” In today’s changing and varied ecosystems, it is important to focus on the effects species have within their ecosystem as opposed to solely where the species originate. Although a species-level analysis can provide useful insights into the extent of invasive behavior, only individual populations should be considered invasive because processes that affect the success of the organism may be independent of species origin (Collacutti et al. 2004). This study focuses on invasive potential at the population level, particularly in horticultural specimens.

The genus *Rubus* is a source of very popular horticultural specimens. It can be divided into 13 subgenera, which include hundreds of species. Most species generally colonize and flourish in conditions of abundant light, soil disturbance and decreased competition created by reductions in tree basal area of recently disturbed areas (Greenberg, Levy and Loftis 2007). The plants spread within populations clonally but migrate outwards by the distribution of seeds.

The flowering raspberry (*Rubus odoratus*) and blackberry (*Rubus allegheniensis*) are two naturalized shrub species which are currently described as expanding their local ranges (Missouri Botanical Gardens, 2010). Their invasive tendencies have been specifically noted in the Nichols Arboretum in Ann Arbor, Michigan. Both species were likely introduced into the Nichols Arboretum for fruit production or as horticultural specimens in the late 1800’s and early 1900’s and have since spread to several key woodland areas. Historical records show that Walter

Nichols raised various raspberries for fruit production in the main valley of the arboretum during the early 1900's (Figure 1). Researching the life histories of *Rubus allegheniensis* and *Rubus odoratus* and determining whether there are specific life history characteristics which lead to invasive tendencies can lead to important insights into management of such species.

### *Rubus odoratus* L.

*Rubus odoratus* is commonly known as the Purple-flowering raspberry or Thimbleberry. The species is native to much of the east coast of the United States. In Michigan, populations are also found primarily along the lake coasts (Figure 4). The plant is a vascular perennial, meaning that it has specialized tissues for conducting water and nutrients, and that its life persists year after year. The plant grows on average up to five feet high. It propagates by root, cutting, seed and sprig (USDA: *Plants Profile: Rubus odoratus*, 2012). The shrub has hairy, cane-like stems and 1-2 inch rose-purple flowers with 5 petals that bloom June-August. Its red fruits appear in summer and although dry and tasteless to humans, they provide food to a variety of small birds and mammals. In the University of Michigan Arboretum and Missouri Botanical Gardens, *Rubus odoratus* has displayed an aggressive suckering behavior that may be responsible for the expansive behavior of their populations (Missouri Botanical Gardens, 2010).

### *Rubus allegheniensis* Porter.

*Rubus allegheniensis* Porter, commonly known as the Allegheny blackberry, is in the same genus as the Purple-flowering raspberry. It is also a vascular perennial that propagates by root, seed or sprig. However, in the United States it has a slightly larger range than the flowering raspberry, extending to the west coast. In this study it is used as a comparison species for *Rubus odoratus* because it has a much larger range in Michigan than *R. odoratus* (Figure 5). The plant has several significant differences from the flowering raspberry. Primarily, its white flowers bloom earlier in May, and the USDA classifies it as having a more rapid vegetative spread rate and higher seedling vigor than the flowering raspberry (USDA: *Plants Profile: Rubus allegheniensis*, 2012). Interestingly, these characteristics are often common among invasive species. I will compare the life history strategies used by these two plants that both seem to be expanding their ranges, perhaps through slightly different methods.

### *Life History Theory*

Life history theory uses natural selection to create a framework for analyzing the life patterns of organisms, which are created by a common mechanism that expresses survival and reproduction. The underlying principle of the theory is that an organism's environment shapes its traits. Principle life history traits include or seed size, growth pattern, age and size at maturity, number, size and sex of offspring, age/size-specific reproductive investments, and age/size-

specific mortality schedules (Stearns, 1992; Roff 1992). This study will focus primarily on analyzing the tradeoffs between certain traits (Roff, 1992). In invasive plants, tradeoffs may lead to properties that emphasize seed quantity over seed size, reproductive growth over mature somatic growth, and a highly efficient use of resources.

### *Horticulture and Invasive Species*

Horticulture and agriculture have the interesting effect of creating new strains of plants which, although they originate from native species, have different characteristics and life histories (Chrobok et al., 2011). The horticulture industry is one of the fastest growing segments of US agriculture and has been the principal pathway for intentional introductions of many invasive plants (Reichard and Hamilton 1997, Reichard and White 2001, Burt et al. 2007). Today, a consumer desire for ornamental plants has created a market that drives the horticultural industry. Horticultural specimens are often chosen for a wide range of morphological characters including large flowers, attractive seeds and fruit, a long blooming season, low maintenance, adaptability and tolerance of a number of environmental extremes (Drew et al., 2010). This selection process leads to increased genetic diversity of the cultivated stock (Trusty et al. 2008).

Horticulture fosters plant invasion in several ways. It can directly involve the importation of non-native species or it can result in multiple invasions and introduce more genetically diverse founders into an environment. Also, different cultivars planted together may cross-pollinate even if they are labeled self-sterile, and may form viable fruit that can then be dispersed. Most importantly, however, selective breeding may unintentionally favor certain traits that mirror those of invasives such as rapid seed germination, increased environmental tolerances and disease resistance (Culley et al. 2011). Chrobok et al. (2011) investigated introduced biases by collecting germination data on native plant species, invasive alien species, and cultivated alien species. They found that cultivars germinated earlier and had more seeds than their non-cultivar equivalents. These in turn may facilitate plant establishment in disturbed habitats by the suppression of slower and less profusely germinating species through asymmetric resource competition and fast population growth. Previously reported differences in germination characteristics between invasive alien species and native species may reflect introduction biases and human-mediated selection for these characteristics. Those very same characteristics might also increase the species' risk of invasiveness (Chrobok et al. 2011).

### *Historical Perspective of Horticulture in the Nichols Arboretum*

The Nichols Arboretum was created with the goal of studying vegetation in natural conditions. It was foreseen in the early 1900s that farmers' land would eventually be drained and put under cultivation for timber. The creation of the arboretum was seen as an opportunity to maintain the original topography and natural groupings of Washtenaw County plants. The early descriptions for the park noted that all plantings would be overseen by a landscape gardener who

would create the layout for the grounds under the supervision of the University of Michigan (Excerpts and summaries..., 1935).

Records from the early 1900s indicate that major plantings were coniferous evergreens in the western hills, an increase of shrubs and lilacs to nearly 150 species, and an increase in deciduous tree species. In the arboretum study site presented here there were plantings of ecological groupings of rhododendrons, azaleas, mountain laurels and other ericaceous plants. It was clear early on that there was a strong interest in making the park attractive to bird species (Histories of Nichols ..., 1935-1945). To fulfill this goal, new plantings of fall and winter fruit-bearing shrubs, which may have included *Rubus* species, were carried out. The number of species and varieties that had been tested in the arboretum approached 2,000 by 1958. The first records of efforts to reign in pest species came in 1992 with efforts to stop buckthorn and honeysuckle (Guerin, 1992).

The earliest University of Michigan Herbarium records of *Rubus odoratus* are from the 1860s. The plant was documented in the eastern portion of Washtenaw County, presumably on a settler's property. The species was first cultivated within the Matthaei Botanical Gardens in 1925 as a new planting from Red Mills, New York (U of M Herbarium collection). However, records of *Rubus odoratus* do not appear in the Nichols Arboretum until 1954 when gifted seeds from the Montreal Botanical Gardens were planted in the greenhouse (Arboretum card file, 1954). This could be a likely ancestor of the escapes from cultivation we see today. No early range maps are available for this species.

*Rubus allegheniensis* has an even more difficult history to track. There are no early cultivation records or even plant diversity records.

## Materials and Methods

### *Study Area*

The Nichols Arboretum in Ann Arbor, MI was created in 1907. Today it consists of 50 hectares of some of the most diverse landscape in southeastern Michigan (Tepley, 2001). A combination of native and exotic species has been crafted into a naturalistic landscape emphasizing the historical glacial topography. In the early history of the Arboretum, emphasis was placed on evaluating both native and horticultural specimens for their adaptability to various habitats. As a result, many exotic species were introduced. Today, some of these species have become pests and have readily invaded natural areas (Matthaei Botanical Gardens, 2007). In addition, the park's urban setting, its vast number of visitors (100,000 people/yr), and its ecological significance for bird migrations create many opportunities for the introduction of exotic species (B. Grese, pers. comm).

There are three significant sites of *Rubus* thickets in the University of Michigan Arboretum (S<sub>1/2</sub> NW<sub>1/4</sub>, Sec. 27, SE<sub>1/4</sub> NE<sub>1/4</sub> Sec.28 and NE<sub>1/4</sub> SE<sub>1/4</sub> Sec.28). One of these sites

was chosen as the location for the research presented in this paper. Tepley (2001) describes the region surrounding my main study site as located on the gently sloping terrain of the valley floor with an average slope of 7% towards the north. The average elevation of the site is 236-258 m. The soil consists of well drained sandy loam with a water table that is below 200-300 cm. The vegetation consists mostly of forest canopy created by black oak, white oak, northern red oak, and pignut hickory. The understory is inhabited by invasive species such as Common Privet (*Ligustrum vulgare*), Honeysuckle (*Lonicera tatarica*), and Buckthorn (*Rhamnus cathartica*), but it is dominated by the Thimbleberry (*Rubus odoratus*) and Blackberry (*Rubus allegheniensis*) (B.Grese pers. comm). Native species such as Running Euonymus (*Euonymus obovata*) and Interrupted Fern (*Osmunda claytonii*) are also present (Tepley, 2001). The average annual precipitation of Ann Arbor is 35.35 inches, evenly distributed throughout the year. Temperatures vary in the summer months but average to 59.6°F, 68.9°F, 72.8°F, and 71.2°F in May, June, July, and August respectively (National Oceanographic and Atmospheric Administration, 2010).

### *Field Procedures*

I carried out all field work in either the study site described above or in the Matthaei Botanical Gardens greenhouses. Data came from mature raspberry plants growing in the arboretum study site and from an experimental plot set up nearby.

To collect data on seed weight, seed number, fruit number, fruit weight, cane length and cane dry weight under natural conditions, I monitored forty mature *R. odoratus* and *R. allegheniensis* plants from May through August 2010. I determined mature second-year plants by examining the stems of the plants. *R. odoratus* second-year stems are characterized by an orange-brown color as well as exfoliating bark (Ladybird Johnson Wildflower Center, 2010). *R. allegheniensis* second year stems are characterized by stipitate-glandular stems that are purple-brown in color and often densely villous (Radford, 1968). To account for phenotypic plasticity, I roughly divided the study site into areas of shade (full tree cover to 2/3 tree cover), partial shade (2/3 tree cover to 1/3 tree cover) and full sun (1/3 tree cover to no tree cover). I made an attempt to sample an equal number of plants in each area. However, due to the fact that *R. odoratus* plants are more prevalent in the full sun habitat and *R. allegheniensis* plants are more prevalent in the shade habitat, the numbers of sampled plants were skewed in these directions.

At the end of June, when flowering was for the most part complete, I placed 4x6 inch breathable pollination bags made from clear, nonwoven polypropylene over fruiting stems to protect the fruit from predators and damage. However, due to high summer rainfall and inadequate protection given by the bags, several were ripped off the plants, and in a majority of the remaining bags the fruits had begun to mold. Collecting data from the fruit in this manner was no longer a viable option. I removed all pollination bags to continue the research.

In mid-July I counted the viable fruit still on the plants and extrapolated the number of fruit that had been lost by counting the petioles which remain attached to the stem. To collect data on fruit and seeds, I took a random sample of fruit from across all the different shade/sun



habitats. While there may be some intrinsic error in this random sampling, a strong attempt was made to sample a variety of fruits in an unbiased manner. I took a sample of 100 fruits per species. Fruits were subsequently dried in a drying oven for 36 hours and promptly weighed using a precision scale. To account for the fact that the receptacle remains attached to the drupes in *R. allegheniensis* plants, I separated the seeds from the receptacle after the initial drying and then reassessed the weights. I determined the number of seeds per fruit by counting the number of drupelets. I determined the seed weight by blending the fruit in water to separate flesh from seed (Ågren, 1989). The pure seeds were dried again and weighed in groups of 10 using a precision scale. I processed the plant canes at the end of August. All canes were cut at the soil level, measured, dried in a drying oven and weighed on a gram scale.

The experimental plants were similarly processed. In April of 2010, I dug up 40 plants of each species next to the transect site. I pruned each plant to 44.29 cm from the root node and pruned the roots to 6.35 cm horizontally and vertically. I then placed wet wraps around the root bundle and set the plant bunches aside. Plants were potted individually in one gallon pots using Sunagro metromix special blend. Twenty pots of each species had a treatment of nitrogen fertilizer added to the soil. I left the plants under a half shade structure at the botanical gardens for three weeks before placing them in a 10x8 grid next to the Arboretum study site. I monitored the plants all summer, allowing water, sunlight, and herbivory to be regulated naturally. At the end of August, I counted the fruiting plants, then uprooted, measured and analyzed the dry weight of all plants.

## Results

The data collected in this study brought to light several differences in life history traits between the two *Rubus* species: they varied considerably in fruit number, fruit weight, cane weight, cane length and morphology (Table 1). These differences point to important differences in energy allocation and growth patterns that make up the very different life history strategies of these two species.

The data collected from the main study area in the Nichols Arboretum reveal significant differences in cane mass (g), length (cm) and overall growth (g/cm). *Rubus allegheniensis* canes are significantly less massive than *Rubus odoratus* canes, with a mean difference in mass of 19.03g ( $p=3.371 \times 10^{-8}$ ) (Figure 8). *R. odoratus* has much heavier canes, meaning that significantly more resources are allocated to cane growth. These heavier canes are also significantly longer than the canes of *R. allegheniensis* ( $p= 1.062 \times 10^{-6}$ ). There is a mean length difference of 29.43 cm between the two (Figure 8).

When mass and length are combined into the overall growth rates for the two species, it is clear that cane growth is far more vigorous in *R. odoratus* than in *R. allegheniensis*. The cane growth of *R. odoratus* is significantly higher with average value of .24 g/cm compared to the .13 g/cm of *R. allegheniensis* ( $p= 5.165 \times 10^{-8}$ ) (Figure 9). Data collected on plant mass, length and

growth all point to significantly more investment in cane development among *R. odoratus* plants than among *R. allegheniensis*.

Fruit production, which is directly related to the reproductive output of the species, also varies significantly between the two species. Morphologically, the fruits are arranged differently along the cane between the species (Figure 2). *R. odoratus* fruits are arranged in clusters close to the flowering buds, and spread out along the cane. In contrast, *R. allegheniensis* fruits are all arranged at the end of the cane in a large cluster. *R. odoratus* produces significantly heavier fruit than *R. allegheniensis* ( $p=1.210 \times 10^{-7}$ ). Two species seem to have a relatively equal amount of variation in fruit weight (Figure 6b). However, *R. odoratus* fruits have an average weight of 169.5 mg while *R. allegheniensis* fruits only average 129.9 mg. The mean number of fruit per cane is significantly different between the two species as well. *R. odoratus* produces an average of 25.4 fruit per cane while *R. allegheniensis* almost doubles this figure with an average 43.6 fruit per cane ( $p=.006$ ; Figure 6a). *R. allegheniensis* varies significantly more in the number of fruits than *R. odoratus* (Levene's test  $p=2.088 \times 10^{-4}$ ).

Reproductive success is also directly correlated with the number of seeds produced per fruit (Herrera, 1991). Therefore, data were collected to estimate the number of seeds produced per fruit as well as the seed weights between the species. There were significant differences in both these categories (Figure 7). Although, as mentioned above, *R. odoratus* fruits are heavier, its seeds are significantly lighter ( $p=1.286 \times 10^{-70}$ ). Figure 7a shows a large number of outliers and very little variation in seed weight (Levene's test of variance  $p=4.186 \times 10^{-10}$ ). Although *R. allegheniensis* produces on average fewer seeds, the seeds tend to be heavier, with an average weight of around 2 mg.

This seeming conflict between the fruit weight and seed weight can be accounted for by the fact that *R. odoratus* produces significantly more seeds per fruit than *R. allegheniensis* ( $p=1.781 \times 10^{-44}$ ) (Figure 7b). The mean difference in the number of seeds per fruit was 41 seeds. The data collected from naturally growing plants in the arboretum study area seem to show a significant amount of trait differences between the two *Rubus* species.

In addition to between-species variation, there was also intraspecies variation based on sunlight levels. *R. odoratus* did not show any significant differences in cane mass, overall growth or fruit production with sunlight in this study. Only cane length showed marginal variation with light treatment ( $p=.093$ ). However, *R. allegheniensis* showed significant variance in cane mass, cane growth and fruit production between full sun habitat and full shade habitat (Figures 12 and 13). Only cane length remained unchanged ( $p=.326$ ). Because cane length displayed a significant amount of variance a Dunnett's post-hoc test was used to test relationships between variables. The other three measures did not show a significant difference in variance according to Levine's test of significance so a Tukeys T3 post-hoc test was used. Most significantly, the variance in the number of fruits produced in the full sun habitat was almost double that of the full shade habitat ( $p=9.887 \times 10^{-6}$ ). Cane mass and growth also increased significantly between the full shade and full sun habitats ( $p=.004$ ,  $.043$  respectively) (Figure 12).

Data from the nitrogen experiment helped analyze the constraining effects of important soil nutrients. There was no significant difference in variance. *R. odoratus* showed a significant increase in cane mass ( $p = .005$ ) with the addition of nitrogen. *R. allegheniensis* did not experience this difference (Figure 10). In terms of cane length, neither species exhibited significant changes among the treatments (*R. odoratus*  $p = .064$ , *R. allegheniensis*  $p = .463$ ). In terms of overall cane growth *R. allegheniensis* displayed a significant difference between the treatments (Figure 11). Interestingly, there seemed to be the slight trend that *R. allegheniensis* growth was greater in the treatment without additional nitrogen ( $p = .031$ ). Outliers are attributed to one plant death and natural variation. In terms of between-species variation, *R. odoratus* re-growth from the sprig again displays higher cane mass, cane growth and fruit production than *R. allegheniensis*.

## Discussion

Both *Rubus odoratus* and *Rubus allegheniensis* are common and variable species. They are extremely difficult to study not only because of their clonal characteristics, but because different species growing in different habitats can have highly different genotypes (Aarssen, 1992). However, both species may have important implications for the future of ecosystem management. With changing climates, shifting ranges and the creation of novel ecosystems, we are beginning to see a growing interest in forest and ecosystem conservation and restoration in developed countries (United Nations Environmental Program, 2010). As ecosystems become more highly disturbed, *Rubus* species fall within the category of native plants that may have an advantage in growth and reproduction due to their life history characteristics. By studying the variable life history strategies of these two *Rubus* species, we can begin to understand trends in future ecosystems as well as come up with more effective and sustainable management strategies.

In addressing the natural variability of *Rubus* species, one must first consider that the classification and study of these plants are complicated by hybridization, polyploidy, angiospermy (enclosing seeds in a vessel) and the lack of a universal species concept (Lawrence and Campbell, 1999). *R. odoratus*, in the raspberry subgenus, is generally strictly diploid, meaning that it has two complete sets of chromosomes ( $2n$ ), with some evidence of hybridization. *R. allegheniensis*, in the blackberry subgenus, includes diploids, polyploids (more than two sets of paired chromosomes) and evidence of apomixis (asexual reproduction through seed) (Reznicek et al., 2011). Polyploidy seems to give species an increased tendency towards speciation as well as a broader tolerance of conditions (Futuyma, 2005). *R. allegheniensis* may, in this case, be able to occupy or spread into a greater variety of niches. These discrepancies are not fully addressed in this study and a further genetic study of the *Rubus* populations in the Arboretum would be an important follow up study. These characteristics very likely influence the invasive potential of the plants.

In comparing two naturalized species in the same habitat, it becomes clearer which mechanisms are used to take advantage of certain ecosystem characteristics. *R. odoratus* can be traced to the eastern United States, while *R. allegheniensis* has had a long history across in the United States and is considered native (Ladybird Johnson Wildflower Center, 2010). In Michigan in general, and in the arboretum site specifically, both species have self-sustaining, naturalized populations.

The amount of energy available to a plant that can be allocated to growth and reproduction is limited by environmental factors. Major resources such as light, water, CO<sub>2</sub>, and mineral resources all influence the dimensions of variation between species (Westoby, 2002). Photosynthesis, which provides the plant with energy, is the limiting factor of growth and reproduction processes. Photosynthesis in turn can be limited by low nitrogen or water availability. Invasive species are often able to maximize net photosynthesis relative to nitrogen and water costs (McDowell, 2002). Data collected from the plants in the Nichols Arboretum suggests that *R. odoratus* and *R. allegheniensis* allocate energy to various functions differently. Data on these life history characteristics were analyzed in terms of energy allocated to growth and reproduction.

There seems to be a clear tradeoff between reproductive traits in these *Rubus* species. *R. odoratus* produces a vast quantity of very small seeds (Table 1). This suggests that there is a tradeoff between the amount of seeds produced and the weight of the seeds. Although the plant is producing many seeds, seed size is limited. This also suggests a tradeoff between the number of seeds and the number of fruit per cane. *R. allegheniensis* seems to use a different reproductive strategy: it produces a smaller number of much heavier seeds, again implying that there may be a tradeoff between these traits (Table 1). Physical and energy constraints are more than likely responsible for the existence of such tradeoffs.

Past research on tradeoffs between seed size and number shows that there are different benefits and disadvantages to each strategy. Quite a few studies have found seed output negatively correlated with seed mass even after adjusting for plant size (Westoby et al., 2002). A larger seed size has been shown to yield a greater tolerance to seed predators (Moles et al., 2003). In addition, larger-seeded species generally establish more successfully under hazardous conditions such as deep shade, defoliation, mineral nutrient shortage, and soil drought during seedling establishment (Westoby et al., 2002). Larger seeds tend to have greater reserves relative to the autotrophic functioning parts of the seedling. However these advantages only apply early during the seedling life. Geritz's model shows that large seeded strategies defeat smaller seed strategies in the competition for space. Plants with smaller seeds and higher seed output are able to persist because their seeds reach some establishment opportunities that are not reached by larger seeds (Westoby et al., 2002). Leishman (2001) reveals that this model may operate off of some assumptions that are not generally found in all vegetation types, such as the actual influence of seedling-seedling competition, and the assumption that small seeded plants were always better colonizers. This game theory perspective of seed strategies can give lots of insight regarding why the plants are able to persist and spread in the patterns one sees.

These results may explain some of the patterns noticed in species' success and distribution in the arboretum study site. *R. allegheniensis* grows primarily in the shaded area of the site, while *R. odoratus* clearly dominates the full sunlight area. The study site was historically a dense thicket of buckthorn and honeysuckle, which was then mowed and burned as part of the management strategy to get rid of these invasives. In the aftermath of this disturbance, woodland herbaceous species dominated for a short time before *Rubus* species quickly became established (B.Grese, pers. comm). Following the literature, *R. odoratus*, with its small seeds was most likely able to establish more quickly than *R. allegheniensis*. *R. allegheniensis*, with its larger seeds, has a higher tolerance for the shaded areas of the disturbed site and may have found its colonizing advantage in this way.

In terms of cane growth, *R. odoratus* clearly displays higher cane lengths and weights, suggesting more energy input to these traits. In addition to simply cane growth, *R. odoratus* puts more energy into larger flower and leaf production. If reproductive traits divert energy from growth and maintenance, the cost can represent a constraint on the evolution of possible life history traits (Snow and Whigham, 1989). More vegetative growth can mean less susceptibility to predation and more vegetative propagation. Additionally, the increased vertical growth favored by *R. odoratus* may take away from its tendency towards clonal growth. Clonal growth seems to provide benefits to plants under stressful growing conditions. However, it is also a sink for resources, and the allocation of energy to clonal growth falls under the same ecological controls as sexual reproduction allocation (Bazzaz et al., 1987).

When considering reproductive growth, *R. odoratus*' numerous lighter seeds may be able to travel further and set seeds more quickly. *R. allegheniensis* produces a mass of fruit at the end of a fairly fragile cane. This causes the cane to bend down towards the ground as the fruits mature. The plant may be able to benefit more from sprig reproduction as well as depositing seeds for local spread. This, along with larger seed size, makes the fruit more accessible and tolerant to small mammals that play a role in distant propagation.

*R. odoratus* is able to fruit on first year re-growth, whereas *R. allegheniensis* is not. This implies that *R. odoratus* will possess a greater tradeoff between reproduction and vegetative growth because the reproductive and vegetative structures are developing at the same time. *R. allegheniensis* on the other hand, has more temporal separation in structural growth, meaning there may be less of a tradeoff. This was exemplified in the nitrogen treatment experiment. Growth in *R. odoratus* was characterized by fruit production on almost all plants, regardless of the nitrogen treatments. *Rubus allegheniensis* did not fruit on a single re-growth.

The nitrogen treatment did, however, generate some other interesting results. Most importantly, *R. odoratus* saw a significant and dramatic increase in cane mass—but not in cane length. *R. allegheniensis* did not show this trend. In fact, *R. allegheniensis* may actually have more mass and growth in the control than in the nitrogen treatment (Figures 14-16). The data only support this claim in terms of overall cane growth. However, further experiments using a larger sample size and repeated tests may provide further insight into this interesting development.

These observed patterns suggest that the life history of *R. odoratus* does involve a greater tradeoff between fruit production and vegetative growth because these growth processes occur at the same time. For this reason, nitrogen may limit the plants more in vegetative growth. Removing this limiting factor did not create longer canes, perhaps due to confounding variables, but instead increased the mass of the cane.

Between-habitat variation and phenotypic plasticity also play an important role in the success of these *Rubus* species. In many species, the mean seed mass is the least variable component of yield (Ågren, 1989). However, light availability can significantly affect the morphology and life history characteristics of *Rubus* plants. Ågren found that fruits in shaded populations had a mean seed mass that was 20-25% larger than that of fruits in open populations. Leaf size can also be affected, with shaded populations having leaves almost twice as large as the ramets of sun populations (Ågren 1989).

At first glance, sunlight is one of the main defining features of the study site. The full sun region of the site is colonized mainly by *R. odoratus* plants, while the full shade habitat is colonized by *R. allegheniensis*. For *R. allegheniensis* plants, cane mass, growth and fruit production were dramatically greater in plants growing in the full sun region when compared to those in the full shade region (Figures 17-19). This suggests that direct sunlight provides better growing conditions, and that light may act as the primary limiting resource in the study site. When this limiting factor is removed, the available energy reserves would increase.

One of the main difficulties with this portion of the data collection was the sample size, because the overwhelming majority of *R. odoratus* plants grew in the full sun habitat, and the inverse was true for *R. allegheniensis*, the sample sizes are skewed. It would be more effective to have larger sample sizes in the non-dominant habitat types. Although these data are relatively inconclusive, they suggest that further tests like this may spread light on whether *R. allegheniensis* is more successful in terms of growth and reproduction in a full sun habitat than *R. odoratus*. This would present either further evidence for or counter-evidence for the colonizing and propagation strategies presented above.

This study is limited in its scope in that it only looked at two single populations of *Rubus* plants, in one localized area. Further research on the topic of invasive behavior in naturalized or native plants would help us better understand its future implications. Genetic studies as well as the inclusion of root growth into consideration of the organism's life histories would be extremely useful in creating a more complete body of research on this subject. Root structures are important in terms of gaining nutrition as well as anchoring the plant in soil - a vital consideration, especially in highly disturbed areas. Root structures between *R. odoratus* and *R. allegheniensis* did vary considerably, with *R. odoratus* roots being much larger and thicker in general. However, due to a lack of time data were not gathered from this aspect of the plants.

## *Bigger Picture*

*Rubus* species are generally regarded in a positive light due to their fruit production and aesthetic qualities. In young regenerated forest stands, a majority of the fruit is mainly produced by species that proliferate in disturbed areas- such as *Rubus* species- and which are generally not found in mature closed-canopy stands (Greenburg et al., 2007). In wild areas, *Rubus* species represent interactions between humans and plants as well as provide important food sources to birds and small mammal populations. These species therefore play an important role in land management. They are generally not associated with invasive behavior. However, today *Rubus* plants are most likely more prolific than they were historically and this may be affecting the biodiversity of our ecosystems.

If forest age and forest size play a large role in determining the amounts of pioneer species, one can safely assume that the pre-settlement forests of Northern America had a much smaller percentage of *Rubus* and similar species (Peterson and Carson, 1996). Today, a majority of the world's forests can be described as "disturbed." In fact, according to the Food and Agriculture Organization (FAO), only 36 percent of the 4 billion hectares of forests are still thought of as primary forests with no to minimal signs of human impact (Pan et al., 2010). North America as a whole, but especially the eastern United States is characterized by forest that is only between 1-70 years old (Figure 3). In addition to disturbances, climactic stability is decreasing due to climate change. Plants and animals that are best adapted to high habitat variation will almost certainly out-compete the rest. Often these plants and animals are either invasive or have strong colonizing behaviors as can be seen with *Rubus* plants (Brown et al., 2004). Peterson and Carson (1996) propose that the abundance of seed bank, pioneer species depends on propagule availability, which in turn is determined by both forest age and size. In terms of these species' dispersal, the rate of spread depends on the size and age of the forest stand, the size of the disturbed area and the rate at which seed rain decreases with distance from the source (Peterson and Carson 1996). With this knowledge, one can assume that forest dynamics at the population, community and ecosystem levels are today much different than they used to be.

A changing vocabulary of ecosystem management is created by changing ecosystem dynamics. It can be argued that *Rubus* species should be considered a weedy agricultural plant; however, it has escaped cultivation, and this term does not reflect the full implications of *Rubus*' invasive behavior in urban natural areas. Today, a large amount of wildlife management plans and strategies are based on native and non-native organism distinctions. This makes sense because habitats composed of only native species have better ecosystem function and health. However, this approach may also become limiting when one does not consider the realities of the ecosystem. The areas we are managing are highly disturbed, have novel species compositions, and are being affected by climate change, just to name a few. In light of these disturbances, we must also consider the changing roles of native and naturalized species. As mentioned above, organisms such as *Rubus* plants are at higher population sizes today than historically recorded.

They are successful under disturbance due to their life history characteristics, which mirror those of an invasive species. In this case the definition of “invasive” loses meaning. Less reliance on this term and further inclusion of life history characteristics into management will perhaps allow us to more effectively manage natural areas in the light of pressing environmental issues.

By studying the life history of an organism, it becomes possible to create a more successful management plan for a site or ecosystem. Shifts in species’ ranges as responses to changing temperatures, hydrological cycles and nutrient levels are in the process of creating novel environments. Management in these areas is best carried out by having a local understanding of individual species’ characteristics. Restoration ecology creates a new field or research by using this detailed information to manage entire ecosystems. Palmer et al. (2004) notes that in the future, research perspectives that incorporate human activity as integral parts of the earth’s ecosystem will have to be used. The main goal of restoration ecology is to “conserve and restore historical ecosystems where viable, while also preparing to design novel ecosystems to ensure maintenance of ecological goods and services” (Jackson et al., 2009). Restoration ecology may be able to provide the most effective ecosystem plans to restore ecosystem services lost due to a shift in ecosystem composition.

The study plot used here is essentially an area of fairly high disturbance due to the high number of visitors, proximity to a roadway and the levels of management necessary to maintain a healthy ecosystem in the urban setting. The area is characterized by many early-successional woody plants; primarily *Rubus* species. Abiotic and biotic disturbances may be stopping the habitat from progressing to a later successional stage. Restoration ecology may provide the techniques to speed up succession by increasing the number of desirable native species and decreasing the number and possible spread of intensive, colonizing species such as *Rubus*. This is especially important with species such as *Rubus* that are clonal and propagate widely.

At the moment, the main control strategies of *Rubus* species are hand pulling and chemical control using glyphosphate (Sandler, 2001). Hand pulling is often very disruptive to the soil, which only increases the chances of future invasion or re-growth. Herbicidal treatments that have been used in the past have had limited success, are labor intensive, expensive and can be detrimental to other species as well (Savannah Oak Foundation, 2011). Burning has also been used to control *Rubus* species but is not always possible in small or densely-vegetated areas. Additionally, clonally reproducing species may actually have an advantage in fire prone habitats (Bazzaz et al. 1987). These methods do nothing to limit the remaining seed bank and leave behind the problem of regeneration. Czarapata (2005) notes that integrated vegetation management (IVM) is one of the most successful control strategies. This involves using two or more control mechanisms simultaneously. Due to the many positive characteristics of raspberries, a broader and less intensive management strategy may be more useful.

Although successful management strategies cannot be determined fully without trials, knowledge of *Rubus* life histories can help inform management strategies for these plants. *Rubus odoratus* has the ability to colonize very quickly; so, taking preventative measures to avoid invasions, in combination with controlling their prolific seed creation may be the most effective



strategy. *Rubus allegheniensis* on the other hand, may be easier to control due to its lack of fruiting during the first year. Addressing this species' clonal propagation may be more successful, keeping in mind that this species may have a much broader tolerance of conditions. Management regimens should be monitored and followed up over several years. Plants with these characteristics should be treated like invasives by using a strategy to prevent spread into un-invaded areas before moving into already affected habitat to remove and control the plants. If at all possible, moving the area on to a later successional stage would decrease opportunities for further colonization and decrease the ability of the plants to proliferate in the area.

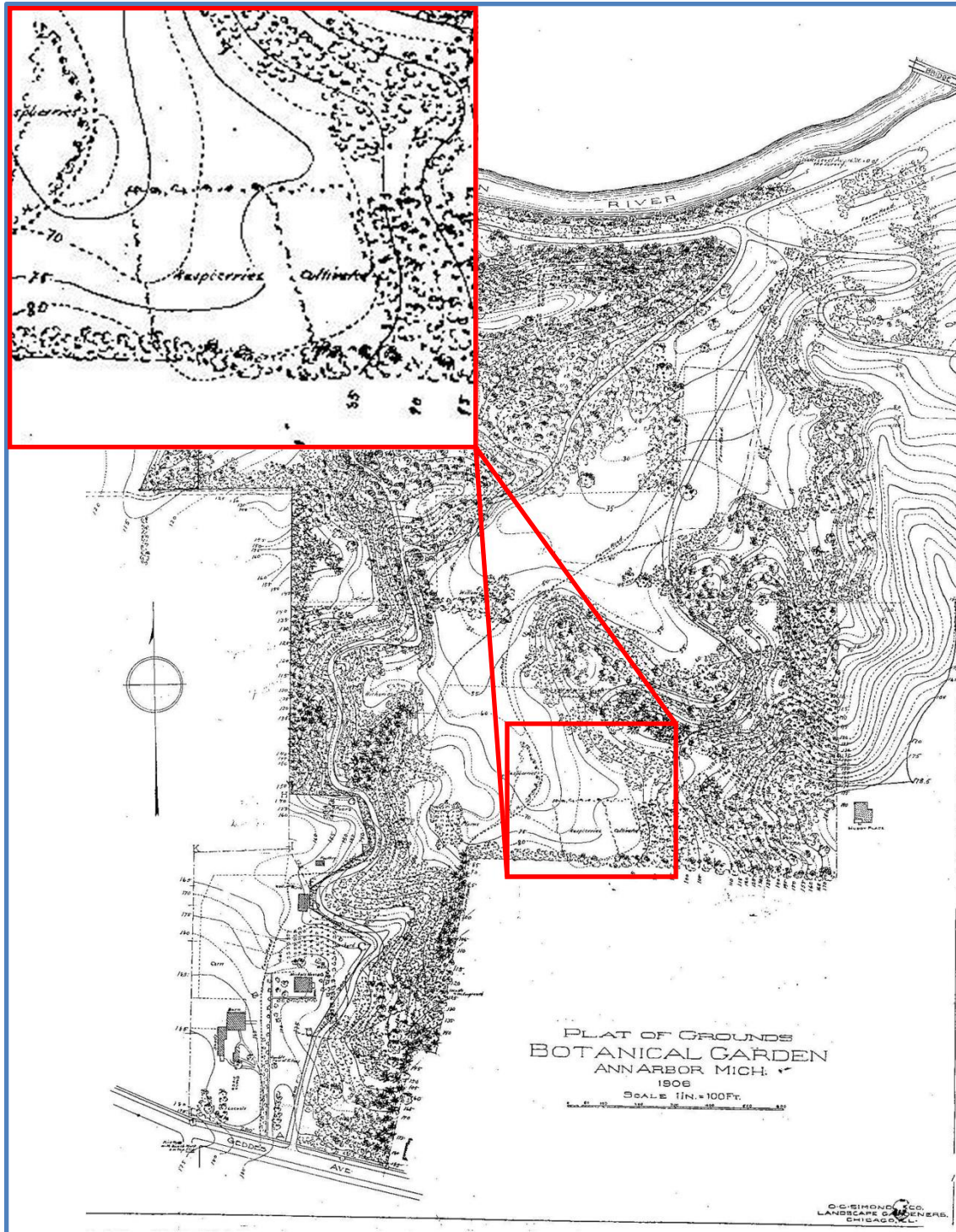
Today when considering management options, we must recognize that it is overwhelmingly important that a restored or reforested area retain strong ecosystem function. The distinction between indigenous and non indigenous plants is very important for the task of choosing plants to be included in restoration efforts. However, when it comes to the control of plant growth for ecosystem management, both non-native as well as aggressive native plants must be viewed as having a potential for negative impacts on biodiversity and ecosystem function.

## Appendix 1: Tables

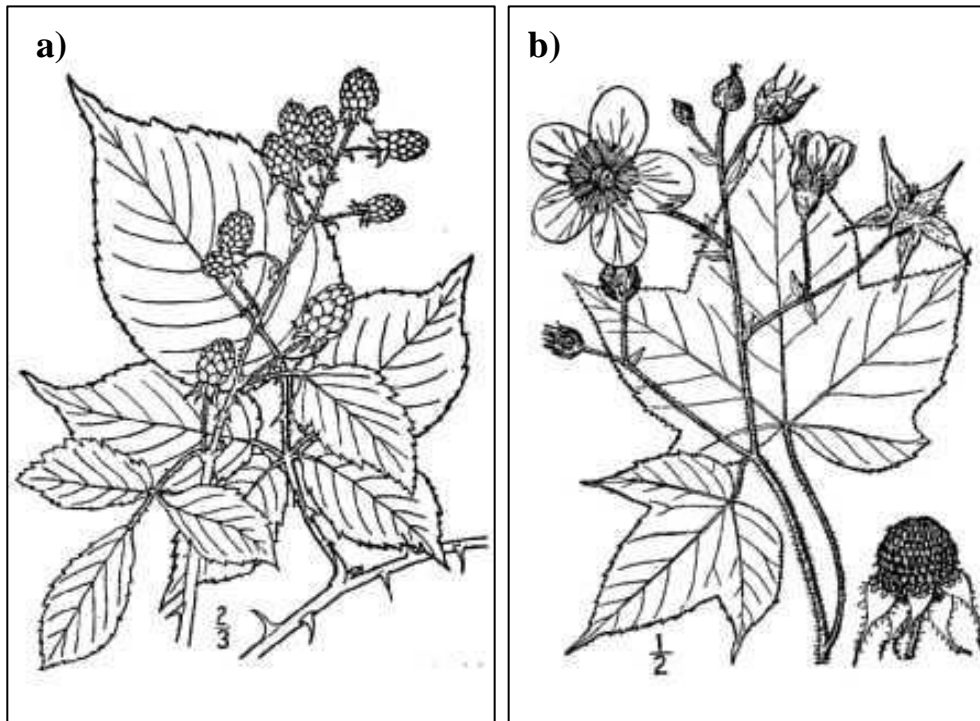
**Table 1:** The between-species differences in *Rubus odoratus* and *Rubus allegheniensis*, including the average values for each trait.

| BETWEEN-SPECIES DIFFERENCES  |                 |                              |                  |
|------------------------------|-----------------|------------------------------|------------------|
| <i>Rubus odoratus</i>        |                 | <i>Rubus allegheniensis</i>  |                  |
| Species Trait                | Average         | Species Trait                | Average          |
| More seeds per fruit         | 80 seeds/fruit  | Fewer seeds per fruit        | 38.5 seeds/fruit |
| Lighter seeds                | .88 mg          | Heavier seeds                | 2.0 mg           |
| Heavier fruit                | 169.5 mg        | Lighter fruit                | 128.9 mg         |
| Few fruit per cane           | 25.4 fruit/cane | More fruit per cane          | 43.6 fruit/cane  |
| Longer canes                 | 137.5 cm        | Shorter canes                | 107.9 cm         |
| Heavier canes                | 34.0 g          | Lighter canes                | 14.9 g           |
| Fruit located along the cane | N/A             | Fruit located at tip of cane | N/A              |

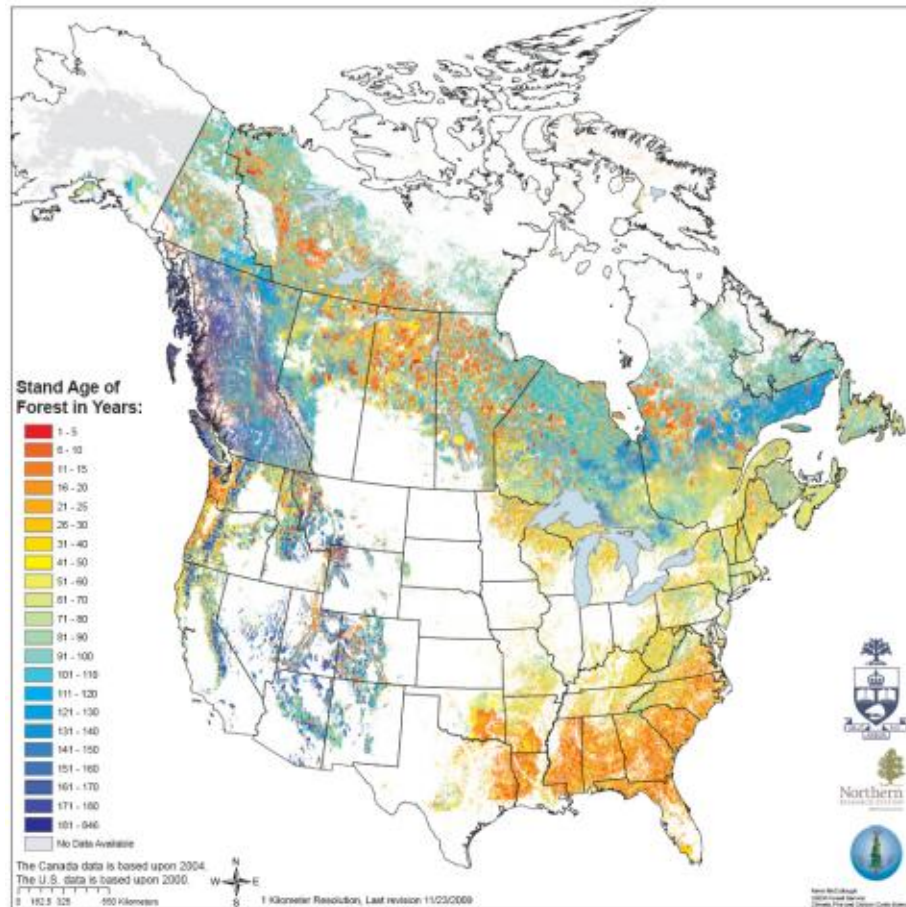
Appendix 2: Figures



**Figure 1:** 1906 Plat Nichols Arboretum grounds drawn by O.C. Simons. The highlighted area depicts the first recorded location of cultivated raspberries [and blackberries] in the Arboretum. All specimens today are considered escapes from cultivation.

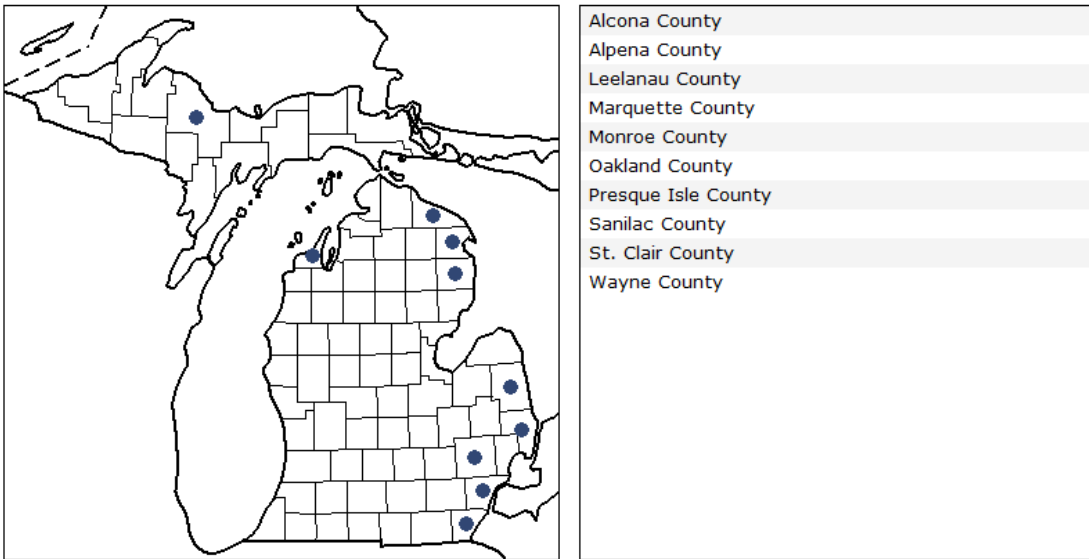


**Figure 2:** (a) The Allegheny blackberry (*Rubus allegheniensis*) is characterized by less vegetative growth than the Purple-flowering raspberry (*Rubus odoratus*) as well as a singular stem with fruits at the cane tip. (b) *Rubus odoratus* is characterized by large purple flowers, and more vegetative growth than *Rubus allegheniensis*, as well as by multiple fruiting stems located along the cane. Courtesy of USDA Plants database.



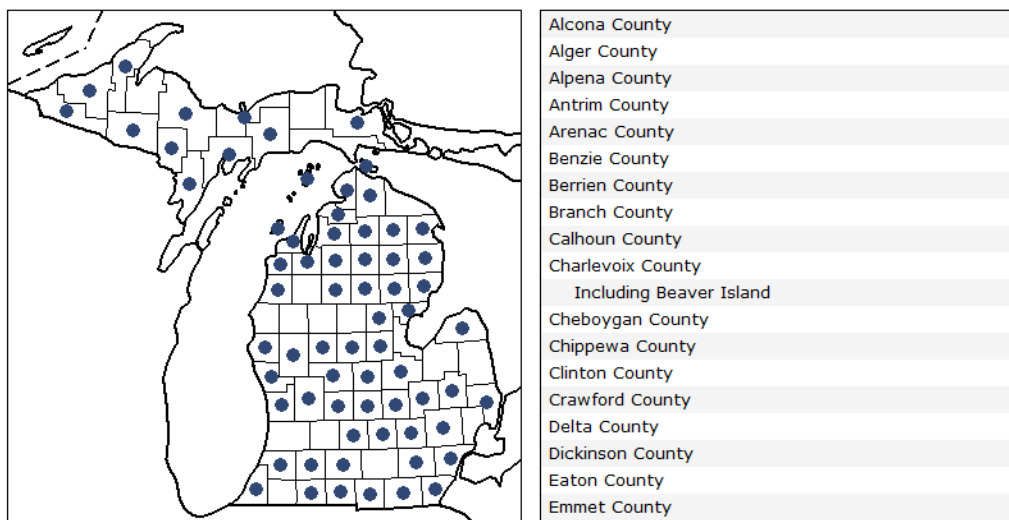
**Figure 3:** This forest age distribution map of North America (excluding Alaska and Mexico) was developed by combining forest inventory data (of US and Canada) with several remote-sensing based disturbance data sources. Figure courtesy of Pan et al. 2010.

**Locations**

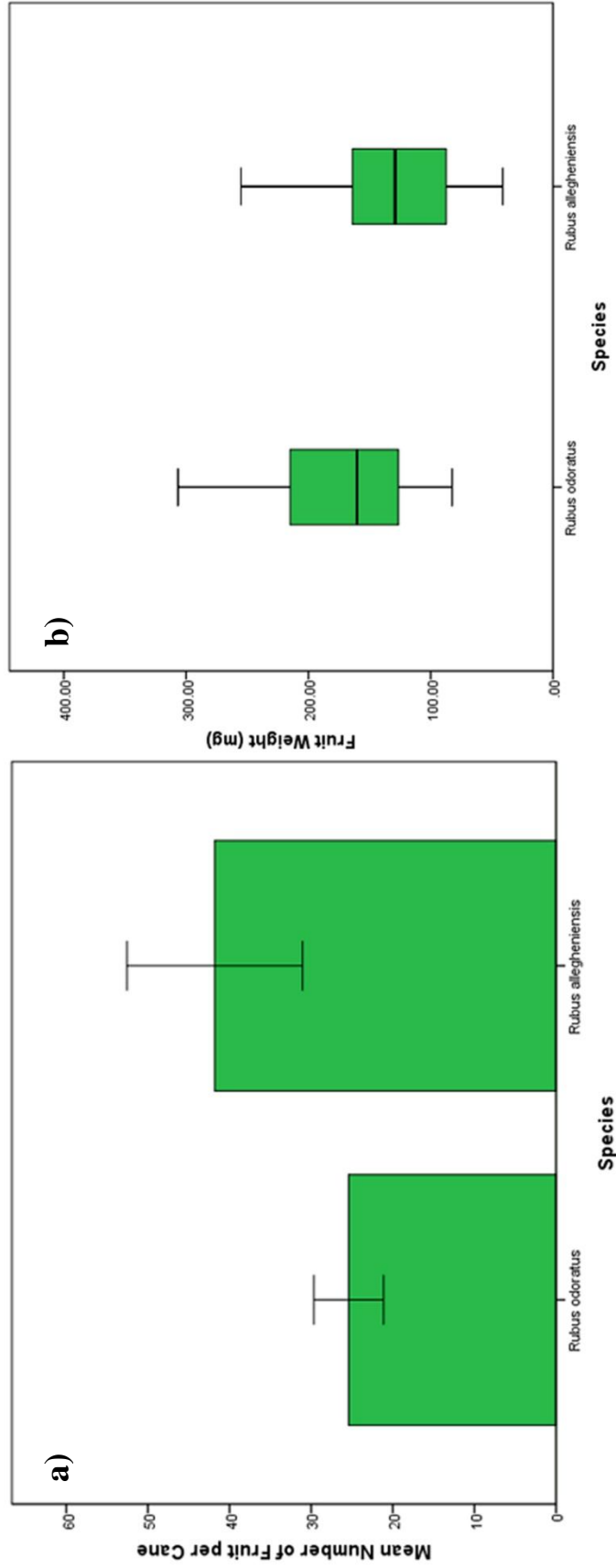


**Figure 4:** Michigan range map of *R. odoratus*. This eastern species with mapped populations in Oakland, Leelanau and Marquette counties most likely represents escapees from cultivation. Courtesy of University of Michigan Herbarium (2011).

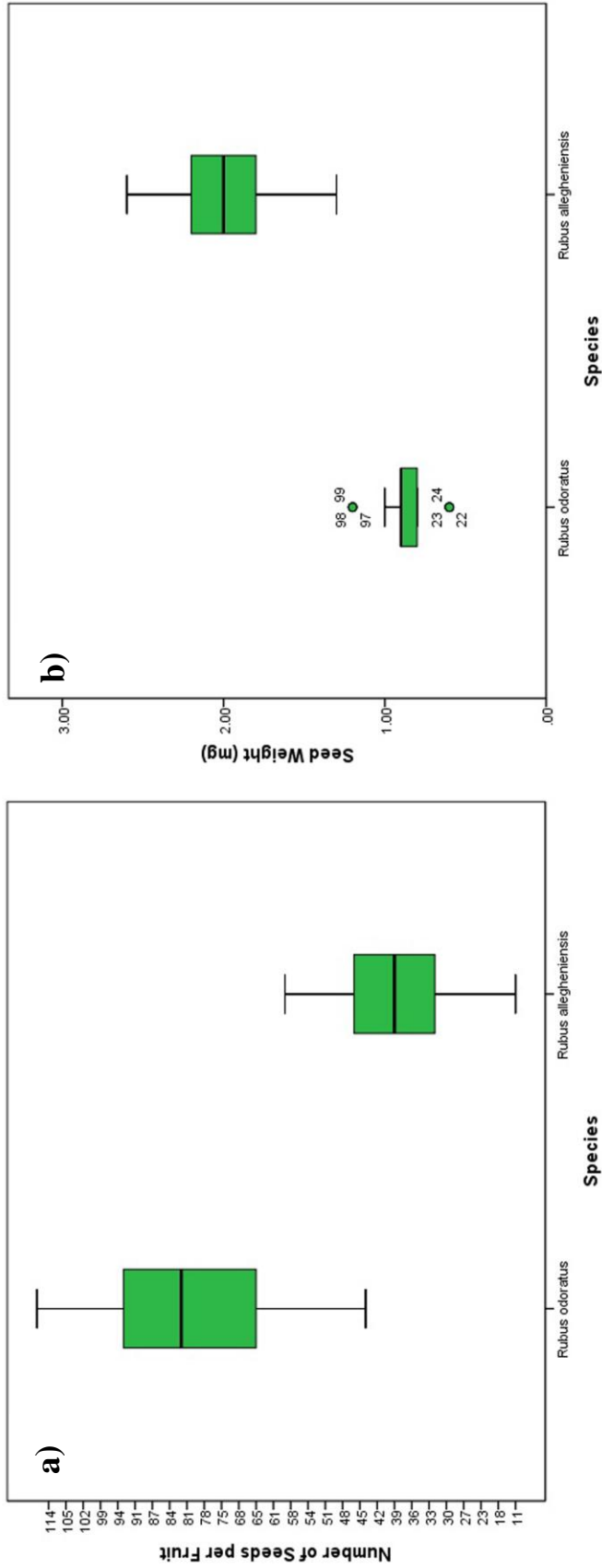
**Locations**



**Figure 5:** Michigan range map of *R. allegheniensis*. This commonly occurring complex species has a wide range throughout Michigan. Courtesy of University of Michigan Herbarium (2011).

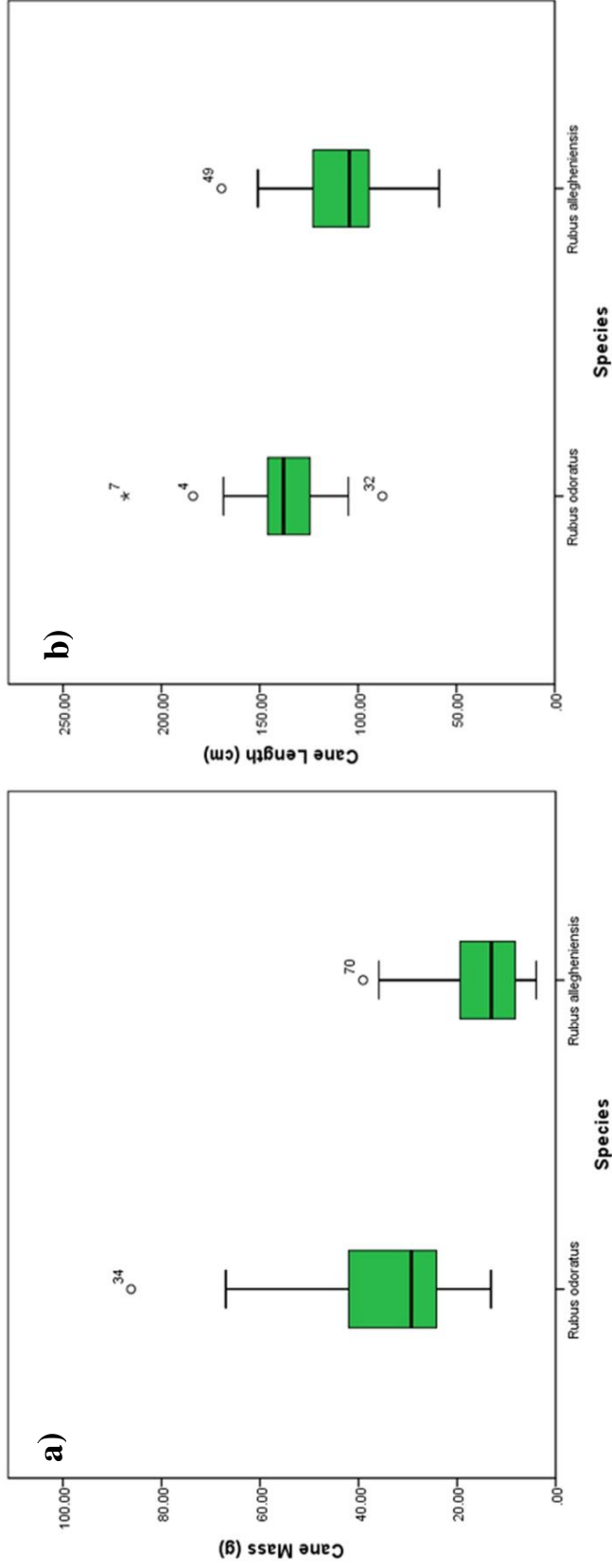


**Figure 6:** (a) *R. odoratus* produced significantly fewer fruit per cane than *R. allegheniensis*. Error bars represent a 95% confidence interval. (b) *R. odoratus* and *R. allegheniensis* both have a similar amount of variation in fruit weight (g). However, *R. odoratus* produces significantly heavier fruits.

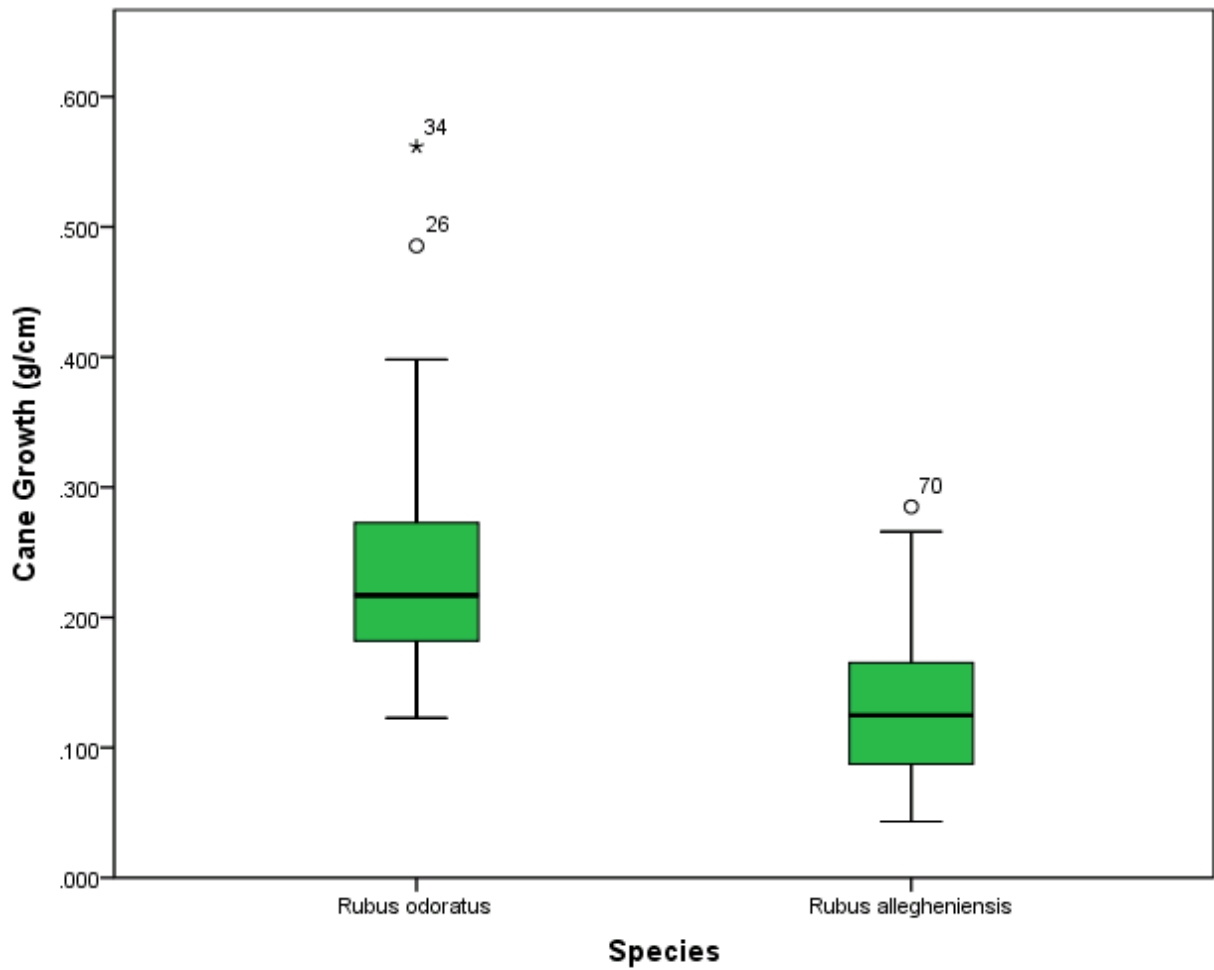


**Figure 7:** (a) *R. odoratus* seeds are significantly lighter than *R. allegheniensis* seeds. The outliers among *R. odoratus* are most likely due to natural variation or confounding factors. (b) The number of seeds produced by each species varies inversely with seed weight. *R. odoratus* produces a significantly greater number of seeds than *R. allegheniensis*.

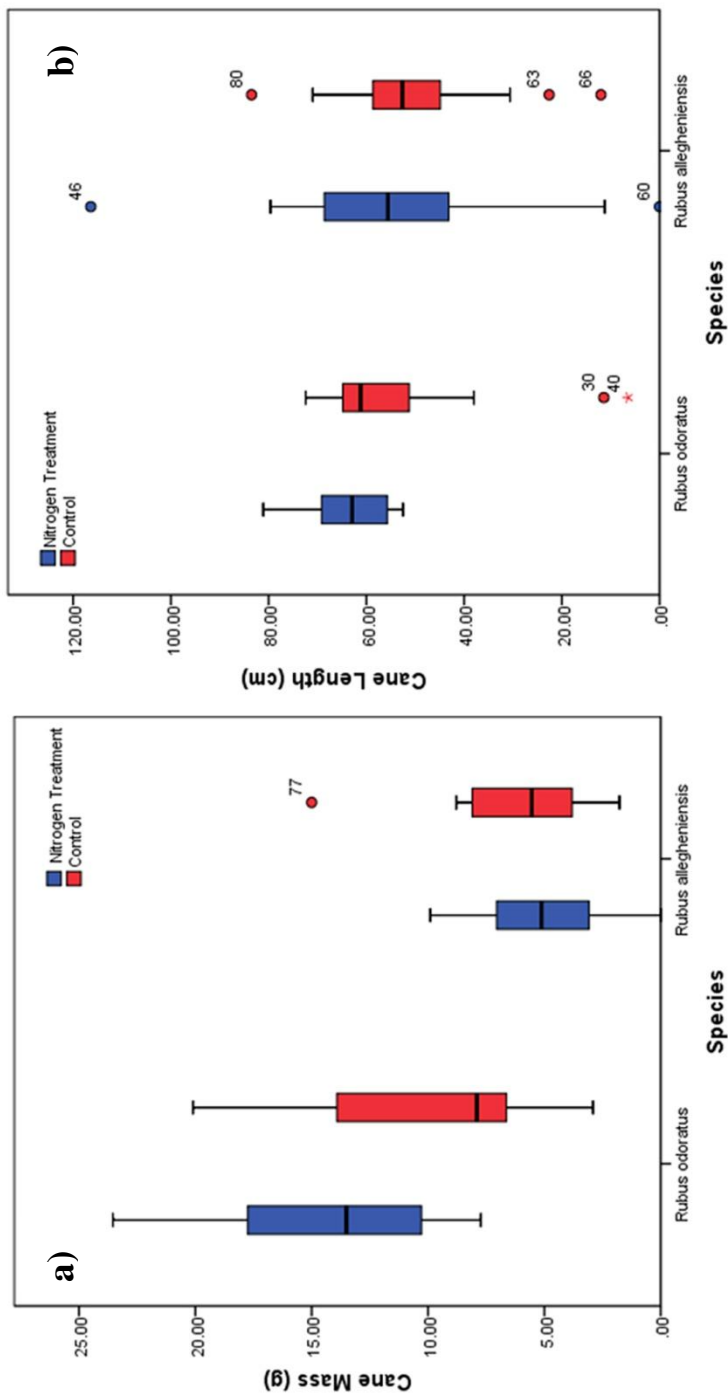




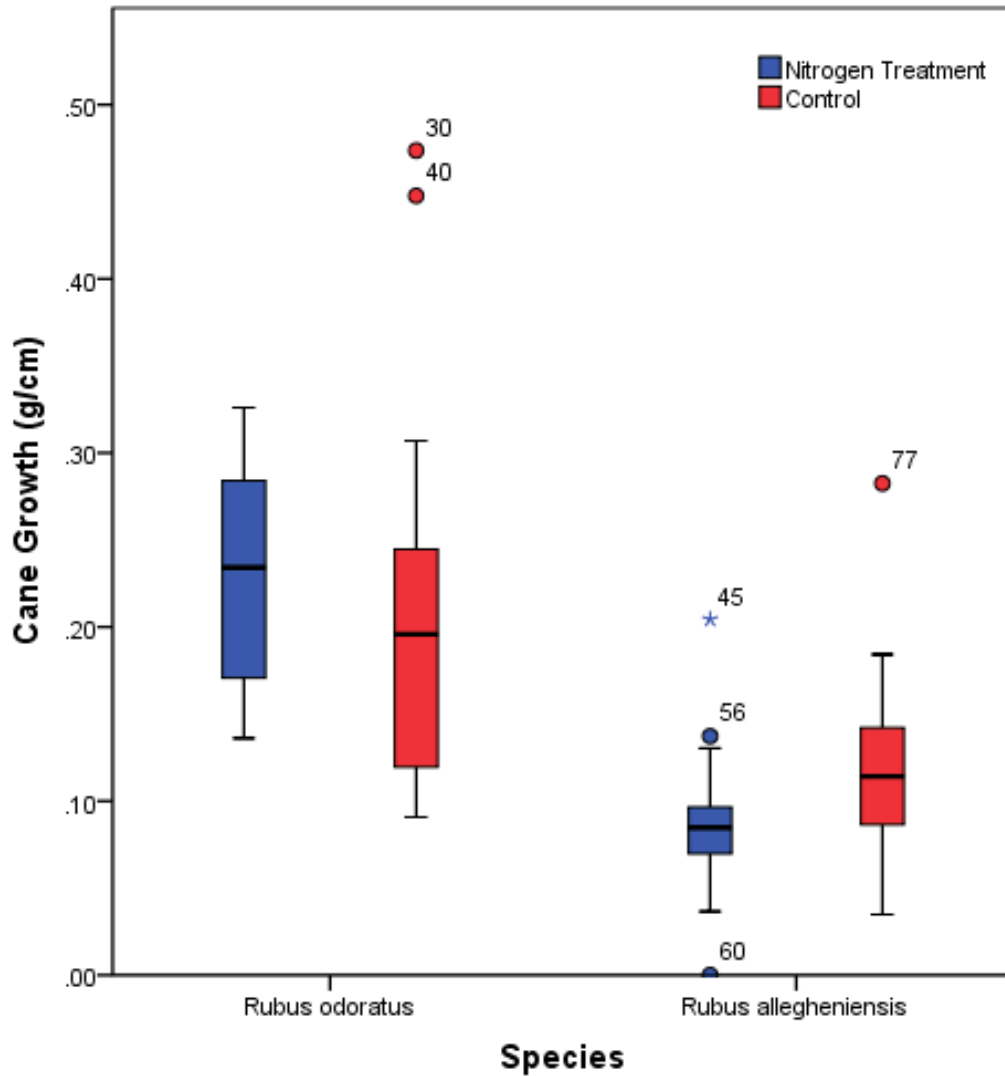
**Figure 8:** (a) *R. odoratus* creates significantly more massive canes than *R. allegheniensis* (g). The range of weights for *R. allegheniensis* is on the whole much lower. Outliers can be attributed to natural variation. (b) *R. odoratus* has significantly longer canes than *R. allegheniensis*, although this species also has more outliers. *R. allegheniensis* has significantly more variation in length.



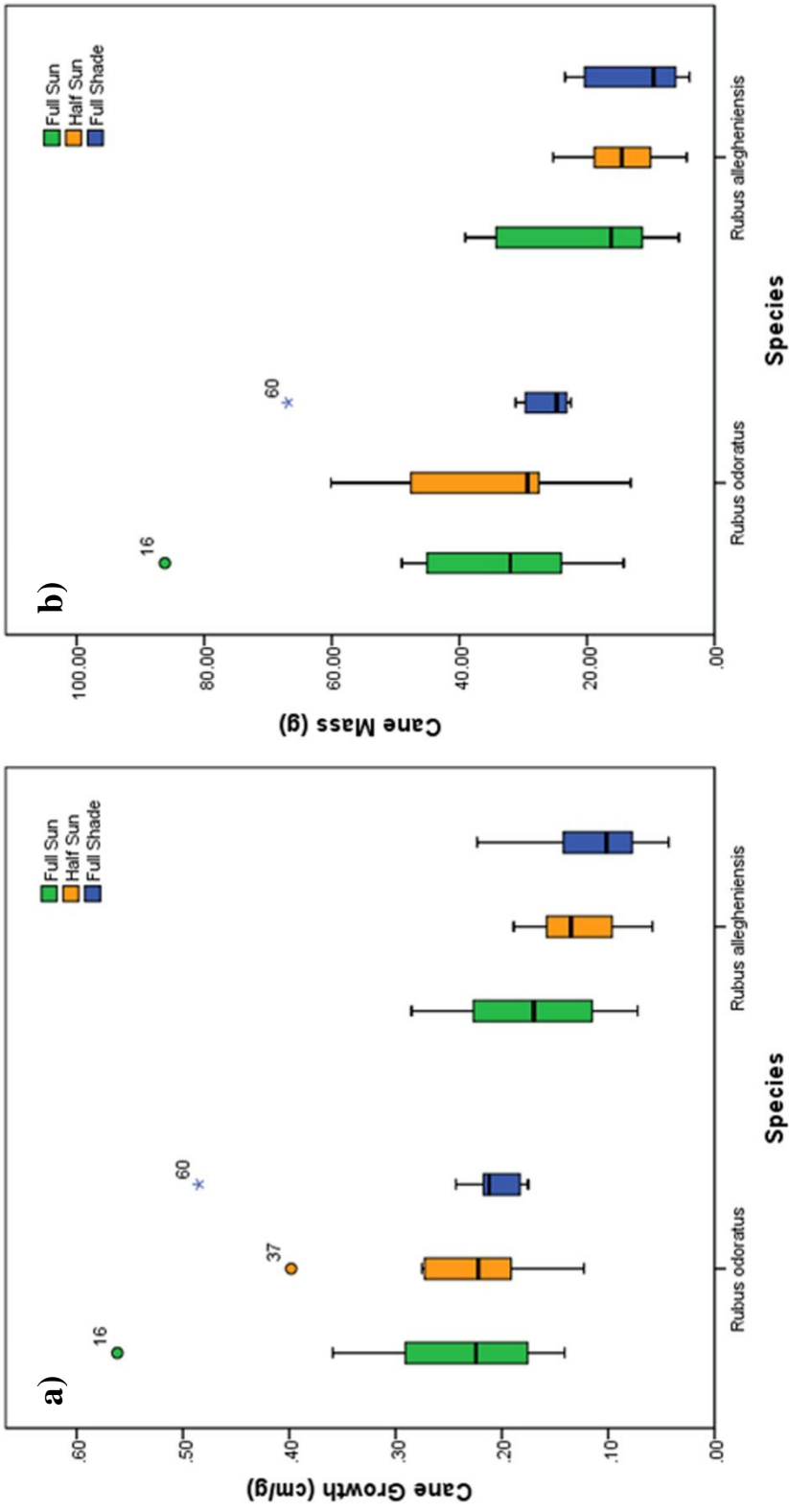
**Figure 9:** When considering both the length (cm) and mass (g), *R. odoratus* has a significantly larger overall growth rate. Outliers can be attributed to natural variation.



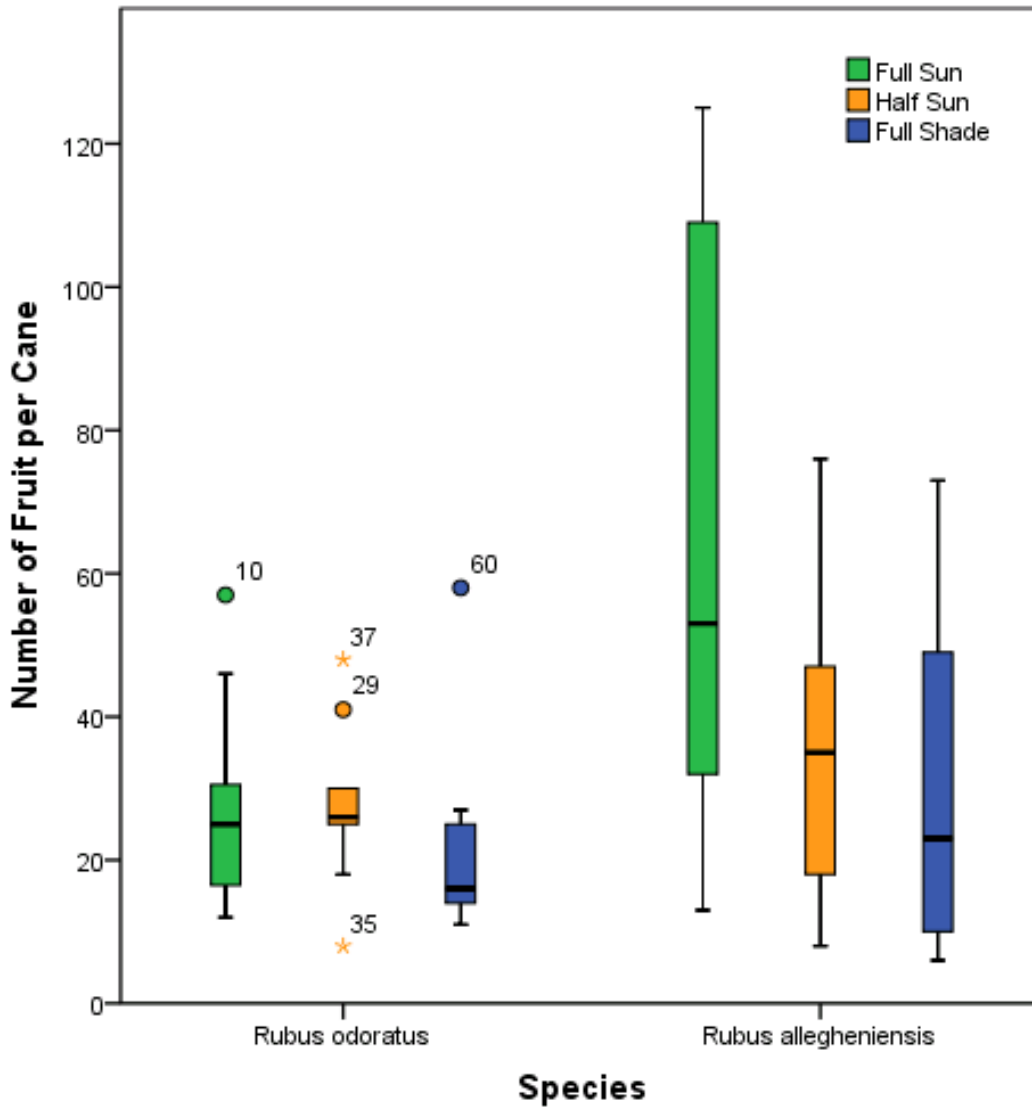
**Figure 10:** (a) Adding nitrogen significantly increased cane mass (g) in *Rubus odoratus*. *Rubus allegheniensis* was not significantly affected by the addition. (b) Neither species showed a significant increase or decrease in cane length (cm). There are significantly more outliers among these results, which may be due to variability in the success of re-growth from the trimmed shoot.



**Figure 11:** *R. odoratus* experienced a significant increase in overall cane growth (g/cm) with the addition of nitrogen, whereas *R. allegheniensis* experienced no significant change. However, there seems to be a slight decrease in growth with the addition of nitrogen in *R. allegheniensis*. Further study is necessary to clarify this possible trend.



**Figure 12:** (a) *Rubus allegheniensis* produced a significant increase in cane growth (g/cm) between the no sun and full sun habitats. *Rubus odoratus* saw no significant change in growth. (b) *R. allegheniensis* again showed a significant increase in cane mass between the no sun and full sun habitat. No significant change in *R. odoratus* was found.



**Figure 13:** *R. allegheniensis*, interestingly, saw a significant increase in the number of fruit produced per cane between the no sun and the full sun habitats, suggesting that sunlight is a limiting factor in this species' fruit production. There is also significantly more variation in the number of fruit produced in this species than in *R. odoratus*. *R. odoratus* saw no significant changes in the number of fruit produced with variation in sunlight.

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