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Effect of Forest Canopy Density on the Distribution of Five *Rubus* Species in Central Pennsylvania

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ABSTRACT

The genus *Rubus*, comprising the raspberries, blackberries and other brambles, includes many familiar plants in Pennsylvania's forests. These species have important effects on the dynamics of the broader ecosystem, and their distribution is impacted by light availability to the understory. In this research, I examined the distribution of five different *Rubus* species at three sites in central Pennsylvania and compared the levels of forest canopy density present over each species. By comparing the results of t-tests between samples of flowering and non-flowering *Rubus* plants, I determined that the invasive *R. phoenicolasius* (wineberry) competes most directly for light with the native *R. allegheniensis* (Allegheny blackberry), a key early-successional species that is important for forest regeneration. These are then followed by *R. occidentalis* (black raspberry) and the low-growing dewberries as the forest develops and its canopy becomes more shaded. Understanding these patterns of *Rubus* succession can help foresters to develop more effective management plans for encouraging native plant regeneration for both economic and wildlife value, while combating the proliferation of invasive species.

Contents

List of Figures

List of Tables

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Introduction

Rubus, comprising the raspberries and blackberries, is a widely distributed genus of plants that are important components of their respective ecosystems. They provide a major food source for wildlife, and many species are likewise cultivated to a great extent for human consumption. In the northeastern United States, *Rubus* is represented by a handful of species that grow as pioneers on ruderal sites and forest edges. These plants exert considerable influence on forest dynamics by encouraging deer browse and allowing new trees to establish themselves on these regenerating sites. *Rubus* competes directly for habitat with several other pioneer species, many of which are invasive and rapidly colonize disturbed sites.

This study was undertaken to compare the ecological niches occupied by five common species of *Rubus* present in central Pennsylvania: *R. occidentalis* L. (black raspberry), *R. allegheniensis* Porter (Allegheny blackberry), *R. hispidus* L. (swamp dewberry), *R. flagellaris* Willd. (northern dewberry), and *R. phoenicolasius* Maxim. (wineberry). The latter of these is of particular interest as an exotic species introduced from Japan; it is listed as a noxious weed in New York and Connecticut (USDA, 2022). A number of papers have been written to survey longitudinal studies of the light ecology of individual *Rubus* species throughout a forest successional cycle; most conclude that the genus is broadly shade-intolerant (Ricard and Messier, 1996; Widen et al., 2018; Donoso and Nyland, 2006; Lautenschlager, 1999). Comparatively few studies have been done to compare the light requirements of various *Rubus* species contemporaneously within a forest. This research aims to answer the following questions:

1) How does the shade tolerance of the five *Rubus* species in this study compare and affect their distribution?

2) Which, if any, native *Rubus* species does *R. phoenicolasius* most directly compete with for light?

It is intended that this research will be useful for forest management and planning to support wildlife populations and encourage forest development, while also limiting the growth of invasive weeds. In order to develop these plans, it will be essential to understand when various *Rubus* species appear in succession to time management activities accordingly.

Review of Scientific Literature

In the northeastern United States, *Rubus* is represented by several species that grow as biennial or perennial shrubs and subshrubs in forest understories, field edges, and roadsides. They are a critical source of food for many wildlife species; *R. allegheniensis* and other blackberry species often comprise the single largest fraction of soft mast in recently timbered areas or other disturbed sites in the Appalachians (Greenberg et al., 2007). In addition, this gives *Rubus* a convenient seed dispersal mechanism, although they are not particularly a high-quality mast and have a low energy content compared to other species (White and Stiles, 1992). Bird dispersal also co-transports the arbuscular mycorrhizae that are associated with *Rubus* (Correia et al., 2019). The plants have several other adaptations that have made them highly successful colonizers of ruderal sites. They reproduce asexually by rooting at the cane tips and form a highly stable seed bank with an exceptionally long viability on the scale of several decades, owing to a hard and impermeable seed coat (Innes 2009). Germination of *R. idaeus*, a red raspberry, requires treatment with concentrated acid to degrade the seed coat, a process that takes many years in nature (Lautenschlager, 1997). Seeds of species such as *R. occidentalis* require multi-year temperature oscillations for germination, staggering emergence over several years to increase the likelihood of growth in ideal conditions (Deno, 1993). However, the seedbank gradually deteriorates over time as trees grow and seeds are lost to predation, decay, or fatal germination under low-light conditions. *Rubus* seedbanks have been found to show a marked drop in density in Pennsylvania hardwood forests at a stand age of around 50-60 years as trees reach maturity and the stored seedbank laid down early in succession is exhausted by decay, predation, or fatal germination (Ristau and Royo, 2020).

As a disturbance-adapted plant, *Rubus* is considered a moderately shade-tolerant to shade-intolerant genus. When forest overstories are removed by major disturbances such as clearcutting or storms, *Rubus* begins to proliferate within 2-3 seasons before gradually becoming a dominant understory species (Donoso and Nyland, 2006). It gradually declines in abundance as trees regenerate and a forest canopy forms over the next 5-20 years (Lautenschlager, 1997). In one forest in Quebec, *R. idaeus* was only present at sampling locations with greater than 7% photosynthetic photon flux density (PPFD), or the percent of total sunlight that reaches through the forest canopy and is intercepted by the plant. Its incidence gradually increased until 25% light penetration, above which it was found at all sites (Ricard and Messier, 1996). Likewise, Lautenschlager (1999) observed that *R. idaeus* growth was inhibited by 70% shading with a shade cloth, while plants grown in 0% or 30% shade showed much greater growth, particularly when fertilized with nitrogen. *R. occidentalis* grew under a wide range of light levels in a study in southern Michigan, but predominantly clustered around a median PPFD of 28.24 $\mu mol\ m^{-2}\ s^{-1}$, approximately 12.8% of full sun. Light intensity over successfully fruiting canes was much higher than that over unproductive canes and correlated with an increasing number of fruits per plant (Bajcz, 2014). These results suggest that *R. occidentalis* will proliferate later in understory succession.

Little research has been focused on the dewberries *R. flagellaris* and *R. hispidus*. As small creeping groundcovers rather than large understory shrubs, they produce less biomass than raspberries or blackberries and are not economically important for production or breeding stock. However, *R. hispidus* is known to follow similar successional patterns to other *Rubus*, although reproductive success through fruit ripening increases with forest maturity (Abrahamson, 1975).

Rubus has profound impacts on the ecology and composition of forests. It competes for understory habitat with the hayscented fern *Dennstaedtia punctilobula*, which, unlike blackberries, deer do not browse. The competition between these two species has major implications for stand regeneration, as deer browse of *Rubus* allows enough light to the ground to promote successful seedling development (Horsley and Marquis, 1983). Conversely, well-established *Rubus* patches can become dense ground cover themselves and interfere with tree establishment (Donoso and Nyland, 2006). This is particularly true of introduced, early-successional species such as *R. idaeus* with high light requirements (Ricard and Messier, 1996). *Rubus* has significant impacts on soil nutrient cycling as well. By shading and cooling soil, they slow organic matter weathering and increase nutrient availability to other plant species. This genus is nitrophilic and the plants' growth is known to be strongly stimulated by soil nitrogen content; N also functions as a plant growth regulator and is essential for chlorophyll formation, so it shows synergistic growth benefits with increased light (Lautenschlager, 1999; Walter et al., 2016). Nitrogen mineralization is frequently increased by the same types of disturbance events that allow *Rubus* to spread (Vitousek and Melillo, 1979). Nitrogen is highly susceptible to loss by runoff, leaching, or denitrification, especially in mature northern hardwood stands of late-successional trees such as sugar maple with low N requirements (Lovett and Mitchell, 2004). Early-successional nitrophiles such as *Rubus* are essential for capturing N in highly erodible soils and thus preventing nutrient loss after disturbance events revert these stands to an earlier phase of succession. As canes die, they recycle N back into the soil to promote establishment and elongation of the young tree stems that eventually replace *Rubus*.

The genetics of the genus is extraordinarily complex, and interspecific hybridization is very common in nature as well as in cultivation (Foster et al., 2019). Authors disagree widely on the distinctions between individual species; frequent revisions to the genus have variously split species or lumped several similar ones together. Rhoads and Block (2000) recognize a total of 18 species in Pennsylvania. The USDA Plants Database (2022) recognizes 67, mostly due to separating blackberries into many more distinct species. For most of the 20th century, the definitive treatment of the genus was a series of monographs by Focke (1910, 1911, 1914) that classified the genus into 12 subgenera, most of which were quite large. This already complex taxonomy was soon made even more so by additional authors describing vastly more species with minute differences. The confusion has become so great that over 5000 Latin names have been published for the blackberries alone, most of which have since been discarded (Jennings, 1988, p. 40). Many of these descriptions were by European botanists working from herbarium specimens sent from North America, and several of their publications have been synonymized (Van de Beek and Widrlechner, 2021). Native blackberries in the eastern United States likely originated as at least five distinct species in the pre-Columbian era, before artificial selection, crossbreeding, and transporting plant materials created the intricate species complex that modern authors recognize (Jennings, 1988, p. 48). This pattern of hybridization creates difficulties for identification, particularly for members of the blackberry subgenus *Rubus*. These individual species (*R. allegheniensis, R. pensilvanicus, R. canadensis,* and several others) occupy nearly identical ecological niches and are only distinguishable by few insignificant morphological features (Hodgdon and Steele, 1962; Rhoads and Block, 2000). For this reason, they will hereafter all be treated as the single species *R. allegheniensis*, the most common of them.

Rubus phoenicolasius, the wineberry, is the only widespread invasive raspberry species in central Pennsylvania. It is easily recognizable by its red fruit, silvery leaves, and stems covered in both prickles and dense red hairs. It was introduced to the United States from Japan in 1890 for use in commercial raspberry breeding, for which it still sees some use (Innes, 2009). It soon escaped cultivation and has now been recorded in at least 21 states of the eastern U.S. (USDA, 2022). Like other members of the genus, it is adapted to ruderal sites and colonizes forest clearings and edges. However, *R. phoenicolasius* shows many adaptations typical of invasive species that allow it to displace native *Rubus* and other plants. Innis (2005) compared several ecophysiological parameters of *R. phoenicolasius* against the native highbush blackberry *R. argutus*. She found that *R. phoenicolasius* had higher photosynthetic efficiency at high light intensity and a lower specific leaf area. The invasive species also showed higher foliar nitrogen content; one of nitrogen's functions as a plant growth regulator is to encourage stem elongation. Her research also found that wineberry produced a higher volume of seed with a higher single-season germination rate. Conversely, other research has found that *R. argutus* seed requires 6-12 months of dry storage or several stratification cycles to produce appreciable germination rates, while the soil seedbank of *R. phoenicolasius* depletes more quickly through germination or decay (Deno 1996; Innes, 2009). Like other raspberries, *R. phoenicolasius* is also adapted to forest gaps and initially requires moderate to high light levels to become established. However, once it becomes established in high-light conditions, it can persist under overgrown canopies even after light availability decreases to levels as low as 5% of full sun (Gorchov et al., 2011). Nearly all the 12 characteristics of weeds described by Baker (1974) apply to this species: rapid growth to flowering, high seed output, self-fertility, seed dispersal mechanisms, vegetative reproduction, etc. Additionally, *R. phoenicolasius* poses a risk to agriculture by serving as an alternate host for many economically devastating raspberry pests and diseases such as raspberry ringspot virus, raspberry bushy dwarf virus, and many species of insects (Martin, 2002; Schilder et al., 2017).

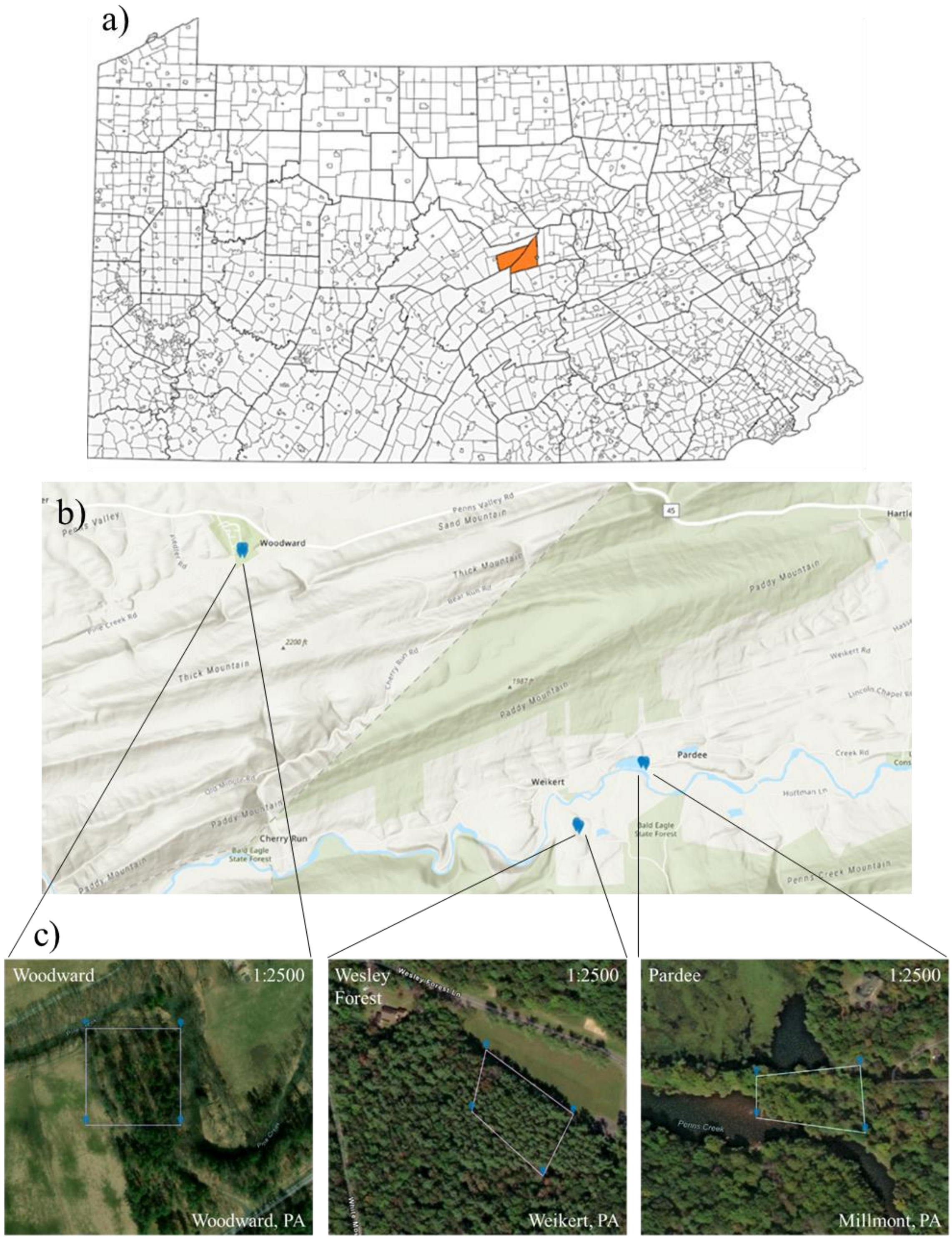
These disruptive effects make it important for land managers to understand the biology and management of this invasive species.

It is evident that *Rubus* is an ecologically important genus in the eastern United States, so there is a need for information on how species interact with one another and develop within forest succession. Most of the existing literature surveyed here focused on only one or two species, so this study aims to capture a more complete picture of the tolerance ranges of the genus as a whole.

Materials and Methods

Three forest sites (Woodward, Wesley Forest, and Pardee) were selected in central Pennsylvania. Woodward is located in Haines Township, Centre County while the other two sites are in Hartley Township, Union County (Figure 1). The site design technique varied slightly from site to site due to the accessibility of each. Soil series data were retrieved from the USDA Web Soil Survey (NRCS, 2023). The dominant trees, shrubs and understory plants, and forbs/herbs at each site are listed in Table 1.

Figure 1. *Locations of survey sites:* ***1a)*** *Map of Pennsylvania, highlighting municipalities of study sites in orange: Haines Township, Centre County (left); Hartley Township, Union County (right);* ***1b)*** *Insert of the above area showing locations of sites;* ***1c)*** *satellite images of sites with corners and edges marked in ArcGIS Pro at 1:2500 scale. Map retrieved from https://upload.wikimedia.org/wikipedia/commons/e/e6/Pennsylvania_Municipalities.svg (public domain).*



Site Descriptions

The site at Woodward, Centre County, PA is a gently sloping, mesic to low-lying forest plot surrounded by a mowed pasture and an intermittent stream at the base of a steep south-facing slope. The soil is a Melvin silt loam, with a high erosivity and shallow depth to the water table. The vegetation consists of a diverse, heterogeneous mixture of native trees and invasive understory plants; the abundance of *Fraxinus americana* seedlings and lack of mature trees indicates that this site recently experienced a heavy disturbance from emerald ash borer invasion. The forest is occasionally used as an equipment storage area, but otherwise experiences little traffic.

The Wesley Forest site is contained within a summer camp ropes course in Weikert, Union County, and accordingly receives heavy traffic throughout the summer months and is crisscrossed by mowed footpaths. It is situated along the lower part of a north-facing slope and borders a mowed sports field. The soil consists of Berks channery silt loam and Buchanan channery loam. The forest was heavily thinned from below in 1992 during the construction of the ropes course to encourage the growth of remaining large trees as structural elements (D. Showalter, personal communication). The stand is heavily dominated by eastern white pine and a dense carpet of hayscented fern over most areas.

The site at Pardee in Union County runs along a cindered path built over an abandoned railroad bed. On one side is a narrow strip of vegetation before a large manmade pond; on the other, a slope drops sharply to a low-lying swampy area until it terminates at the bank of Penns Creek. The soil is a Holly silt loam, found on floodplains. The area was essentially clearcut at the end of the 19th century by the Pardee Lumber Company before being reforested by a Civilian Conservation Corps camp in the 1930s (Shively, 2020; Bastian, 2013, p. 64). A forest inventory of the lumber company's land around the site in 1900 listed several abundant species (American chestnut, white walnut, ash) that have since been eliminated by disease (Bastian, 2013, p. 69). Today it experiences infrequent floods as the main source of disturbance (NOAA, 2020). It also contains a large number of dead ash stems due to emerald ash borer invasion.

Table 1. *Dominant vegetation at each of the three study sites.*

Site	**Trees**	**Shrubs/Vines**	**Forbs/Herbs/Grasses**
Woodward	*Pinus strobus* *Prunus serotina* *Juglans nigra* *Acer saccharum* *Fagus grandifolia* *Tsuga canadensis*	*Berberis thunbergii* *Fraxinus americana*	*Microstegium vimineum* *Mitchella repens* *Dennstaedtia punctilobula*
Wesley Forest	*Pinus strobus*	*Berberis thunbergii*	*Dennstaedtia punctilobula* *Microstegium vimineum*
Pardee	*Lindera benzoin* *Juglans nigra* *Tilia americana* *Fraxinus* sp. (dead)	*Celastrus orbiculatus* *Rosa multiflora* *Ligustrum obtusifolium*	*Impatiens capensis* *Urtica dioica*

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At Woodward, the plot was bounded on three sides by a horse pasture and a streambed. These landmarks were used to roughly estimate the placement of the corners of the plot, which were marked with GPS coordinates and then adjusted as needed to form a rectangular plot 114.59 m x 105.65 m, as measured in ArcGIS Pro. The longer side of the plot was divided into 60 sections (roughly 2 meters wide each). The plots at Wesley Forest and Pardee were bordered by easily walkable terrain (a mowed field and a footpath, respectively). In these cases, the width of the plot was marked by placing one corner and walking 100 paces. The plot was then divided into 100 sections. At Wesley Forest, the length of the plot ran from the field to the southern edge of the ropes course partway up the slope (approximately 75 m); at Pardee, the plot terminated at the banks of Penns Creek and the pond on opposite sides of the path (variable distance).

After dividing each plot into sections, they were blocked into adjacent groups of 10, and one randomly generated section was chosen from each block to find the starting point for each transect[1]. At Woodward these points were determined by calculating their position from GPS coordinates; at the other two sites it was done by walking the respective number of paces along the edge from the initial corner. The length of the transects were then followed using a compass (Silva Systems, Sandy, UT). Every *Rubus* plant within 1 m of either side of the transect was measured; the sample sizes collected are listed below in Table 2.

Table 2. *Total sample sizes of* Rubus *species collected at three sites.*

Abbr.	Species	Common name	Woodward	Wesley Forest	Pardee	Total
o	*occidentalis*	black raspberry	51	1	21	**73**
a	*allegheniensis*	Allegheny blackberry	10	27	12	**49**
h	*hispidus*	swamp dewberry	3	52	0	**55**
f	*flagellaris*	northern dewberry	55	108	18	**181**
p	*phoenicolasius*	wineberry	0	23	30	**53**
		Total	**119**	**211**	**81**	**411**

The following data were collected for each plant: species, percent forest canopy cover, length of the longest cane, and whether the plant had reached the flowering stage (denoted binarily as a 1 or 0 for flowering or not). Forest canopy cover was sampled with a convex spherical densiometer from four directions (north, east, south, and west) and averaged in accordance with the procedure described by Lemmon (1956). Several *Rubus* species, particularly *R. hispidus* and *R. flagellaris*, are known for forming dense, low-growing patches of many closely packed crowns that propagate asexually by stolons (Rhoads and Block, 2000, p. 624). In these cases, where it would not have been feasible or useful to measure every individual crown, several representative

[1]Two transects were taken in the first block of 10 at Woodward, with the intention of doing so in every subsequent block as well; the number of transects to be taken was reduced after this block was sampled due to an abundance of plants and time constraints.

measurements were taken at various spots within the patch. Data on each site were compiled and analyzed in Microsoft Excel.

Results

Complete data tables can be found in Appendix 1. Figure 2 below summarizes the distribution of forest canopy cover over each *Rubus* species, separated into flowering and non-flowering life stages. The descriptive statistics for this figure are presented in Table 3.

Figure 2. *Relative forest canopy openness over five* Rubus *species in central Pennsylvania, in both flowering and non-flowering life stages.*

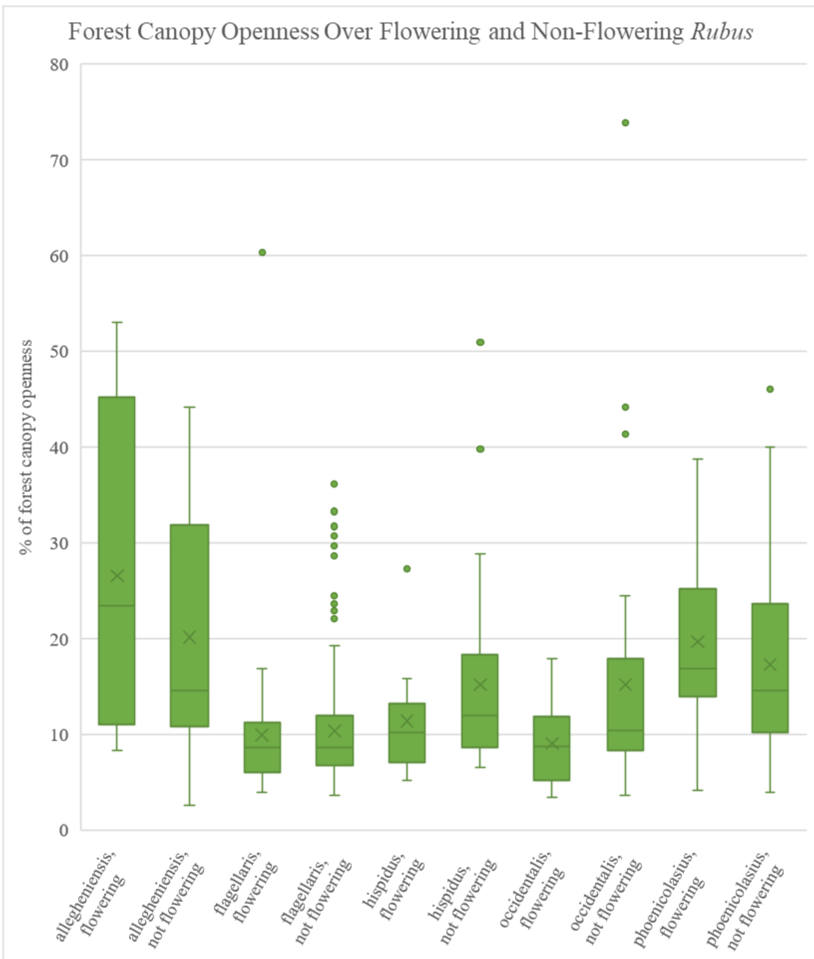

Table 3. *Descriptive statistics of relative forest canopy openness over five* Rubus *species in central Pennsylvania.*

Forest Canopy Openness Over Five ***Rubus*** Species										
	R. allegheniensis		R. flagellaris		R. hispidus		R. occidentalis		R. phoenicolasius	
Flowering?	yes	no	yes	no	yes	no	yes	no	yes	no
Sample Depth	20	29	47	134	19	36	38	35	22	31
Mean	26.55	20.15	9.90	10.37	11.40	15.19	9.06	15.19	19.65	17.28
SE	3.50	2.24	1.19	0.54	1.48	1.61	0.67	2.31	1.85	1.83
Median	23.4	14.56	8.58	8.58	10.14	11.96	8.71	10.4	16.9	14.56
SD	15.64	12.04	8.18	6.22	6.47	9.64	4.14	13.65	8.67	10.20
Min	8.32	2.6	3.9	3.64	5.2	6.5	3.38	3.64	4.16	3.9
Max	53.04	44.2	60.32	36.14	27.82	50.96	17.94	73.84	38.74	46.02
Skewness	0.525	0.39525	5.292	2.117	1.751	2.066	0.475	2.907	0.49	1.288595

Due to the great differences in sample size and variance between the flowering and non-flowering populations of each species, performing an analysis of variance was not feasible, as the test loses power under these conditions. Instead, to determine which species compete with each other, additional two-tailed t-tests were performed on each pair of samples to determine if a significant difference existed between mean light levels ($p<0.05$), with the assumption of unequal variances. The results are presented below in Table 4. Only *R. occidentalis* showed a significant intraspecific difference between light received by flowering and non-flowering individuals.

Table 4*. P-values for two-tailed t-test of forest canopy openness above various* Rubus *species (p<0.05). Yellow shading indicates statistically significant differences; blue shading indicates insignificant differences. "Yes" and "no" indicate whether plants in sample are flowering.*

		R. allegheniensis		*R. flagellaris*		*R. hispidus*		*R. occidentalis*		*R. phoenicolasius*	
		yes	no	yes	no	yes	no	yes	no	yes	no
R. phoenicolasius	yes	9.205E-02	8.637E-01	7.395E-05	5.904E-05	1.272E-03	7.459E-02	1.084E-05	1.369E-01	3.658E-01	
	no	2.591E-02	3.239E-01	1.377E-03	9.216E-04	1.616E-02	3.945E-01	1.494E-04	4.814E-01		
R. occidentalis	yes	8.438E-05	3.809E-05	5.399E-01	1.317E-01	1.628E-01	4.565E-03	1.460E-02			
	no	1.034E-02	1.274E-01	4.676E-02	4.864E-02	1.728E-01	9.991E-01				
R. hispidus	yes	4.835E-04	2.111E-03	4.363E-01	5.198E-01	8.941E-02					
	no	6.474E-03	7.696E-02	1.024E-02	6.765E-03						
R. flagellaris	yes	1.464E-04	2.073E-04	7.235E-01							
	no	1.846E-04	1.781E-04								
R. allegheniensis	yes	1.328E-01									
	no										

Figure 3 on the following page shows the relationship between total light availability and length of the longest cane per plant; the data are separated into flowering and non-flowering individuals within each species. The plants generally showed inconsistent relationships between light and length; trendline slopes were variously positive or negative for each sample, with no clear pattern emerging between species, and correlation was very low (R^2 <0.5 for non-flowering *R. allegheniensis*, and <0.1 for all other samples).

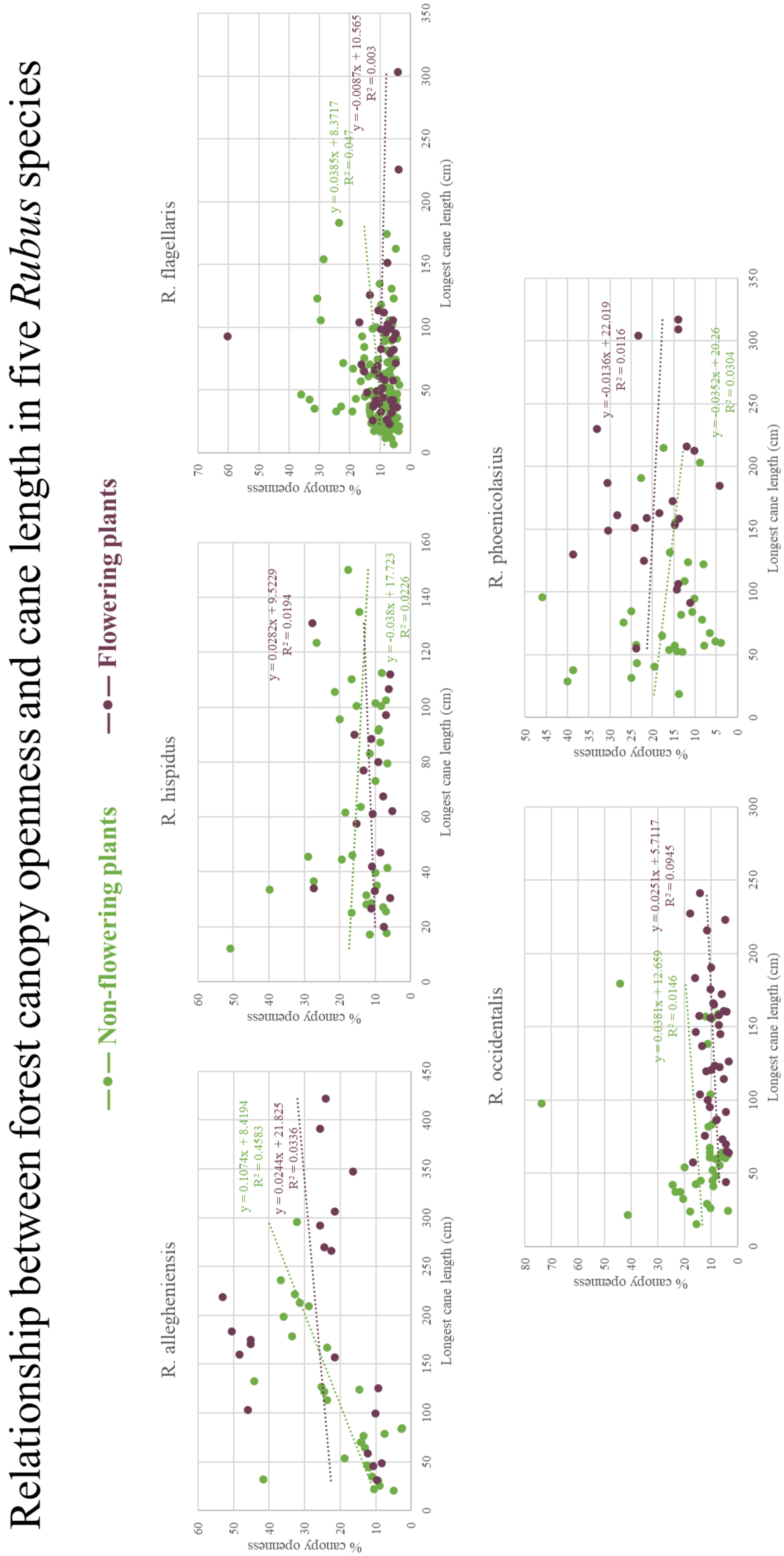

Figure 3. *Comparison of forest canopy openness and cane length in* Rubus.

Discussion

The data indicate that increasing forest canopy cover is associated with a change in the composition of *Rubus* species in Pennsylvania forests. Of the five species studied, all except *R. occidentalis* do not show a significant difference in forest canopy cover at different life stages (non-flowering primocanes versus flowering floricanes). *R. occidentalis* plants showed a higher shade tolerance after producing reproductively mature floricanes; this pattern was also observed in *R. flagellaris* and *R. hispidus*, albeit not at significant levels. This may indicate that survivorship to reproduction is lower in *R. occidentalis* than its relatives as the forest matures and shading increases. Bajcz (2014) also found that reproductive success (in terms of surviving floricanes and fruit per cane) was correlated with light availability in this species, and that it grew under an average of 12.8% of full sunlight. My results corroborate these, as average forest canopy openness over *R. occidentalis* plants was 9.06% in non-flowering plants and 15.19% in flowering plants. Mean light received by *R. allegheniensis* and *R. phoenicolasius* was higher than the other three species; flowering plants received more light than non-flowering individuals, although the difference was not significant for either species. Gorchov et al. (2011) reported that *R. phoenicolasius* can persist and reproduce under shade that would not permit its establishment. My data did not show a significant difference in either direction between the two life stages, but also was based on a single season while the aforementioned study followed individual plants over several years; as such, my results neither contradict nor confirm theirs. However, I was able to reproduce this paper’s observation that *R. phoenicolasius* persists at a lower bound of approximately 5% forest canopy openness. The minimum openness over plants I measured was 4.16% and 3.9% for flowering and non-flowering plants of this species, respectively, and this supports their conclusion that *R. phoenicolasius* is troublesome for its ability to persist as an invasive species in mid-successional forests.

To determine which species *R. phoenicolasius* most directly competes with for habitat, we can use the t-test results in Table 2 and compare which species showed the least significant differences from this one. Three of the four t-tests against *R. allegheniensis* showed no significant difference, more than any other species. The exception was where *allegheniensis* is flowering and *phoenicolasius* is not. *R. occidentalis* and *hispidus* in the primocane stage also were found in similar habitats to both stages of *phoenicolasius* before available light decreases as succession continues. *R. flagellaris* did not appear to occupy the same niche in any case, growing under much lower light than *phoenicolasius*. It follows that *R. phoenicolasius* is a direct competitor of *R. allegheniensis*. The latter native species serves as an important food source for deer, one of the main keystone species in the eastern United States and creates gaps for trees to regenerate as it is browsed (Horsley and Marquis, 1983; Royo and Stanovick, 2019). Deer browse of invasive shrubs such as *R. phoenicolasius* is lower than their native counterparts, and this species becomes more abundant with the presence of deer (Ward et al., 2016; Shen et al., 2016). This means that *R. phoenicolasius* is likely to slow forest regeneration by outcompeting native blackberries and compromise forest health. It also appears to interfere with the establishment of *R. occidentalis* and *hispidus*, which are less ecologically significant but still important for wildlife and forest understory dynamics. These two species were less strongly correlated with *R. allegheniensis*, with insignificant differences found only when neither species was flowering. This suggests that *R. phoenicolasius* occupies an intermediate niche in succession, proliferating after *R. allegheniensis* and before either *occidentalis* or *hispidus*.

These results can be used to construct a rough timeline of when various *Rubus* species may appear sequentially after a disturbance. Species with higher light demands typically appear earlier in succession before the forest canopy closes in. As such, *R. allegheniensis* will typically be the first species of the genus to appear; it is adapted to disturbance well enough that it frequently occurs as a weed in no-till agronomic crops (Glenn and Anderson, 1993). It will most often be followed by *R. phoenicolasius*, its closest competitor for light. *R. occidentalis* will establish thereafter as the overstory begins to develop and displace *allegheniensis*; the late-successional *hispidus* and *flagellaris* will be the final species to proliferate. This timeline is not absolute; the distribution of the three later-successional species displayed a strong positive skew ($\tilde{\mu}_3 > 1$) towards a few individuals receiving much more light. This likely indicates that while these species are adapted to survive and reproduce under low light, they have a high light saturation point and can effectively utilize additional light.

Plant vigor was evaluated in this study by measuring the longest cane of each plant. While this experimental design is intuitive, and was somewhat well correlated with forest canopy openness over flowering *R. allegheniensis* plants, it did not prove useful for the other samples. Most regression lines showed a very low R^2 value and there was not a reliable pattern of either positive or negative correlations between light and length. While light exerts a very strong influence on plant growth rates, there are several other important factors that can influence cane length: soil nitrogen, temperature, or even excessive shade and etiolation. In many flowering plants, the longest cane was a second-year primocane that was not itself flowering. Other related research has measured criteria such as flowers per plant, seed volume, or shoot/root ratio (Bajcz, 2014; Innis, 2005; Lautenschlager, 1999). These techniques may be more useful for future research to employ.

There were several possible sources of error in this experiment that ought to be considered. The first is the possibility of misidentification of plants, a problem that was encountered between the myriad of blackberry species and *R. flagellaris,* which are quite visually similar and mainly distinguished by their upright or trailing habit (Rhoads and Block, 2000). No research could be found that separated the light requirements of blackberry species within *Rubus* subgenus *Rubus*, but it is possible that differences exist. Site selection bias may also have affected data. Not all species were present at all sites – importantly, no *R. phoenicolasius* plants were found at Woodward. Collecting data at more sites would also help to increase sample sizes and give more reliable statistical analyses, as the sample sizes collected here were highly uneven.

The choice of a spherical densiometer for data collection may also have influenced results. Several techniques exist for estimating forest canopy cover, including ceptometry (measuring photosynthetically active radiation), leaf area index with high-resolution hemispherical photography, vertical sighting tubes and visual estimation. This method was chosen for cost-effectiveness, efficiency, and ease of use compared to the alternatives. Ceptometry is highly weather- and time-dependent and would have been impractical over the two-month window during which this study was conducted; leaf area index is highly precise, but it requires sophisticated equipment and cumbersome data processing. Although spherical densiometers are widely used in forestry for estimating canopy cover, their efficacy is the subject of ongoing debate. Some research concludes that they variously systematically overestimate or underestimate forest canopy cover compared to other methods (Ganey and Block, 1994; Cook et al., 1995; Korhonen et al., 2006). Others have found that they give comparable results to hemispherical photography, although they are less accurate than ceptometry at extreme values of heavily shaded forests (Englund et al., 2000; Russavage et al., 2020). Densiometry results are also less influenced by weather than photography (Beeles et al., 2021). As all results were obtained by the same operator and with the same instrument, this may counteract some of the bias, but it remains possible that some systematic error was introduced.

This research creates several further questions for further investigation. While deer preferentially browse native shrubs over invasives like *R. phoenicolasius* as a group, there is scant research on whether this species individually is less palatable than *allegheniensis* (Shen et al., 2016). This study also did not examine all species of *Rubus* present in Pennsylvania, even if the blackberry subgenus is not further divided. Several of these other species including *R. laciniatus* (cutleaf blackberry) and *R. discolor* (Himalayan blackberry) are also invasive and could be managed more effectively with more information on their ecology. Other factors such as soil composition and water availability also influence *Rubus* distribution and are beyond the scope of this research but deserve further study.

Conclusion

Rubus is a highly important genus in the forest understories of central Pennsylvania. This observation of how these species develop, and how *R. phoenicolasius* interferes with native vegetation, can be helpful for developing weed management plans. This species can be managed effectively by mowing, pruning or nonselective broadleaf herbicides such as glyphosate or triclopyr (Innes, 2009). Gorchov et al. (2011) suggests that monitoring treefall gaps within three years of a disturbance event to remove any *R. phoenicolasius* seedlings should effectively control the species in the long term. There is still a great deal of the genus's biology to be investigated in more detail, but these results construct a timeline of when several major species become established throughout forest succession.

References

Abrahamson, W. G. (1975). Reproduction of *Rubus hispidus* L. in different habitats. *American Midland Naturalist*, *93*(2), 471. https://doi.org/10.2307/2424184

Bajcz, A. W. (2014). Reproductive ecophysiology of Rubus occidentalis in southeastern Michigan I. A survey of tolerance ranges. *Rhodora*, *116*(967), 249–266. https://doi.org/10.3119/13-16

Baker, H. G. (1974). The evolution of weeds. *Annual Review of Ecology and Systematics*, *5*(1), 1–24. https://doi.org/10.1146/annurev.es.05.110174.000245

Bastian, J. D. (2013). *Lumbering: A Way of Life at Pardee: Stripping the Forests of Union, Snyder, and Mifflin Counties Through Prosperity and Turmoil*. CreateSpace Independent Publishing Platform.

Beeles, K. L., Tourville, J. C., & Dovciak, M. (2021). Characterizing canopy openness across large forested landscapes using spherical densiometer and smartphone hemispherical photography. *Journal of Forestry*, *120*(1), 37–50. https://doi.org/10.1093/jofore/fvab046

Cook, J. G., Stutzman, T. W., Bowers, C. W., Brenner, K. A., & Irwin, L. L. (1995). Spherical Densiometers Produce Biased Estimates of Forest Canopy Cover. *Wildlife Society Bulletin*, *23*(4), 711–717.

Correia, M., Heleno, R., Silva, L. P., Costa, J. M., & Rodríguez-Echeverría, S. (2019). First evidence for the joint dispersal of mycorrhizal fungi and plant diaspores by birds. *New Phytologist*, *222*(2), 1054–1060. https://doi.org/10.1111/nph.15571

Deno, N. C. (1993). *Seed germination theory and practice* (2nd ed.).

Deno, N. C. (1996). *First supplement to the second edition of seed germination theory and practice.*

Donoso, P. J., & Nyland, R. D. (2006). Interference to hardwood regeneration in northeastern North America: The effects of raspberries (*Rubus* spp.) following clearcutting and shelterwood methods. *Northern Journal of Applied Forestry*, *23*(4), 288–296. https://doi.org/10.1093/njaf/23.4.288

Englund, S. R., O'Brien, J. J., & Clark, D. B. (2000). Evaluation of digital and film hemispherical photography and spherical densiometry for Measuring Forest Light Environments. *Canadian Journal of Forest Research*, *30*(12), 1999–2005. https://doi.org/10.1139/x00-116

Focke, W. O. (1910-1914). *Species ruborum: Monographiae Generis rubi prodromus* (Vol. 1-3). Schweizerbartsche.

Foster, T. M., Bassil, N. V., Dossett, M., Worthington, M. L., & Graham, J. (2019). Genetic and genomic resources for *Rubus* breeding: A roadmap for the future. *Horticulture Research*, *6*(1). https://doi.org/10.1038/s41438-019-0199-2

Glenn, S., & Anderson, N. G. (1993). Hemp dogbane (*Apocynum cannabinum*) and wild blackberry (*Rubus allegheniensis*) control in no-tillage corn (*Zea mays*). *Weed Technology*, *7*(1), 47–51. https://doi.org/10.1017/s0890037x0003685x

Gorchov, D. L., Thompson, E., O'Neill, J., Whigham, D., & Noe, D. A. (2011). Treefall gaps required for establishment, but not survival, of invasive Rubus phoenicolasius in deciduous forest, Maryland, USA. *Plant Species Biology*, *26*(3), 221–234. https://doi.org/10.1111/j.1442-1984.2011.00317.x

Greenberg, C. H., Levey, D. J., & Loftis, D. L. (2007). Fruit production in mature and recently regenerated forests of the Appalachians. *Journal of Wildlife Management*, *71*(2), 321–335. https://doi.org/10.2193/2005-747

Hodgdon, A. R., & Steele, F. (1962). Glandularity in *Rubus allegheniensis* Porter. *Rhodora*, *64*(758), 161–168. http://www.jstor.org/stable/23306538

Horsley, S. B., & Marquis, D. A. (1983). Interference by weeds and deer with Allegheny Hardwood Reproduction. *Canadian Journal of Forest Research*, *13*(1), 61–69. https://doi.org/10.1139/x83-009

Innes, Robin J. (2009). *Rubus phoenicolasius*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: https://www.fs.usda.gov/database/feis/plants/shrub/rubpho/all.html [2022, December 22].

Innis, A. F. (2005). *Comparative ecology of the invasive* Rubus phoenicolasius *and the native* Rubus argutus (dissertation). University of Maryland, College Park, MD.

Jennings, D. L. (1988). *Raspberries and blackberries: Their breeding, diseases and growth*. Academic Press.

Korhonen, L., Korhonen, K., Rautiainen, M., & Stenberg, P. (2006). Estimation of forest canopy cover: A comparison of field measurement techniques. *Silva Fennica*, *40*(4). https://doi.org/10.14214/sf.315

Lautenschlager, R. A. (1997). Effects of perturbations and stimulants on red raspberry (Rubus idaeus L.) seed germination. *The Forestry Chronicle*, *73*(4), 453–457. https://doi.org/10.5558/tfc73453-4

Lautenschlager, R. A. (1999). Environmental resource interactions affect red raspberry growth and its competition with white spruce. *Canadian Journal of Forest Research*, *29*(7), 906–916. https://doi.org/10.1139/x99-078

Lemmon, P. E. (1956). A Spherical Densiometer for Estimating Forest Overstory Density. Forest Science, 2(4), 314–320.

Lovett, G. M., & Mitchell, M. J. (2004). Sugar maple and nitrogen cycling in the forests of eastern North America. *Frontiers in Ecology and the Environment*, *2*(2), 81–88. https://doi.org/10.1890/1540-9295(2004)002[0081:smanci]2.0.co;2

Martin, R. R. (2002). Virus diseases of *Rubus* and strategies for their control. *Acta Horticulturae*, (585), 265–270. https://doi.org/10.17660/actahortic.2002.585.43

National Oceanic and Atmospheric Administration. (2020, January 21). *Historical floods: Penns Creek at Penns Creek, PA*. National Weather Service. Retrieved January 6, 2023, from https://www.weather.gov/media/marfc/FloodClimo/MSL/PennsCreek.pdf

Mr. Matté. (2008). *Pennsylvania Municipalities*. Wikimedia Commons. Retrieved January 5, 2023, from https://upload.wikimedia.org/wikipedia/commons/e/e6/Pennsylvania_Municipalities.svg.

Rhoads, A. F., & Block, T. A. (2000). The plants of Pennsylvania: An illustrated manual. University of Pennsylvania Press.

Ricard, J.-P., & Messier, C. (1996). Abundance, growth and allometry of red raspberry (*Rubus idaeus* L.) along a natural light gradient in a northern hardwood forest. *Forest Ecology and Management*, *81*(1-3), 153–160. https://doi.org/10.1016/0378-1127(95)03643-1

Ristau, T. E., & Royo, A. A. (2020). Influence of stand age, soil attributes, and cover type on *Rubus* (Rosaceae) seed bank abundance. *The Journal of the Torrey Botanical Society*, *147*(3). https://doi.org/10.3159/torrey-d-17-00015.1

Royo, A. A., & Stanovick, J. S. (2019). Deer browsing overwhelms extended leaf phenology benefits: A test case with Rubus allegheniensis and a recalcitrant hay-scented fern layer. *Forest Ecology and Management*, *448*, 294–299. https://doi.org/10.1016/j.foreco.2019.06.019

Russavage, E., Thiele, J., Lumbsden-Pinto, J., Schwager, K., Green, T., & Dovciak, M. (2020). Characterizing canopy openness in open forests: Spherical densiometer and canopy photography are equivalent but less sensitive than direct measurements of solar radiation. *Journal of Forestry*, *119*(2), 130–140. https://doi.org/10.1093/jofore/fvaa052

Schilder, A. C., Hall, H. K., Tzanetakis, I. E., & Funt, R. C. (2017). Diseases, Viruses, Insects, and Weeds of Blackberries and Their Hybrids. In H. K. Hall & R. C. Funt (Eds.), *Blackberries and their hybrids* (pp. 202–244). essay, CABI.

Shen, X., Bourg, N. A., McShea, W. J., & Turner, B. L. (2016). Long-term effects of white-tailed deer exclusion on the invasion of exotic plants: A case study in a Mid-Atlantic Temperate Forest. *PLOS ONE*, *11*(3). https://doi.org/10.1371/journal.pone.0151825

Shively, T. L. (2020). *Nature and history in the west end of Union County, Pennsylvania*. Union County Historical Society.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available online at http://websoilsurvey.nrcs.usda.gov/ accessed 1/4/2023.

USDA, NRCS. 2022. The PLANTS Database (http://plants.usda.gov, 10/23/2022). National Plant Data Team, Greensboro, NC USA.

Van de Beek, A., & Widrlechner, M. P. (2021). North American species of *Rubus* L. (Rosaceae) described from European Botanical Gardens (1789-1823). *Adansonia, 43*(8). https://doi.org/10.5252/adansonia2021v43a8

Vitousek, P. M., & Melillo, J. M. (1979). Nitrate losses from disturbed forests: Patterns and mechanisms. *Forest Science, 25*(4), 605–619. https://doi.org/10.1093/forestscience/25.4.605

Ward, J., Williams, S., & Linske, M. (2016). Independent effects of invasive shrubs and deer herbivory on plant community dynamics. *Forests, 8*(1), 2. https://doi.org/10.3390/f8010002

White, D. W., & Stiles, E. W. (1992). Bird dispersal of fruits of species introduced into eastern North America. *Canadian Journal of Botany, 70*(8), 1689–1696. https://doi.org/10.1139/b92-208

Widen, M. J., Petras O'Neil, M. A., Dickinson, Y. L., & Webster, C. R. (2018). *Rubus* persistence within silvicultural openings and its impact on regeneration: The influence of opening size and advance regeneration. *Forest Ecology and Management*, *427*, 162–168. https://doi.org/10.1016/j.foreco.2018.05.049

Appendix 1: Complete Raw Data Tables

Species abbreviations are as listed in Table 2: o=*R. occidentalis*; a=*R. allegheniensis*; h=*R. hispidus*; f=*R. flagellaris*; p=*R. phoenicolasius*.

				Woodward			
Species	**Transect**	**N**	**E**	**S**	**W**	**Length (cm)**	**Flowering?**
o	4	56	74	75	79	97.5	0
o	4	65	17	21	56	21.5	0
o	6	8	20	14	27	23.8	0
o	6	13	17	13	36	32.3	0
o	6	18	8	5	46	53.8	0
o	6	19	8	3	53	36.9	0
o	6	15	10	5	25	157.5	1
o	6	18	10	3	31	183	1
o	6	25	8	4	28	57.7	1
f	10	27	25	84	96	92.3	1
f	10	11	65	62	1	46	0
a	10	5	9	20	20	69.8	0
o	10	14	6	34	36	37.2	0
o	10	8	3	19	31	42.6	0
a	10	3	10	13	46	53.5	0
o	10	9	3	6	35	45.1	0
o	10	7	5	7	21	64.1	0
o	10	7	6	1	3	44.1	1
o	10	6	4	4	3	69.3	1
o	10	7	10	6	7	86.5	1
o	10	10	4	7	5	122.3	1
o	10	9	9	10	7	41.2	0
o	10	6	7	10	8	48.2	0
o	10	11	7	15	7	60.6	0
o	10	11	7	15	7	67.6	0
o	10	11	7	15	9	81.3	0
o	10	10	6	13	7	44.8	0
o	10	3	3	10	10	55.7	0
o	10	3	5	8	11	150.8	1
o	10	3	6	7	4	114	1
o	21	27	8	3	22	15	0
f	21	5	5	8	26	27.5	0
f	21	6	3	8	27	42.1	1
f	21	0	8	12	10	24	0
f	21	4	5	25	7	63.4	0
f	21	0	2	25	7	18.1	0
f	21	4	5	13	4	61.6	0
f	21	3	9	5	7	31.5	1
f	21	3	3	3	5	20.8	0
o	21	3	3	1	7	24.5	0
f	21	4	5	3	3	17.1	0
f	21	6	6	6	5	81.5	1
f	21	8	5	4	5	90.5	1
f	21	6	8	5	7	39.9	0
o	21	5	9	5	20	175.5	1
o	21	11	10	10	6	83	0
o	21	9	11	10	15	119.4	1

o	21	9	11	7	11	120.5	1
o	21	6	5	7	9	60.6	0
o	21	0	4	10	9	172	1
o	21	9	8	4	6	158	1
f	21	8	8	4	5	41.5	1
o	21	10	11	6	7	165	1
o	21	8	9	2	4	64	0
o	21	5	8	1	3	91.5	1
o	21	6	9	4	3	73	1
o	21	11	13	6	6	52	0
o	21	15	8	4	6	123.5	1
o	21	9	13	3	6	86	1
o	21	12	20	11	11	103.5	1
f	21	11	4	7	1	36	0
o	21	9	5	8	17	156	1
o	21	9	8	9	9	166	1
o	21	13	8	8	9	190.5	1
o	21	18	8	7	7	95	1
o	21	7	15	8	21	136.5	1
o	21	7	16	5	19	75.5	1
o	21	3	16	7	17	100	1
h	35	18	11	10	15	63.5	0
h	35	5	5	16	37	46	0
f	35	7	14	11	7	18.5	0
f	35	10	20	12	10	70	0
f	35	7	9	13	12	61.5	0
h	35	5	8	7	5	41.5	0
f	35	2	6	4	5	47	0
f	35	5	6	5	6	35.5	0
f	35	1	10	9	8	15.5	0
f	35	3	7	9	10	72	0
f	35	0	4	10	7	6.5	0
f	35	8	5	14	9	39	0
f	35	18	6	5	10	60.5	1
f	35	8	9	9	8	41.5	0
f	35	7	10	6	8	96	1
f	35	15	15	11	5	17	0
f	35	11	7	4	4	40.5	0
f	35	9	17	6	4	18.5	0
f	35	10	8	12	6	19.5	0
f	35	9	5	10	6	15	0
f	35	7	4	7	6	11	0
f	35	12	5	8	12	51	0
f	35	8	13	6	11	16.5	0
f	35	9	5	7	19	40	0
f	35	14	6	3	12	23	0
f	35	10	11	6	19	63.5	0
f	35	8	12	6	16	69	1
f	35	9	9	9	13	30.5	0
f	35	3	14	11	9	50	1
f	35	2	8	6	3	71.5	1
f	35	7	18	16	4	66	1
f	35	5	8	11	5	50.5	0
f	35	5	10	10	5	26	1
f	35	10	9	8	5	11.5	0
f	35	5	7	6	4	57.5	1

f	35	6	16	6	6	24.5	0
a	35	10	16	8	3	31	1
a	35	3	6	6	4	20.5	0
a	35	6	16	6	6	25.5	0
a	35	12	16	7	4	99	1
f	35	9	17	15	10	29.5	0
a	35	7	9	11	5	48.5	1
a	35	10	19	7	12	46	0
a	35	3	9	10	14	30.5	0
a	35	7	16	11	7	45.5	1
f	49	14	8	4	15	22.5	0
f	49	24	6	5	15	23.5	0
f	49	19	15	3	22	64.5	1
f	49	14	68	27	5	105.5	0
o	49	8	66	13	7	42	0
f	49	8	53	43	6	154	0

Wesley Forest

Species	Transect	N	E	S	W	Length (cm)	Flowering?
h	4	96	77	1	22	12.2	0
h	4	67	22	7	9	36.6	0
h	4	47	12	4	1	24.8	0
f	4	52	10	5	7	32.9	0
f	4	33	11	5	4	60.6	0
f	4	30	5	4	4	20.1	0
f	4	29	14	10	7	65.6	0
f	4	34	2	6	8	46.5	0
f	4	8	3	6	9	48.9	0
f	4	11	5	8	9	88.5	0
f	4	11	15	13	13	32.5	0
h	4	14	9	9	11	88.7	1
f	4	14	5	9	9	118	0
p	4	16	10	12	12	52.2	0
f	4	11	9	6	2	18.5	0
f	4	13	9	8	4	24.1	0
h	21	67	28	2	8	34	1
h	21	14	7	4	5	67.5	1
f	21	19	6	9	7	45.4	0
f	21	11	9	12	12	99.8	0
p	21	16	17	25	17	40.5	0
h	40	37	12	4	6	57.5	1
f	40	26	13	5	8	34.1	0
f	40	5	5	4	12	39.5	0
f	40	6	7	3	2	57.8	0
f	57	41	6	3	12	70.5	1
f	57	21	4	1	3	151.5	1
f	57	56	1	2	14	67	0
f	57	51	4	0	10	104	1
f	57	47	2	0	11	66.5	0
f	57	20	4	2	6	36	0
f	57	13	4	5	4	98.5	0
f	57	8	5	4	2	74	0
f	57	6	3	9	6	74	0
f	57	10	7	11	4	63	0
f	57	5	2	8	11	51	0
f	57	6	4	2	5	91	0

f	57	11	12	19	10	35	0
f	57	14	8	19	10	49	0
a	57	14	8	8	13	35	0
p	57	5	15	11	14	123.5	0
f	60	60	3	2	4	43	0
f	60	27	3	2	5	40	0
f	60	16	2	3	8	98	1
f	60	17	2	5	5	102	1
f	60	8	3	4	7	105.5	1
f	60	6	4	5	4	36	0
f	60	15	3	5	4	23	1
f	60	12	2	6	2	37.5	1
f	60	12	2	6	2	31.5	0
f	60	14	1	6	1	42	1
f	60	7	1	6	2	17.5	0
f	60	11	4	9	6	63	0
f	60	7	1	11	8	105.5	0
f	60	10	4	10	10	111.5	1
f	60	12	6	9	9	51	1
h	60	12	14	15	15	134.5	0
h	60	13	4	13	11	61	1
h	60	6	3	10	6	79.5	0
h	60	9	2	12	10	47	1
h	60	7	4	13	10	92	0
h	60	5	3	7	7	30.5	1
h	60	2	5	5	10	112	1
f	60	5	10	7	10	53.5	0
f	60	8	6	3	12	21	0
h	60	6	7	4	14	112.5	0
f	60	5	6	3	4	18.5	0
o	60	11	10	7	8	156	0
a	60	14	9	11	12	44	0
p	60	15	16	17	8	155.5	0
p	60	14	11	22	7	309	1
f	60	13	10	20	12	48	1
p	60	17	10	21	13	131.5	0
f	60	7	7	15	8	98	1
p	60	10	15	19	11	102	1
p	60	5	6	8	11	57	0
p	60	12	13	17	11	18.5	0
p	60	12	7	9	11	94.5	0
a	60	15	7	7	11	21.5	0
h	15	51	12	0	12	44.5	0
h	15	29	3	3	8	26.5	1
f	15	29	10	2	7	99	0
h	15	29	10	2	7	31.5	0
h	15	19	2	4	2	25.5	0
h	15	16	6	4	3	20	1
h	15	14	7	5	4	27	0
h	15	16	9	11	8	17	0
h	15	15	11	9	8	28.5	0
h	15	13	7	11	7	39.5	0
h	15	17	8	13	10	28	0
h	15	14	9	7	9	33	1
a	15	13	11	12	14	64	0
f	15	6	10	6	8	174	0

h	15	3	2	10	12	97	1
p	15	5	10	10	6	122	0
h	15	7	7	6	6	17.5	0
h	15	10	9	13	5	35	0
h	15	6	7	13	9	91.5	0
f	15	4	12	13	10	61.5	0
h	15	7	9	11	11	73	0
p	15	10	12	13	11	216	1
p	15	13	7	15	13	108.5	0
p	15	13	11	15	15	106.5	1
p	15	15	14	13	15	153	1
p	15	13	14	15	17	172	1
a	15	14	12	11	15	76	0
a	15	16	13	11	15	70	0
h	37	34	7	5	5	77	1
f	37	17	8	7	13	43	0
f	37	13	6	7	9	35.5	0
f	37	24	6	7	10	37	1
f	37	15	6	8	6	43	0
f	37	9	2	3	4	41.5	0
f	37	3	6	7	10	20	0
f	37	5	6	8	5	27	0
f	37	4	7	8	7	20	0
f	37	5	2	9	10	32	0
f	37	5	5	5	9	25	0
f	37	4	4	8	5	25	0
f	37	12	7	7	2	25.5	0
f	37	20	7	8	3	26	0
f	37	9	9	9	6	21	0
f	37	9	9	7	8	35.5	0
f	37	10	5	8	6	26.5	1
f	37	9	9	10	7	44	1
f	37	11	9	9	8	32	1
f	37	11	10	9	10	39	1
f	37	14	10	10	9	49	1
f	37	14	10	9	11	62	0
f	37	15	8	12	11	38.5	1
f	37	14	10	12	12	25.5	1
a	37	16	11	10	10	58	1
f	37	10	9	5	6	42	0
f	37	5	8	8	6	30	0
f	37	4	12	5	6	17	0
f	37	7	12	6	5	38	0
f	79	82	17	4	25	42.5	0
h	79	91	20	9	33	33.5	0
f	79	61	9	1	14	71.5	0
f	79	64	8	2	14	36.5	0
f	79	81	15	6	20	35	0
h	79	74	11	4	18	130.5	1
f	79	47	4	4	8	57	0
f	79	36	3	5	8	37.5	0
h	79	42	4	3	10	100.5	0
h	79	10	2	6	9	102.5	0
h	79	19	3	7	4	87	0
f	79	16	2	4	3	99	1
h	79	5	0	6	9	62	1

f	86	11	7	6	8	93	0
h	86	19	3	5	11	101.5	0
f	86	7	6	5	9	65	0
f	86	7	3	4	9	102	0
f	86	7	5	7	5	89.5	0
f	86	6	2	5	8	123	0
h	86	7	3	7	7	106.5	1
f	86	7	2	7	8	130.5	0
f	86	4	2	7	6	162.5	0
f	86	4	3	8	4	95	1
f	86	3	4	8	5	93	0
f	86	5	3	10	3	82	1
f	86	6	2	9	9	79	1
f	86	7	5	12	9	58	1
f	86	8	9	10	10	82.5	1
h	95	75	6	4	17	123.5	0
h	95	81	10	3	17	45.5	0
h	95	30	4	6	4	83	0
h	95	29	6	5	2	42	1
h	95	11	6	9	6	100.5	0
h	95	9	7	12	7	80	1
p	79	11	11	14	21	57	0
p	79	22	18	15	30	124.5	1
p	79	26	16	19	31	55	1
p	79	30	15	17	34	84.5	0
f	79	19	4	5	13	113.5	1
f	79	19	4	5	13	73.5	0
f	79	26	7	2	17	125.5	1
f	79	21	4	3	11	134.5	0
a	79	12	14	17	13	124	0
a	79	21	10	15	17	347	1
a	79	26	18	19	24	266	1
a	79	30	21	21	21	422	1
a	79	20	24	20	19	306.5	1
a	79	26	24	17	16	156.5	1
a	79	23	25	23	23	269.5	1
p	86	9	11	19	16	52.5	0
p	86	24	26	24	18	58	0
a	86	34	18	20	19	113	0
a	86	31	19	23	26	391	1
f	86	29	23	23	16	183	0
a	86	28	24	20	22	121.5	0
f	95	19	14	15	11	75.5	0
h	95	19	13	14	15	90	1
h	95	23	15	13	13	110	0
h	95	18	16	18	16	150	0
h	95	17	27	23	15	105.5	0
h	95	10	24	23	14	61.5	0
h	95	14	21	24	18	95.5	0
p	95	16	18	16	17	214.5	0
f	95	41	32	20	25	123	0
a	95	27	27	17	20	166.5	0
a	95	45	34	25	25	178.5	0
a	95	40	33	21	32	221.5	0
a	95	44	36	23	35	198.5	0
a	95	48	33	22	38	235.5	0

a	95	39	33	26	26	295.5	0
a	95	41	31	17	32	213	0
a	95	39	28	21	23	209	0
a	95	34	27	18	18	126.5	0
a	95	31	19	23	26	292	1
f	95	14	11	16	20	92.5	0

Pardee

Species	Transect	N	E	S	W	Length (cm)	Flowering?
p	4	38	4	27	85	29	0
p	4	43	6	55	73	96	0
p	4	50	4	21	74	37.5	0
p	4	47	3	8	45	75.5	0
p	4	31	1	4	51	190.5	0
o	4	39	12	51	68	179.5	0
p	4	33	3	13	69	186.5	1
p	4	13	0	4	3	60.5	0
p	4	4	1	6	4	59.5	0
p	4	27	5	40	55	229.5	1
p	4	1	1	31	38	162.5	1
o	4	3	6	8	1	223	1
o	4	3	4	11	2	160.5	1
o	4	8	6	11	14	26	0
o	4	24	9	6	5	29	0
o	15	10	8	5	2	145	1
o	15	10	0	3	0	126	1
o	15	9	3	3	1	65	1
p	15	14	35	43	4	31.5	0
p	15	0	3	22	0	67.5	0
p	15	25	25	0	3	158.5	1
p	15	5	7	1	3	184.5	1
p	15	8	38	5	3	317	1
p	15	34	42	35	38	130	1
p	15	19	69	16	5	161	1
p	15	32	42	34	9	148.5	1
p	15	18	24	19	32	151	1
f	21	4	15	7	33	84	0
o	21	3	6	9	10	158.5	0
f	21	1	3	6	6	303.5	1
o	21	2	6	3	5	160	1
f	21	1	4	4	5	54	0
f	21	4	5	2	6	36	1
f	21	2	3	3	7	225.5	1
f	21	6	3	5	8	21.5	0
f	21	9	3	2	6	23.5	0
f	21	7	3	4	5	20	0
f	37	30	6	18	4	44.5	0
o	37	20	6	11	2	103.5	0
o	37	33	19	15	2	227	1
o	37	6	3	7	2	60	0
o	37	5	0	3	5	64	1
o	37	5	0	3	6	62.5	0
f	37	5	4	13	7	81.5	0
f	37	15	37	32	10	33	0
f	40	6	9	2	0	28	0
f	57	9	1	7	7	48	0

f	57	3	2	11	7	68.5	0
f	60	13	0	3	20	23.5	0
f	60	15	1	5	26	26	0
f	60	14	0	2	26	74	0
f	60	14	3	3	7	46	0
a	79	96	35	6	37	170.5	1
a	79	96	40	8	30	175	1
a	79	96	32	3	29	31.5	0
a	79	96	43	2	36	103	1
a	79	96	61	6	41	218.5	1
a	79	96	38	7	45	159.5	1
a	79	96	44	7	47	183.5	1
a	79	96	39	7	28	132	0
a	86	11	6	6	13	125	1
a	86	6	0	2	2	84.5	0
a	86	3	6	1	1	83.5	0
a	86	5	0	14	10	78.5	0
o	86	30	1	1	12	215.5	1
o	86	19	0	2	11	59.5	0
o	86	27	1	3	15	157	0
o	86	38	1	3	12	241	1
p	86	50	0	5	13	65	0
p	86	43	1	4	14	54	0
p	86	21	0	4	16	84	0
o	86	36	1	7	17	146.5	1
o	86	29	2	4	8	138	0
p	95	16	14	37	23	304	1
p	95	24	14	28	25	43.5	0
p	95	29	14	22	17	159	1
p	95	27	5	6	1	212.5	1
p	95	17	5	10	2	203	0
p	95	14	8	8	2	78	0
p	95	21	5	9	8	91.5	1
p	95	22	11	7	11	81.5	0

Appendix 2: Academic Vita

LEVI J. SHOWALTER

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Education

The Pennsylvania State University, University Park, PA

- B.S. in Plant Sciences – Horticulture; Schreyer Honors College
  - Honors Thesis: Effect of Forest Canopy Density on the Distribution of Five *Rubus* Species in Central Pennsylvania
  - Minors in Forest Ecosystems and Agronomy
  - Anticipated Graduation: May 2023
- Academic Presentations:
  - "Food Insecurity in Arctic Inuit Communities: Causes, Impacts, and Opportunities", 2022 Undergraduate Exhibition
  - "Effect of Forest Canopy Density on the Distribution of Five *Rubus* Species in Central Pennsylvania", 2023 Undergraduate Exhibition
  - "Breeding Hybrid Maize for Endogenous Flavonoid Expression to Improve Fall Armyworm Resistance", 2023 Undergraduate Exhibition and 2023 Gamma Sigma Delta Research Expo
- Extracurricular Activities:
  - Horticulture Club
    - 2022 Horticulture Show Manager: Coordinated donations of over $1200 worth of plant material from local nurseries; helped supervise construction of large demonstration landscape for sale to public to raise funds for club activities
  - Reformed University Fellowship
  - Boy Scouts of America (Eagle Scout, current Venture Crew Associate Advisor)
  - Club Wrestling

Mifflinburg Area High School - Diploma (2019)

Professional Experience

- **Undergraduate Researcher** – Chopra Maize Genetics Laboratory (Nov 2022 – Present)
  - Evaluated hybrid maize lines for flavonoid expression and fall armyworm resistance
  - Performed feeding assays, collected plant tissue samples, and followed extraction protocols to gather data on chemical composition of plant tissues
  - Catalogued seed samples

    - Managed laboratory research greenhouse
    - Prepared findings into a poster for public presentation at research exhibitions
- **Independent Forestry Research** – Penn State Department of Ecosystem Science and Management (July – Aug 2022)
    - Conducted research on the ecology of five species of native and introduced raspberry species in Pennsylvania forests
    - Designed sampling methodology and collected data on over 400 individual plants
    - Statistically analyzed data to prepare results into a finalized honors thesis
- **Poultry Farm Worker** – Penn State Poultry Education & Research Center (Aug 2021 – May 2022)
    - Handled all steps of chicken and turkey production for meat and eggs, including pen setup, feeding and egg collecting, egg processing, and slaughter under USDA guidelines
    - Performed artificial insemination
    - Kept records of egg production, environmental conditions, and mortality
    - Assisted with scientific research projects on avian nutrition