

The Pennsylvania State University

The Graduate School

**HABITAT AND FLORA ASSOCIATED WITH TWO “RAMP/LEEK” SPECIES (*ALLIUM*
TRICOCCUM AND *A. BURDICKII*) IN PENNSYLVANIA**

A Thesis in

Forest Resources

by

Cassie Stark

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The thesis of Cassie Stark was reviewed and approved by the following:

Eric Burkhart

Associate Teaching Professor, Ecosystem Science and Management
Program Director, Appalachian Botany and Ethnobotany Program, Shavers
Creek Environmental Center
Thesis Advisor

Jonathan Duncan

Assistant Professor of Hydrology, Ecosystem Science and Management

Douglas A. Miller

Research Professor Emeritus, Landscape Science and Informatics

Sarah Nilson

Assistant Professor of Biology, Pennsylvania State Beaver

Bradley Cardinale

Department Head, Ecosystem Science and Management

ABSTRACT

Allium tricoccum Ait., is a perennial, herbaceous forest plant known as a ramp or wild leek in Pennsylvania (PA). Ramps are a popular, foraged, non-timber forest product, and are consumed for their edible bulbs and leaves which have an onion or garlic flavor. For nearly the past century, a second “ramp” taxon, has been variously recognized outside of PA as a separate race, variety, or species. Recent floristic treatments now address it as a separate species, narrow-leaf ramp (*Allium burdickii* (Hanes) A.G. Jones). Little is known about the forested site conditions associated with both ramp species in PA. This habitat information could be useful for guiding *in situ* cultivation (i.e., forest farming) of *A. tricoccum* and for discovery and conservation of *A. burdickii*. The latter species is currently only known from a handful of sites in southwestern PA. In this study, habitat and association data was collected from 30 wild *A. tricoccum* populations on forestlands located in PA. Four additional *A. burdickii* populations were included and paired with nearby *A. tricoccum* populations for a comparison of habitats. At each field site, five plots were placed throughout the population area and the following data were collected: floristic associates (all strata), soil chemistry, soil moisture content, topographic position, elevation, and aspect.

Results indicate *A. tricoccum* commonly occurs on moist, east, and north facing lower slopes or floodplains with slightly acidic and fertile soil chemistry. The flora associated with *A. tricoccum* populations was 50% (27-65%) similar when compared throughout PA. Sugar maple (*Acer saccharum* Marsh.) and blue cohosh (*Caulophyllum thalictroides* (L.) Michx.) were frequently occurring species at ramp sites and an indicator species analysis (ISA) identified them as indicators for ramp habitat on north aspects. Wood nettle (*Laportea canadensis* (L.) Wedd.) was commonly found later in the season at sites with blue cohosh. This is likely due to the wet, calcium rich habitat these species prefer. Species such as bitternut hickory (*Carya cordiformis*

(Wang) K. Koch), mayapple (*Podophyllum peltatum* L), and jack-in-the-pulpit (*Arisaema triphyllum* (L.) Schott) were associated with ramps on floodplains. These site factors and associated flora can be used for ramp site selection for cultivation.

Habitat comparisons between *A. tricoccum* and *A. burdickii* at field sites in southwestern PA revealed soil moisture content was significantly higher at *A. tricoccum* populations while soil pH and nutrients were all greater at *A. burdickii* populations. Flora associated with *A. tricoccum* and *A. burdickii* populations were 44% (35-75%) similar. The most frequent and dominant tree species was sugar maple. The ISA and NMS results were consistent with the statewide *A. tricoccum* results with blue cohosh, and wood nettle being associated with *A. tricoccum* populations. The ISA and NMS revealed species such as mayapple, false Solomon's seal (*Maianthemum racemosum* (L.) Link), and stonecrop (*Sedum ternatum* Michx.) were associated with *A. burdickii* populations. Species associated with *A. tricoccum* were those that require moist or mesic habitat conditions whereas species associated with *A. burdickii* can tolerate drier conditions.

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Chapter 1

Introduction

Ramps, also known as wild leeks, are perennial wild onions in the Alliaceae botanical family (Weakley, 2020). They are now regarded to be two species of “ramps” in eastern North America: *Allium tricoccum* Ait. and *A. burdickii* (Hanes) A.G. Jones. Of these *A. tricoccum* appears to be the more popular non-timber forest product (NTFP) and is foraged for its’ edible bulb and leaves. Ramps are a slow growing species and reproduce sexually through seeds and asexually through clonal bulb division (Nault and Gagnon, 1993). Dion and Lapointe (2015) observed 7-10 years of growth may be required from seed germination to reach reproductive maturity. Ramps have short photosynthetic and reproductive phases that can be easily impacted by environmental factors, such as light availability which can contribute to slow population recovery after a harvest (Dion and Lapointe, 2015; Nault and Gagnon, 1993). Increased media coverage and ramp culinary usage has increased ramp popularity during the past 50 years and has also raised conservation concerns (Chamberlain and Baumflek, 2019).

Forest farming is a type of agroforestry that focuses on the cultivation and management of NTFP’s under a forest canopy (Chamberlain et al., 2009; NAC 2022). This practice can reduce foraging pressures off wild NTFP’s by providing a more reliable “cropping” system with the potential for income generation and quality control (Chamberlain et al., 2009). As wild ramp populations are primarily foraged, and few populations are being cultivated and farmed, implementation of forest farming could increase supply to meet consumer demands. Especially due to growth in ramp popularity which now extends far outside of its wild harvest region (Baumflek and Chamberlain, 2019). Forest farming of ramps could reduce foraging pressure on wild ramp populations and provide income generating possibilities for private forest landowners (Chamberlain et al., 2014; Davis and Greenfield, 2001; Dion and Lapointe, 2015). However,

understanding the habitat and microenvironmental conditions required for ramps is necessary for successful implementation of forest farming and site selection for cultivation (Burkhart, 2013; Gillespie et al., 2006).

In addition to the importance of understanding ramp habitat for agroforestry cultivation and *in situ* restoration purposes, this study aims to compare habitat between two ramp species, *A. tricoccum* and *A. burdickii*, in southwest PA where their range has been found to overlap (this study). This information will serve to guide location of additional populations by generating field “search” conditions and better establish their conservation status. Narrow-leaf ramp (*A. burdickii*) can be confused with *A. tricoccum* due to a lack of knowledge surrounding the species and visual similarities. *A. burdickii* was not recognized as a valid taxon until the mid-nineteenth century (Jones, 1979). Hanes and Ownbey (1946) were the first to suggest two ramp taxa exist based on observations in Michigan and Ohio. Since then, it has been referred to as a separate race, variety, or species based on differences in morphology, phenology, and habitat (Sitepu, 2018; Weakley, 2020). Most recently, *A. burdickii* it has been recognized as a separate species (Sitepu, 2018; Weakley, 2020); therefore, in this study it will be referred to as such. *A. burdickii* is listed as highly threatened as it is vulnerable or imperiled in many states where it has been documented, or its conservation status is unknown and listed as “no rank” (NatureServe, 2022) Prior to the initiation of this study, *A. burdickii* had not been confirmed in Pennsylvania (PA) (Rhoads and Klein, 1993; Rhoads and Block, 2007; The Pennsylvania Flora Project, 2022).

A. tricoccum can be found throughout the northeastern United States (U.S.) and adjacent regions of eastern Canada (Figure 1-1) (BONAP, 2021; NatureServe, 2022; Weakley, 2020). However, the distribution of *A. burdickii* is unclear and unresolved, although has been suggested to occur from Maine to North Dakota and south of New Jersey (Figure 1-1) (NatureServe, 2022; Plants of the Northeastern U.S., 2004; USDA Plants Database, 2022; Weakley, 2020). While information on *A. burdickii* is limited, it’s been suggested habitat between *A. burdickii* and *A.*

tricoccum differs (Bernatchez et al., 2013; Hanes, 1953; Jones 1979). Research examining habitat between these two species can help guide future population discovery and further research development by providing important modeling criteria as well as field “indicators” that can be used to identify possible supportive habitat(s) (Dufrêne and Legendre, 1997).



Figure 1-1: *Allium burdickii* (top) and *A. tricoccum* (bottom) distribution throughout the United States.

This thesis contains two chapters, each written as a manuscript to be further developed and formatted for peer-reviewed journal submission. The first (Chapter 2) chapter “A study on ramp habitat: Site factors and flora associated with *Allium tricoccum* Ait., in Pennsylvania”

outlines site characteristics and floristic associates of wild ramp populations in Pennsylvania (PA). Chapter 3, “*Allium tricoccum* Ait. and *A. burdickii* (Hanes) A.G. Jones occurrences in Pennsylvania may be driven by differences in soil moisture, pH, and fertility” is a habitat comparison between the two ramp species in the southwestern portion of the state where *A. burdickii* has been found to date. This chapter compares site factors, soil moisture, soil chemistry, and flora associated with each ramp species.

Chapter 2

A study of ramp habitat: Site factors, soil, and flora associated with *Allium tricoccum* Ait. in Pennsylvania

Introduction

Allium tricoccum Ait., is a wild onion in the Alliaceae botanical family, also known as ramps or wild leeks (Weakley, 2020). Ramps are indigenous to the eastern United States (U.S.) and southern parts of Canada where they are a wild, collected, non-timber forest product (NTFP) harvested for their flavorful leaves and bulbs (Baumflek and Chamberlain, 2019). The species is perennial, slow growing, and is usually harvested in its entirety---meaning the bulb, leaves, and roots are all gathered (Dion and Lapointe, 2015; Rock, 2003). These factors can contribute to overharvesting (Dion and Lapointe, 2015; Rock, 2003). In some parts of the range (e.g., Canada), ramp harvesting is prohibited for commercial purposes (Bernatchez et al., 2013; Rock et al., 2003). The species is listed as “secure” in Virginia and New York (NatureServe, 2022).

Ramps have been identified as a forest “crop” in the eastern U.S. with potential for commercial production on forestlands (Chamberlain et al., 2014). Forest farming is a type of agroforestry practice defined as “the cultivation of high-value crops under the protection of a managed tree canopy” (NAC, 2022). The adoption of forest farming can lead to more sustainable production by providing incentive for intensive management of populations to meet consumer and market demand (Burkhart and Jacobson, 2009; Chamberlain et al., 2014; Chamberlain and Predny, 2003). An important component of forest farming site evaluation is the use of so called “indicator species” (Burkhart, 2013; NAC 2022; Davis and Persons, 2014.). Indicator species are used to characterize habitats and assess habitat suitability (Dufrêne and Legendre, 1997). An indicator value is the product of the relative abundance and frequency of a given species (Dufrêne and Legendre, 1997; Peck, 2016). If an indicator occurs in an area, then the local habitat is likely

suiting for the species of interest. Selected indicator species should be sensitive to certain environmental conditions to represent ideal habitat conditions (Hager, 1998).

The habitat and flora associated with wild ramps in the eastern U.S. has not been fully investigated, although there is anecdotal and observational information available in regional or state floras, and some technical publications. Collectively, these existing accounts describe ramp habitat as mesic, deciduous forests, along flat stream sides, or on moist slopes (Bernatchez et al., 2013; Rhoads and Block, 2007; Rock et al., 2003; Vasseur and Gagnon, 1993). Recent floristic guides note *A. tricoccum* is found in “cove forests and mesic slope forests” (Weakley, 2020). Horticultural guides for cultivation purposes suggest ramps occur with species such as trout lily, trillium, wood nettle, and black cohosh (Chamberlain et al., 2014; Davis and Greenfield, 2001).

Habitat descriptions often state that ramps prefer moist, well-drained soil (Bernatchez et al., 2013; Rock, 2003). Many members of the genus *Allium* have shallow root systems which only penetrate the top 12 in./30 cm of soil (Geries et al., 2020). Ramps similarly have a shallow bulb and root system (Nault and Gagnon, 1993; Sitepu, 2018). Because of this, onion (*A. cepa*) yields can be severely reduced under water stress (Geries et al., 2020). It has been suggested that soil moisture may be the most important factor on ramp growth and survival (Vasseur and Gagnon, 1993).

Previous work on soil nutrients suggests ramps favor soil with a lower pH (4.9 to 5.5) and a high calcium to magnesium ratio (Bernatchez et al., 2013; Davis and Greenfield, 2002). A study on forb species (including *Allium tricoccum*) showed a correlation between greater calcium content (ppm) and increased species richness (Catella et al., 2019) suggesting sites derived from limestone or other base contributing parent materials may be preferred substrate. Furthermore, when studying ramp survival in North Carolina, an increase in ramp survival was observed in soils with greater calcium content (greater than 3,300 ppm) (Davis and Greenfield, 2002). In

horticultural experiments application of gypsum and slaked lime have resulted in increased ramp growth (Bernatchez et al., 2013, Ritchey and Schumann, 2005).

A better understanding of habitat and associated flora would help landowners and technical service providers identify existing ramp populations for conservation and monitoring and recognize suitable forested sites for ramp forest farming where populations do not already occur. The objectives of this study were to characterize the following habitat conditions associated with wild ramp populations in PA:

- 1) Site factors: aspect, topographic position, and elevation
- 2) Hydrologic properties: drainage class, hydrologic soil group, and soil moisture content
- 3) Soil chemistry: pH and fertility
- 4) Associated vegetation: over and understory species, similarity, indicator species value

This data will be helpful for modeling and locating populations and to determine site traits to be examined for forest farming.

Methods

Population solicitation and criteria for inclusion

Ramps occur on forestlands through a combination of sexual (e.g., seeds) and asexual (e.g., bulblets) reproduction and growth (Vasseur and Gagnon, 1993). Asexual clonal growth can make discerning individual plants difficult without excavation of the bulb to look for the presence of a shared basal plate (Nault and Gagnon, 1993). Due to clonal growth, it was difficult to discern genet numbers with precision in each population study area and so only estimates were made using ramets. Population ramet estimates in this study ranged from 1,000 to 100,000 with most study populations averaging 5,000-10,000 ramets. Inclusion of ramp populations was based on the following criteria: (1) Each population occupied at least an acre in size and consist of at least

1,000 ramets; and (2) each population exhibited both asexual and sexual recruitment (the latter evidenced by the presence of all demographic stages (e.g., seedling to adult); and (3) each study population represented a new geographic area within PA, contributing to a goal of achieving statewide representation.

Beginning in 2017, ramp study populations were solicited from professional contacts and the public using a variety of media (e.g., social media, newsletter articles, internet blogs) and botanical networks in PA. iNaturalist and herbarium records were also reviewed, and populations were visited if sufficient information existed for field location. A total of 30 populations and 150 understory plots were eventually included in this study and visited over a three-year period. These populations were in most regions and all major physiographic provinces of PA (Figure 2-1).

Study location

This study was conducted in PA, U.S.A. (39°43'-42°16' N; 74°41'-80°31' W). Four different forest types occur in PA but two predominate: northern hardwood and oak-hickory forests (Pennsylvania Natural Heritage Program, 2019). PA includes seven major physiographic provinces with the Appalachian Plateau, Ridge and Valley, and Piedmont regions comprising most of the state. The climate is “humid continental” and “human subtropical” with a mean annual precipitation of between 34 in./86 cm and 52 in./132 cm and an average annual temperature of 47°F/8°C to 57°F/14 °C (The Pennsylvania State Climatologist, 2021).

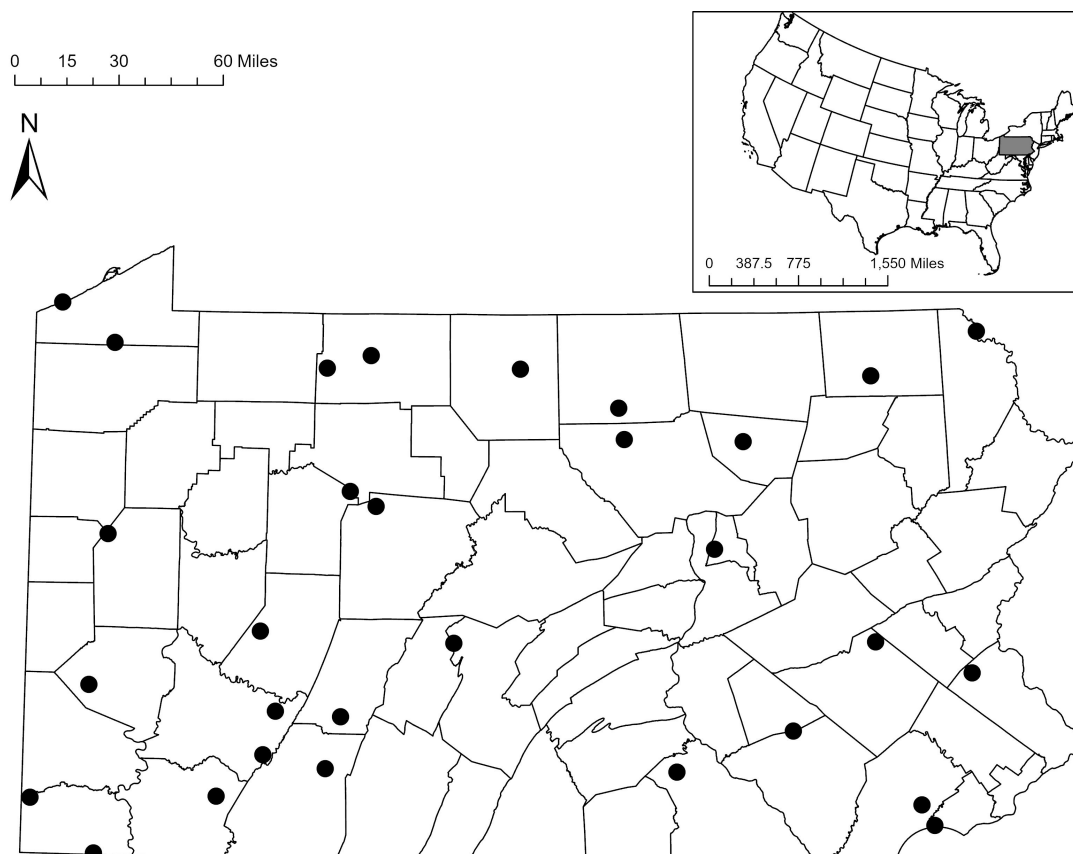


Figure 2-1: Ramp populations (n=30) throughout the state of Pennsylvania. All points are larger than scale to obscure locations.

Site factor data collection and analysis

Topographic data collection and analysis

At each study location, plots were located subjectively (e.g., visually) within populations with a goal of capturing the breadth of the site with five plots. In most cases, plots transected a slope or were spread upon a floodplain. Topographic position was recorded at each plot as the position on the slope (upper, middle-upper, middle, middle-lower, lower, toe-slope) or “bottom/flat” if the plot was on a floodplain. Elevation and aspect were recorded for each plot. Global Position System (GPS) coordinates taken at each plot allowed for calculation and comparison of aspect, slope in degrees, and elevation using ArcGIS Pro (ArcGIS pro v. 29,

Environmental Systems Research Institute (ESRI) Redlands, CA). These calculations were compared alongside field collected data for accuracy and consistency. Soil drainage class and hydrologic soil group were compiled using Web Soil Survey (Web Soil Survey, 2022).

Soil moisture data collection and analysis

At one site, in each understory floristic sampling plot, 30 measurements were taken with a ML3 Theta Soil Moisture Probe (Dynamax Inc. Houston, TX) every 8-weeks beginning in April and concluding in December 2021 (April 23, June 16, August 21, October 8, and December 10). Soil moisture data were averaged across the entire site for each sampling date.

Canopy density data collection and analysis

To examine tree canopy openness throughout the ramp growing season, hemispherical light photographs were taken and averaged at the center of each understory vegetation plot when soil moisture data was being collected. This was done using a Nikon D90 digital camera with a Nikon 10.5 mm Fisheye lens, mounted on a tripod. Gap Light Analyzer (Gap Light Analyzer, Version 2.0) was used to calculate Global Site Factor (GSF), which is the percent of canopy openness (Hemiview Manual 2.1,1998)

Soil sample collection and analysis

At each site, five soil samples were collected. In each understory floristic sampling plot, one sample was collected from the top 8 in./20 cm of soil (A horizon) and within 6 in./15 cm proximity to ramp bulbs and roots. Each sample was therefore a single rather than composite soil sample. This sampling method was used to ensure that samples (1) accurately represented only the localized soil from the rhizosphere; and (2) to examine any fine scale rooting zone variation between plots within each site.

Samples were submitted to the Pennsylvania State Agricultural Analytical Services Laboratory (University Park, PA) for chemical analysis. The following protocol was used to analyze samples: soil pH was determined using the Water method (Eckert and Sims, 1995) and

macro-nutrient content (available P, K, Ca, Mg) of samples was determined using the Melich 3 (ICP) method (Wolf and Beegle, 1995).

A total of 150 soil samples were collected and analyzed. Because data was nonnormally distributed, a Kruskal Wallis with pairwise post-hoc tests was calculated using SPSS (IBM Statistics for Macintosh, v. 28) with a significance level of $p < 0.01$. Sites were grouped according to physiographic province to test if there was a difference in soil chemistry (pH, Ca, Mg, P, K) between provinces.

Floristic sampling and analysis

Over and understory flora associated with ramps were documented using a combination of plot and plot-less sampling methods. The overstory layer included dominant or co-dominant tree species while, understory included resident woody species (e.g., small trees, shrubs, vines) and herbaceous plants (Gilliam, 2014).

Between 2018 and 2021, repeat visits were made to study sites to ensure documentation of seasonal changes in flora and to confirm identification of taxa where necessary. Specifically, visits were timed to document spring-early summer (April-May) and late summer-early fall (July-August) flora. Herbarium voucher specimens were collected for all ramp populations and deposited at the Carnegie Museum of Natural History (CM), The Morris Arboretum of the University of Pennsylvania (MOAR), and the Pennsylvania State University Herbarium (PAC). All plant nomenclature follows “Flora of the Southeastern U.S.: Pennsylvania” (Weakley, 2020).

For overstory documentation, each plot was divided into four quarters using the Point-Centered-Quarter-Method (Causton, 1987; Kent and Coker, 1992). Using this method, only the nearest dominant or co-dominant canopy tree (stems ≥ 3 in./ 7.6 cm diameter at breast-height (4.5 ft/1.4 m) and height ≥ 4.5 ft/1.4 m) within each quarter was recorded, yielding one tree per quarter and four trees per plot. Diameter at breast-height (dbh) was recorded for each tree species to calculate importance values (IV) (Curtis and McIntosh, 1951; McCune and Grace, 2002). IVs

were calculated for all overstory tree species recorded by summing relative frequency, relative density, and relative dominance (Curtis and McIntosh, 1951).

For understory documentation, five plots (628 m²/687 yards²/ (d=40 m/ 44 yards, r=20 m/ 22 yards) were established at each site throughout the population using a stratified nonrandom approach. Plot size was based on the goal that only “nearest neighbors” were to be recorded and to examine microvariability in associates by topographic position. In addition to noting presence, the local abundance of each floristic element was recorded within the plot and the immediate vicinity (i.e., within vision) using the following scale: (1) one plant observed; (2) 2-10 plants observed; (3) 11-49 plants observed; (4) 50 or more observed. If the abundance of a floristic associate changed over the growing season the greatest abundance value was used.

Sorenson coefficients (S_s) (also known as Bray-Curtis) were calculated for all vegetative layers to determine percent similarity between floristic associates at sites and plots (McCune and Grace, 2002). A Sorenson coefficient is calculated using $S_s = 2a/(2a+b+c)$, where “a” is the number of species in both samples and “b” and “c” are the number of species unique to each sample. Binary, presence/absence data was used with a Sorenson (Bray-Curtis) distance measure and city block geometry.

Indicator species analysis (ISA) was used to assess the degree to which an associate is correlated with ramp occurrence. Dufrêne and Legendre methodology with a Monte Carlo randomization test were done to determine significance (Dufrêne and Legendre, 1997; Peck, 2016). Abundance data per plot was analyzed with the following geographic factors of interest: region (north, south, east, west), province, (Appalachian Plateau, Piedmont, and Ridge and Valley), aspect (north or south) and topographic position (floodplain, lower, middle, or upper slope). A significance level of $p < 0.01$ was used for examining floristic associations.

Four general regions of PA (NW, NW, SW, SE) were created for ISA analyses, using State College as the geographic center. When divided, all populations were clearly within one

region or another except for one occurring due north of State College and was treated as NW in ISA analyses. For physiographic province, one population located in the Central Lowlands that was reclassified as Appalachian Plateau. Aspects that were either N/NW/E/NE were classified as N and S/SE/SW/W were S. Topographic positions recorded as toe slope were redefined as lower slope, those as middle-upper were defined as upper and middle-lower as lower.

ISA and similarity indices (Sorenson's coefficient) were calculated using PC-ORD (Multivariate Analysis of Ecological Data, v. 7.0, MJM software design, Glenden Beach, Oregon).

Results

This is the first scientific study of ramp habitat associations in PA, and the first of its kind within the range of the species. The primary objective was to identify site factors and flora associated with ramps in PA. Due to the stratified, non-random approach in which ramp sites were located statewide using informants, and targeted plot placement for sampling, results from this study should be regarded as suggestive of habitat preferences and indicators (Kent and Coker, 1992). No extrapolation is possible as paired "control" plots without ramp populations were not included, and therefore, sampling bias is inherent (McGraw et al., 2003). Nevertheless, the results obtained in this study help to highlight and identify additional research areas for future ramp habitat studies and provides practical guidance to those interested in assessing forested sites for introductions or forest farming.

Site factors

Topographic and soil moisture results

PA ramp populations were most frequently found on lower slopes with east and north aspects and floodplains (Figure 2-2). The mean elevation across all ramp populations was 1,151 ft. Average elevation was lowest in the southeastern portion of the state at 433 ft. ArcGIS pro results indicate median aspect was northeast, average slope was 13 degrees, and average elevation

was 1,167 ft. At BSP site, soil moisture content remained consistently high from April to December (Figure 2-3). Soil moisture content was the lowest in April at 35% volume (% vol) then continued to rise until August where it was the highest at 50% vol. Soil moisture then slightly declined in October and increased again in December (Figure 2-3). Percent canopy openness was the highest in April and December at 48% and lowest in June at 5% (Figure 2-3). Results on drainage class indicate ramps were predominantly found on “well-drained” soil with 22 out of 30 sites in this category and the rest being either “poorly drained” or “excessively drained”. Hydrologic soil group results were non-definitive as the range of results were so broad.

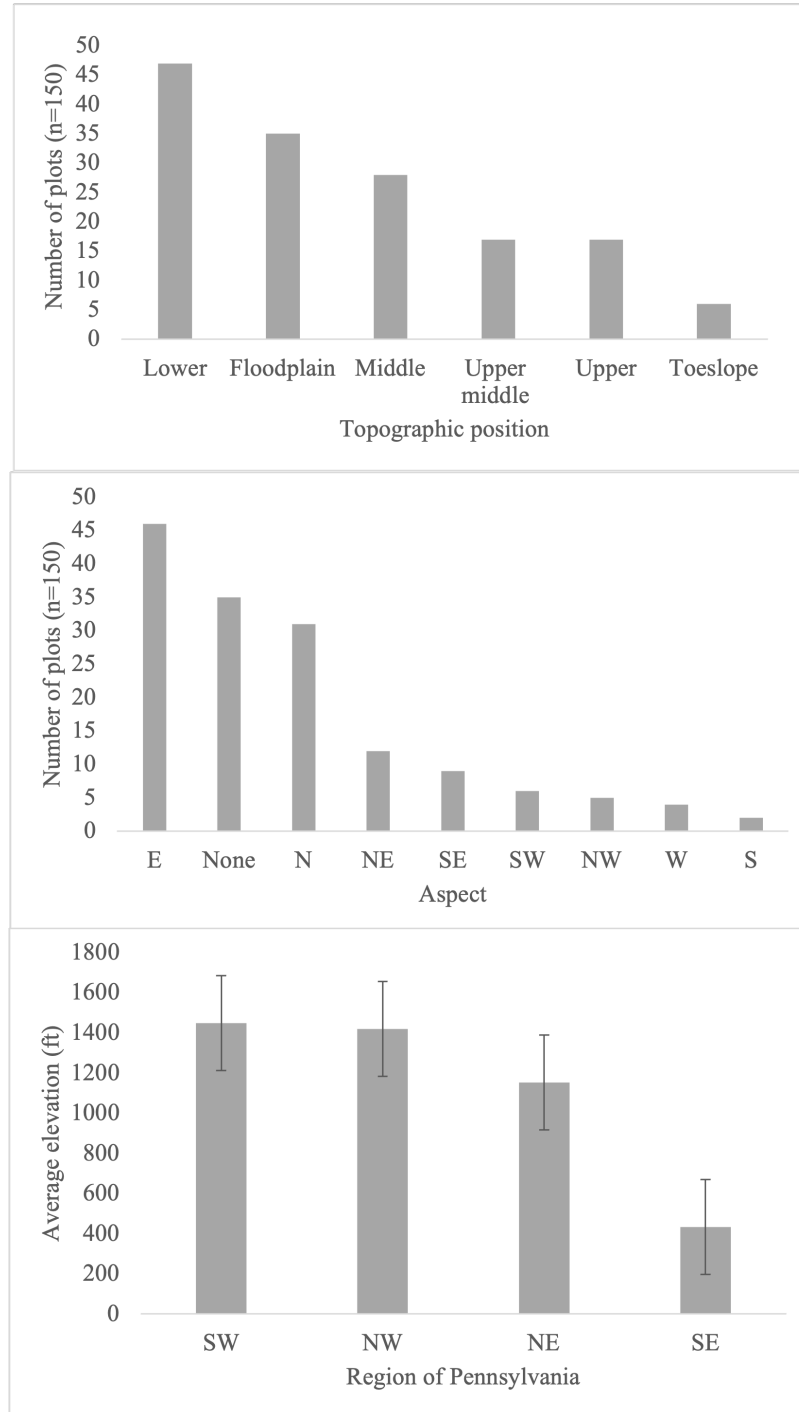


Figure 2-2: Topographic position (slope or floodplain), aspect, and elevation (ft) summaries at Pennsylvania ramp populations. Bars represent standard error (σ/\sqrt{n}).

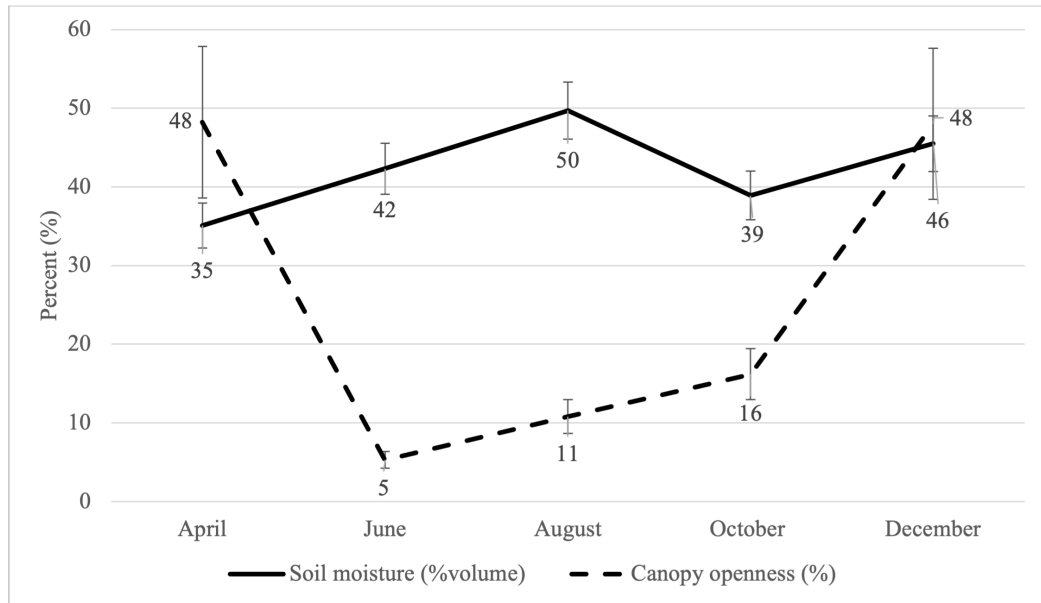


Figure 2-3: Percent soil moisture content and canopy openness at a single Pennsylvania ramp population ($n=1$). Bars present standard error (σ/\sqrt{n}).

Soil chemistry results

Soil pH revealed soils to be neutral to slightly acidic with an average of 5.7 (Table 2-1). Ramp populations throughout PA had high soil calcium contents (ppm) (Table 2-1). The Kruskal Wallis results indicate pH, magnesium, and phosphorus are statistically significantly different depending on physiographic province (Table 2-2). Potassium content (ppm) and pH were the highest in the Piedmont region and magnesium content (ppm) was the highest in the Ridge and Valley.

Table 2-1: Soils summary data from Pennsylvania ramp populations.

Soil characteristics	pH	Phosphorus ppm	Potassium ppm	Magnesium ppm	Calcium ppm
Mean	5.7	54	238	460	3306
Min	5.0	7	44	60	356
Max	7	141	649	2392	9448
Standard deviation	0.5	40	146	460	2141

Table 2-2: Mean and standard deviation (μ , s) of soil nutrients at Pennsylvania ramp populations sorted by province. Subscript letters (^{a, b, c}) denote statistical significance ($p < 0.01$) from Kruskal Wallis with pairwise post hoc results on province ($df=2$): Appalachian Plateau ($n=110$), Piedmont ($n=25$) and Ridge and Valley ($n=15$). Statistical significance reads down the columns, if letters (^{a, b, c}) are shared then there is no statistical difference, if letters are different than there is a statistical difference.

	pH	Phosphorus ppm	Potassium ppm	Magnesium ppm	Calcium ppm
Appalachian Plateau (μ , s)	5.5, 0.7 ^a	52, 58	198, 119 ^{ac}	328, 273 ^b	2938, 2535
Ridge and Valley (μ , s)	5.9, 0.9 ^{ab}	47, 42	201, 97 ^a	914, 1114 ^{ab}	4306, 4033
Piedmont (μ , s)	6.1, 0.7 ^b	50, 46	400, 174 ^b	676, 374 ^a	3620, 2121

Flora

A total of 252 species were recorded in this study: 25 overstory tree species, 41 small trees, shrubs, lianas, or vines, and 186 herbaceous species (entire species lists located in Appendix A). Summary data can be found in tables: 2-3, 2-4, 2-5, and 2-6. Sugar maple (*Acer saccharum* Marsh.) was the most dominant and frequent overstory tree species with an importance value of 95 and occurring at 90% of sites (Table 2-3, Table 2-4). Multiflora rose (*Rosa multiflora* Thunb. Ex.Murr) and Japanese barberry (*Berberis thunbergii* A.P. de Candolle) were the most frequent understory woody species documented with ramp populations at 80% and 63% of sites (Table 2-5). Following was spicebush (*Lindera benzoin* L. Blume) which was present at 50% of sites (Table 2-5). The most frequent herbaceous species recorded with ramp populations was blue cohosh (*Caulophyllum thalictroides*. (L.) Michx.), which was on 83% of sites and 66% of plots (Table 2-6). Following was yellow trout lily (*Erythronium americanum* Ker-Gawl.) and mayapple (*Podophyllum peltatum* L.) (Table 2-6).

Table 2-3: The 10 most frequent (ranked by site) overstory tree species associated with ramps in Pennsylvania

Common name	Scientific name	Percentage of sites and (n)	Percentage of plots and (n)
Sugar maple	<i>Acer saccharum</i> Marsh.	90 (27)	77 (116)
American basswood	<i>Tilia americana</i> L.	67 (20)	33 (50)
Black cherry	<i>Prunus serotina</i> Ehrh.	57 (17)	26 (39)
Tulip poplar	<i>Liriodendron tulipifera</i> L.	50 (15)	23 (34)
Bitternut hickory	<i>Carya cordiformis</i> (Wang) K. Koch	50 (15)	21 (31)
Northern red oak	<i>Quercus rubra</i> L.	40 (12)	17 (26)
White ash	<i>Fraxinus americana</i> L.	40 (12)	13 (19)
American beech	<i>Fagus grandifolia</i> Ehrh.	30 (9)	10 (15)
Shagbark hickory	<i>Carya ovata</i> (P. Miller) K. Koch	30 (9)	8 (12)
Slippery elm	<i>Ulmus rubra</i> Muhl.	30 (9)	8 (12)

Table 2-4: Relative abundances and importance values (IV) for the top 10 dominant or co-dominant overstory tree species associated with ramps in Pennsylvania.

Species		Relative abundance			IV
Common name	Scientific name	Frequency	Density	Dominance	
Sugar maple	<i>Acer saccharum</i> Marsh.	27	39	29	95
Tulip poplar	<i>Liriodendron tulipifera</i> L.	6	11	19	35
American basswood	<i>Tilia americana</i> L.	8	11	8	27
Black cherry	<i>Prunus serotina</i> Ehrh.	7	9	7	22
Bitternut hickory	<i>Carya cordiformis</i> (Wang) K. Koch	6	7	6	19
Northern red oak	<i>Quercus rubra</i> L.	4	5	8	17
American beech	<i>Fagus grandifolia</i> Ehrh.	3	4	4	11
American ash	<i>Fraxinus americana</i> L.	3	3	3	9
Slippery elm	<i>Ulmus rubra</i> Muhl.	3	2	2	7
Shagbark hickory	<i>Carya ovata</i> (P. Miller) K. Koch	2	2	1	5

Table 2-5: The 20 most frequent (ranked by site) woody understory species associated with ramps in Pennsylvania. An asterisk (*) denotes non-native exotic species.

Common name	Scientific name	Percentage of sites and (n)	Percentage of plots and (n)
Multiflora rose	<i>Rosa multiflora</i> Thunb. Ex. Murr. *	80 (24)	43 (64)
Japanese barberry	<i>Berberis thunbergii</i> A.P. de Candolle*	63 (19)	34 (51)
Spicebush	<i>Lindera benzoin</i> L. Blume	50 (15)	35 (52)
Gooseberry	<i>Ribes sp.</i>	47 (14)	20 (30)
Blackberry	<i>Rubus sp.</i>	47 (14)	16 (24)
Red elderberry	<i>Sambucus racemosa</i> L. var. <i>pubens</i>	43 (13)	15 (22)
Witch hazel	<i>Hamamelis virginiana</i> L.	37 (11)	11 (16)
Choke cherry	<i>Prunus virginiana</i> L.	33 (10)	12 (18)
Grape vine	<i>Vitis sp.</i>	33 (10)	11 (17)
Poison ivy	<i>Toxicodendron radicans</i> L. Kuntze	27 (8)	12 (18)
Musclewood	<i>Carpinus caroliniana</i> Walter	27 (8)	9 (13)
Virginia creeper	<i>Parthenocissus quinquefolia</i> (L.) Planch.	23 (7)	13 (20)
American hophornbeam	<i>Ostrya virginiana</i> (P. Miller) K. Koch	23 (7)	11 (17)
Wineberry	<i>Rubus phoenicolasius</i> Maxim. *	20 (6)	11 (16)
Black haw	<i>Viburnum prunifolium</i> L.	20 (6)	7 (11)
Oriental bittersweet	<i>Celastrus orbiculatus</i> Thunb. *	17 (5)	9 (14)
Hawthorn	<i>Crataegus sp.</i>	17 (5)	5 (8)
Morrow or bell's honeysuckle	<i>Lonicera morrowii</i> A. Gray or <i>bella</i> Zabel *	17 (5)	5 (8)
Amur honeysuckle	<i>Lonicera maackii</i> (Rupr.) Herder *	13 (4)	5 (8)
Autumn olive	<i>Elaeagnus umbellata</i> Thunb. *	13 (4)	5 (7)

Table 2-6: The 20 most frequent (ranked by site) herbaceous species associated with ramps in Pennsylvania. Asterisk (*) denote non-native, exotic species.

Common name	Scientific name	Percentage of sites and (n)	Percentage of plots and (n)
Blue cohosh	<i>Caulophyllum thalictroides</i> . (L.) Michx.	83 (25)	66 (100)
Yellow trout lily	<i>Erythronium americanum</i> Ker-Gawl.	83 (25)	51 (77)
Mayapple	<i>Podophyllum peltatum</i> L.	80 (24)	51 (76)
Christmas fern	<i>Polystichum acrostichoides</i> (Michx.) Schott	77 (23)	59 (88)
Violet	<i>Viola</i> sp.	77 (23)	53 (80)
White wood aster	<i>Eurybia divaricata</i> (L.) G.L. Nesom	73 (22)	45 (67)
Enchanter's nightshade	<i>Circaea canadensis</i> L. Hill	70 (21)	39 (58)
Intermediate woodfern	<i>Dryopteris intermedia</i> (Muhl. Ex Willd.) A. Gray	70 (21)	47 (71)
Bedstraw	<i>Galium</i> sp.	70 (21)	42 (63)
Hairy sweet cicely	<i>Osmorhiza claytonii</i> (Michx.) C. B. Clarke	70 (21)	41 (61)
Hairy Solomon's seal	<i>Polygonatum pubescens</i> (Willd.) Pursh.	70 (21)	37 (56)
Garlic mustard	<i>Alliaria petiolata</i> (Bieb.) Cavara & Grande *	67 (20)	48 (72)
Jack-in-the-pulpit	<i>Arisaema triphyllum</i> (L.) Schott	67 (20)	45 (67)
Broadleaf toothwort	<i>Cardamine diphylla</i> (Michx.) Alph. Wood	67 (20)	44 (66)
White avens	<i>Geum canadense</i> Jacquin	67 (20)	29 (43)
False Solomon's seal	<i>Maianthemum racemosum</i> (L.) Link	67 (20)	25 (38)
Jumpseed	<i>Persicaria virginiana</i> (L.) Gaert.	67 (20)	41 (61)
Jewelweed	<i>Impatiens</i> sp.	66 (20)	42 (63)
Cut-leaf toothwort	<i>Cardamine concatenata</i> (Michx.) O. Schwarz	63 (19)	46 (69)
Common blue violet	<i>Viola sororia</i> Willde.	63 (19)	29 (44)

Sorenson coefficients for overall flora indicated an average of 38% (43-76%) for sites and 50% (27-65%) for plots (Table 2-7). For overstory species, average Sorenson coefficient was 47% (62-90%) for sites and 57% (41-88%) across plots (Table 2-7). Understory woody species had an average Sorenson coefficient of 53% (44-86%) between sites and 57% (23-63%) between plots (Table 2-7). Sorenson coefficient for herbaceous species was 43% (39-81%) between sites and 53% (22- 61%) between plots (Table 2-7).

The ISA revealed 37 species were indicators with $p < 0.01$ (Table 2-8, 2-9, 2-10). Sugar maple, black cherry (*Prunus serotina* Ehrh.), American beech (*Fagus grandifolia* Ehrh.), tulip popular (*Liriodendron tulipifera* L.), and white oak (*Quercus alba* L.) were significant indicators depending on region ($p < 0.01$) (Table 2-8). Eighteen understory woody species and 13 herbaceous species were identified as indicators depending on region, province, aspect, or topographic position (Table 2-9, Table 2-10).

Table 2-7: Sorenson coefficient, mean, standard deviation, minimum, and maximum associated with flora at Pennsylvania ramp populations.

	Sorenson coefficient (S_s)		
	mean, s.d.	min	max
Between sites (n = 30)			
Overstory trees species	47%, 19%	0%	100%
Understory woody species	53%, 16%	0%	100%
Herbaceous species	43%, 17%	0%	95%
Overall	38%, 13%	0%	87%
Between plots (n = 150)			
Overstory tree species	57%, 14%	0%	100%
Understory woody species	57%, 14%	0%	100%
Herbaceous species	53%, 10%	0%	100%
Overall	50%, 11%	0%	100%

Table 2-8: Statistically significant indicator species analysis (ISA) results for overstory tree species for Pennsylvania ramp study populations. Significance denoted by: P<0.001***, P<0.01**. Latitude (Lat.) is grouped by north (N) and south (S) while longitude (Long.) is west (W) and east (E). Physiographic provinces included are: Appalachian Plateau (AP), Piedmont (P), and Ridge and Valley (RV). Aspect was broken into three categories: N/E/NE/NW (N), S/W/SW/SE (S), and none (None). Topographic positions are: lower slope (L), middle slope (M), upper slope (U), and floodplain (F).

Common name	Species	ISA				Topographic position
		Lat.	Long.	Province	Aspect	
Sugar maple	<i>Acer saccharum</i> Marsh.	N**		AP***	N**	
Bitternut hickory	<i>Carya cordiformis</i> (Wang) K. Koch				None**	F**
American beech	<i>Fagus grandifolia</i> Ehrh.	S***		P***		
Tulip poplar	<i>Liriodendron tulipifera</i> L.	S***		P***		
Black cherry	<i>Prunus serotina</i> Ehrh.	N**				
White oak	<i>Quercus alba</i> L.	S**	E**			

Table 2-9: Statistically significant indicator species analysis (ISA) results for woody understory species at Pennsylvania ramp populations. Significance denoted by $P < 0.001^{***}$, $P < 0.01^{**}$. Latitude (Lat.) is grouped by north (N) and south (S) while longitude (Long.) is west (W) and east (E). Physiographic provinces included are: Appalachian Plateau (AP), Piedmont (P), and Ridge and Valley (RV). Aspect was broken into three categories: N/E/NE/NW (N), S/W/SE/SW (S), and none (None). Topographic positions are: lower slope (L), middle slope (M), upper slope (U), and floodplain (F).

Common name	Species	ISA				Topographic position
		Lat.	Long.	Province	Aspect	
Striped maple	<i>Acer pensylvanicum</i> L.		W**			
Japanese barberry	<i>Berberis thunbergii</i> A.P. de Candolle*	S**				
Musclewood	<i>Carpinus caroliniana</i> Walter		E**	RV**	None*	F**
Oriental bittersweet	<i>Celastrus orbiculatus</i> Thunb. *	S***		P**	S**	
Autumn olive	<i>Elaeagnus umbellata</i> Thunb. *			P**	None*	F**
Running strawberry bush	<i>Euonymus obovatus</i> Nutt.					L**
Spicebush	<i>Lindera benzoin</i> L.	S***		RV*		
Japanese honeysuckle	<i>Lonicera japonica</i> Thunb. *	S***	E***	P***	S***	
Amur honeysuckle	<i>Lonicera maackii</i> (Rupr.) Herder*	S**			None*	
Morrow or Bella honeysuckle	<i>Lonicera morrowii</i> A. Gray or bella Zabel *				*	
American hophornbeam	<i>Ostrya virginiana</i> (P. Miller) K. Koch	N***				
Virginia creeper	<i>Parthenocissus quinquefolia</i> (L.) Planch.		E***	RV*	None*	F**
Multiflora rose	<i>Rosa multiflora</i> Thunb. Ex. Murr. *				None*	F**
Wineberry	<i>Rubus phoenicolasius</i> (Maxim.)*	S***	E***	P***	None*	
Red elderberry	<i>Sambucus racemosa</i> L. var. <i>pubens</i>		W**			
Bladdernut	<i>Staphylea trifolia</i> L.			RV**		
Black haw	<i>Viburnum prunifolium</i> L.				None*	F**
Gooseberry	<i>Viburnum</i> sp.				S**	

Table 2-10: Statistically significant indicator species analysis (ISA) results for herbaceous species at Pennsylvania ramp populations. Significance denoted by $P < 0.001$ ***, $P < 0.01$ **.

Latitude (Lat.) is grouped by north (N) and south (S) while longitude (Long.) is west (W) and east (E). Physiographic provinces included are: Appalachian Plateau (AP), Piedmont (P), and Ridge and Valley (RV). Aspect was broken into three categories: N/E/NE/NW (N), S/W/SW/SE (S), and none (None). Topographic positions are: lower slope (L), middle slope (M), upper slope (U), and floodplain (F)

Common name	Species	ISA				Topographic position
		Lat.	Long.	Province	Aspect	
Jack-in-the-pulpit	<i>Arisaema triphyllum</i> (L.) Schott	N**	E**			F**
Cut-leaf toothwort	<i>Cardamine concatenata</i> (Michx.) O. Schwarz		W**	RV**		
Broad-leaf toothwort	<i>Cardamine diphylla</i> (Michx.) Alph. Wood	N***	W**	AP**		
Blue cohosh	<i>Caulophyllum thalictroides</i> (L.) Michx.	S**	W***		N**	
Enchanter's nightshade	<i>Circaea canadensis</i> L. Hill		E***		None*	F**
Intermediate woodfern	<i>Dryopteris intermedia</i> (Muhl. Ex Willd.) A. Gray		W***			
Yellow trout lily	<i>Erythronium americanum</i> Ker Gawl.	N***				
White wood aster	<i>Eurybia divaricate</i> (L.) G. L. Nesom	N**	E***			
Orange jewelweed	<i>Impatiens capensis</i> Merrb.		E***		None*	F**
Wood nettle	<i>Laportea canadensis</i> (L.) Wedd.			RV**		
Mayapple	<i>Podophyllum peltatum</i> L.					F**
Christmas fern	<i>Polystichum acrostichoides</i> (Michx.) Schott			AP**		
Red trillium	<i>Trillium erectum</i> L.	N**	W***	AP**		

Discussion

Site and soil results

This study confirms soil moisture is an important factor influencing ramp occurrence and suggests seasonal soil moisture might be a limiting factor on ramp distribution on forestlands. Ramp populations most frequently occurred on east and north facing slopes or floodplains in PA. Additionally, soil moisture content remained consistently at or above 35% volume throughout the year at a study site where it was measured every 8 weeks during 2021 (Figure 2-3). Slope and aspect can alter environmental conditions and species richness, slopes exposed to higher levels of sunlight are drier and have less plant cover (Osman and Barakbah, 2011). In the northern hemisphere, south facing slopes receive longer, and more intense insolation compared to north facing slopes (Nevo et al., 1999). Ramps likely prefer north aspects because they are prone to water stress due to their shallow root systems (Geries et al., 2020). When comparing light availability, soil nutrients, and soil moisture content on ramp survival it was determined soil moisture was the most important environmental factor (Vasseur and Gagnon, 1993). Additionally, it has been observed that ramps had greater growth rates on nutrient poor sites that were moister compared to nutrient rich sites that were drier, suggesting ramps are more dependent on water availability than soil nutrient levels (Bernatchez et al., 2013).

Soil nutrient content differed according to physiographic province (Table 2-2), this is undoubtedly due to different underlying rock types and geologic histories. The Appalachian Plateau and Ridge and Valley provinces are predominantly sandstone, shale, siltstone, and some limestone while the Piedmont province is schist, dolomite, limestone, and gneiss (Pennsylvania Natural Heritage Program, 2019). This study found that soil pH and nutrient content was consistent with other research that suggests ramps can be cultivated in soils with a slightly acidic pH (5-7) and abundant soil calcium content (Table 2-1, Table 2-2) (Bernatchez et al., 2013; Sitepu, 2018). Ramps are often labeled as “calciphytes,” meaning their growth is positively

correlated with calcium content and horticultural experiments have indicated that application of calcium can positively influence ramp growth and survival (Bernatchez et al., 2013; Ritchey and Schumann, 2005). Therefore, it is suggested sites have a calcium rich soil for cultivation purposes. However, too much calcium can inhibit the uptake of magnesium and ramps prefer soil with a high calcium to magnesium ratio (Bernatchez et al., 2013).

Associated flora

Although there were 252 plants associated with ramps in PA, on average 50% were shared between sites suggesting a similar associated flora with some consistent indicator candidates (Table 2-7).

Sugar maple was the most frequent and dominant tree species occurring at ramp sites (Table 2-3, 2-4). It has been observed that ramps planted under sugar maple stands had greater annual leaf width due to increased sunlight availability (Bernatchez et al., 2013). ISA identified this species as a significant indicator for ramps on north aspects (Table 2-8), likely because these slopes are cool, wet, and high in calcium content. Sugar maple is both a calcium demanding species and has high calcium content in its' leaf litter (Ott and Watmough, 2021) Other popular NTFPs such as goldenseal (*Hydrastis canadensis* L.) and American ginseng (*Panax quinquefolius* L.) are also commonly found on calcium rich soil and growing under sugar maple (Burkhart, 2013; Zuiderveen et al., 2019). However, ginseng and goldenseal were not found to be common ramp associates in PA (only on 17% and 10% of sites, respectively) (Appendix A-3). Therefore, differences in habitat suitability may be attributed to other environmental factors, such as soil moisture. While ramps require consistently high soil moisture content throughout the year, goldenseal and ginseng may not (Figure 2-3). This could be why overlap between these species was infrequent.

Bitternut hickory (*Carya cordiformis* (Wang) K. Koch) was found on 50% of ramp sites and was an indicator species for ramp habitat on floodplains (Table 2-3, Table 2-8). This is likely

because bitternut hickory is associated with wet, riparian areas (Weakley, 2020). It's been observed ramps found under hickory (*Carya* sp.), experienced a later canopy closure, and were exposed to higher levels of sunlight for a longer time, this increase in resources resulted in greater carbon accumulation, seed production, and bulb width (Dion et. al., 2017). Sugar maple and black cherry were significant indicators for northern PA; this portion of the state is classified as "northern hardwood" forests which is dominated by maple and cherry trees (Table 2-8) (Pennsylvania Natural Heritage Program, 2019). American beech, tulip poplar, and white oak were indicators for southern PA which is classified as "Appalachian oak" forests dominated by tulip poplar and oak species (Table 2-8) (Pennsylvania Natural Heritage Program, 2019). This is likely why sugar maple was an indicator in the Appalachian Plateau and American beech and tulip poplar were significant indicators in the Piedmont region (Table 2-8). These significant associations are not simply due to "forest type" but also habitat suitability. Geographical history such as previous glaciation presence, local diversity, species competition and interactions, and regional environmental differences can all have an impact on species diversity (Rhoads and Block, 2005; Ricklefs and He, 2016).

Spice bush was the most frequently occurring native understory woody species. Floristic guides note spicebush grows in rich alluvial and mesic forests on slopes, bottomlands, or swamps (Weakley, 2020). When found on upland slopes, it can be an indicator of base rich soils, which usually refers to high levels of calcium or magnesium (Weakley, 2020). It was significant indicator in both the Ridge and Valley and southern part of the state (Table 2-8).

Blue cohosh was the most frequent herbaceous species found on ramp sites and plots (Table 2-6) and was a significant ISA indicator in the southern and western parts of PA and on north aspects (Table 2-10). At sites where blue cohosh was present in the spring, wood nettle (*Laportea canadensis* (L.) Wedd.) was observed later in the season. Blue cohosh and wood nettle may be good plant indicators in site selection as they are easy to see at both ends of the season. In

a study on identifying two mesic forest community types, “*Acer saccharum- Allium tricoccum- Caulophyllum thalictroides*”, was identified as main vegetative group, suggesting these species are frequently found in similar habitats (Bellemare et al., 2005). Additionally, the environmental factor that had the greatest effect on these species was solar insolation, further suggesting aspects that are cooler and moister may be an important factor governing the habitat conditions these species require (Bellemare et al., 2005).

Yellow trout lily was the second most frequent herbaceous species at ramp sites and an indicator for northern PA (Table 2-6, Table 2-10). Trout lily is a spring ephemeral and present when ramps begin to emerge, therefore, it could be a key identifier for forest farming site selection during ramp season. Previous work suggests ramps and trout lily share a similar niche (Bernatchez and Lapointe, 2012). Mayapple was observed at 80% of ramp sites (Table 2-6). Recent floristic guides note this species can be found upslope or on bottomlands, however it was a significant indicator of ramp habitat on floodplains (Table 2-10) (Weakley, 2020). Jack-in-the-pulpit (*Arisaema triphyllum* (L.) Schott) was also frequently observed at ramp sites was identified as an indicator species on floodplains (Table 2-6, Table 2-10).

Summary

In conclusion, ramps in PA were most frequently found on lower slopes, east and north facing aspects, and floodplains (Figure 2-2). Ramps were found on sites with high soil calcium contents and a neutral to slightly acidic pH; this information should be used as a guide for ramp cultivation (Table 2-1). Ramps require high soil moisture content throughout year not just during the growing season (Figure 2-3). Therefore, it is likely soil moisture is a key determinant in ramp habitat suitability and other species that require cool, moist environments should be prioritized as indicator species such as yellow trout lily (Table 2-9, Table 2-10). Yellow trout lily can be used for site selection during ramp season as it is a spring ephemeral. For ramp cultivation on north aspects, use indicator species such as sugar maple and blue cohosh. (Table 2-8, 2-10). At sites

where blue cohosh is present, wood nettle may be more valuable as an indicator later in the season as it is more apparent and flowering/fruitleting in late summer and early fall (Table 2-10).

Where ramps are to be forest farmed on floodplains, the use plant indicators such as bitternut hickory, mayapple and jack-in-the-pulpit (Table 2-8, Table 2-10).

Chapter 3

***Allium tricoccum* Ait. and *A. burdickii* (Hanes) A.G. Jones occurrences in Pennsylvania may be driven by differences in soil moisture, pH, and fertility**

Introduction

Allium tricoccum Ait. (Alliaceae), known as a ramp or wild leek, is a perennial forest plant that is widely distributed in the eastern United States (U.S.). Hanes and Ownbey (1946) were the first to formally recognize two “ramp” taxa and suggested a variety *burdickii* (versus var. *tricoccum*) based on morphological, phenological, and habitat differences. It has been suggested that var. *burdickii*, often referred to as narrow-leaf ramp, be recognized as a separate species, *Allium burdickii* (Hanes) A.G. Jones. Recent floristic treatments support it as a separate species (Sitepu, 2018; Weakley, 2020).

Despite recognition of two ramp taxa, geographic distribution remains unclear. The Biota of North America Program (BONAP, 2021), for example, does not recognize *A. burdickii* and therefore no maps have been produced from its database. Distribution maps of *A. burdickii* that do exist are contradicting (NatureServe, 2022; USDA Plants Database, 2022). Limited current understandings, and anecdotal observations, suggest sporadic and overlapping occurrences between the two taxa in the eastern U.S. Misidentification of *A. burdickii* as *A. tricoccum* may also contributed to uncertainty surrounding the distribution of *A. burdickii*. The range of *A. tricoccum* is along the east coast, down south to Georgia and across the Mississippi River into North and South Dakota and Nebraska (Figure 3-1) (BONAP, 2021). By contrast, *A. burdickii* can be found west as far as *A. tricoccum*, but distribution further south is only known to Tennessee (Figure 3-1) (NatureServe, 2022). Sources contradict on whether it is present in Virginia, and North Carolina (NatureServe, 2022; USDA Plants Database, 2022; Weakley, 2020). Eight states currently list *A. burdickii* as vulnerable, imperiled, or extinct. Ten states list the

conservation as “no rank” because its distribution and population status remain unknown, including Pennsylvania (PA) (NatureServe, 2022). Until this study, *A. burdickii* had not been officially documented in PA (Rhoads and Block, 1993; Rhoads and Block, 2007; The Pennsylvania Flora Project, 2022). Identification of key habitat determinants for *A. tricoccum* and *A. burdickii* would aid in the continued understanding of these two taxa and possibly in the conservation of *A. burdickii*.



Figure 3-1: *Allium burdickii* (top) and *A. tricoccum* (bottom) distribution throughout the United States.

Spring ephemeral abundance is associated with fertile soil because their short photosynthetic phase requires a surplus of nutrients (Rothstein and Zak, 2001). While ramps are perennials, their photosynthetic phase is like spring ephemerals since they leaf out before the overstory tree canopy to take advantage of high levels of sunlight. Nault and Gagnon (1988) have reported high levels of calcium in ramp reproductive structures at the end of the growing season. However, when comparing growth habits between the two species, Bernatchez et al. (2013) noted *A. burdickii* had a greater calcium leaf concentration and invested more resources in bulb growth and produced more bulbs. This calcium increase was correlated with a greater seed set (Bernatchez et al., 2013). Sitepu (2018) noted environmental factors associated with *A. tricoccum* and *A. burdickii* and determined populations of both species are often found at the same sites in different microhabitats. Soil pH of both species was within the same range of 4.5 to 7.6 with *A. tricoccum* found on loam to sandy soils and *A. burdickii* on mostly sandy and silty soils (Sitepu, 2018). Anecdotal results of associated flora report *A. burdickii* was commonly found under pine, maple, and oak species (*Pinus*, *Acer*, and *Quercus* spp.) (Sitepu, 2018).

It is possible that indicators occurring with *A. tricoccum* and *A. burdickii* may differ according to each species habitat preferences and tolerances. Anecdotal observations suggest that *A. tricoccum* may require greater soil moisture content than *A. burdickii*. Early descriptions of *A. burdickii* suggested it grew in drier, more upland areas compared to *A. tricoccum* (Hanes, 1953; Jones, 1979). More recent floristic treatments describe *A. burdickii* habitat as, “rich upland woods” (NatureServe, 2022) and “hardwood forests at higher elevations than *A. tricoccum* in cove forests or rich mount slopes” (Weakley, 2020). Whereas *A. tricoccum* habitat has been described as mesic, moist slopes, or depressions (Bernatchez et al., 2013; Rock et al., 2003). When describing *A. tricoccum* habitat for site selection it has been described as “damp, east or north facing slopes with well drained organic soils” (Chamberlain et al., 2014).

Allium species have short roots with bulbs that grow close to the soil surface. (Geries et al., 2020). Therefore, they only draw soil moisture from the upper 12 in./30 cm of the soil profile, making them vulnerable to water stress (Geries et al., 2020). Due to shallow root systems, soil moisture content has been implicated as important for ramp growth and survival (Bernatchez et al., 2013; Dion et al., 2017; Vassuer and Gagnon, 1993). Vassuer and Gagnon (1993), even suggested soil moisture as being the most influential variable on ramp survival. Bernatchez et al. (2013), found that wetter sites with less nutrient availability had greater ramp growth rates compared to drier sites with more nutrients available, suggesting moisture is more important for ramp growth than soil nutrients. *A. tricoccum* exhibited greater growth rates when found at sites that had a soil water potential of greater than -50 kilopascals (kpa) (Bernatchez et al., 2013). Soil water potential (kpa) relates to how tightly the water is held in the soil based on soil texture (Adhikary et al., 2008). Sitepu (2018), calculated soil moisture using wet and dry weight data from soil samples and noted *A. tricoccum* soil moisture ranged from 44-91% volume (% vol) and *A. burdickii* from 64-91% vol.

In this study, the habitat associated with *A. tricoccum* and *A. burdickii* populations occurring in southwest PA was documented and compared. Accordingly, the following habitat and flora data was collected and analyzed:

- 1) Site factors: aspect, elevation, topographic position, soil moisture, and other hydrologic characteristics associated with *A. tricoccum* and *A. burdickii* populations
- 2) Soil chemistry: pH and fertility associated with *A. tricoccum* and *A. burdickii* populations
- 3) Associated flora: most frequent over and understory species, similarity between flora, dominant tree species, “indicators species”, and flora correlated with *A. tricoccum* and *A. burdickii* populations

This information could be used to predict *A. burdickii* occurrences in PA and the region and to identify site factors that might explain why these two closely related taxa appear to differ in habitat.

Methods

Population solicitation and criteria for inclusion

Ramps are capable of colonizing forestlands through a combination of sexual (e.g., seeds) and asexual (e.g., bulblets) reproduction and growth (Nault and Gagnon, 1993). Asexual clonal growth can make discerning individual plants difficult without excavation of the bulb to look for the presence of a shared basal plate (Nault and Gagnon, 1993). Due to this clonal growth, it was difficult to discern genet numbers with precision in each population study area and so estimates were made using ramets. Populations ramet estimates in this study ranged from 500 to 50,000 ramets with most study populations averaging 1,000 ramets. Inclusion of ramp populations was based on the following criteria: (1) Each population occupied at least an acre in size and consist of at least 500 ramets; and (2) each population exhibited both asexual and sexual recruitment. The latter was evidenced by confirming the presence of all demographic stages (e.g., seedling to adult).

Beginning in 2017, ramp study populations were solicited from professional contacts and the public using a variety of media (e.g., social media, newsletter articles, internet blogs) and botanical networks in PA. iNaturalist and herbarium records were also reviewed, and populations were visited if sufficient information existed for field location. A total of eight sites and 40 understory plots were included and visited in this study (four *A. burdickii* sites and four *A. tricoccum* sites with 20 understory plots). These sites were all located outside of Pittsburgh, PA (Figure 3-2). Due to the frequent references to *A. burdickii* and *A. tricoccum* throughout this paper they will hence be referred to as AB (*Allium burdickii*) and AT (*Allium tricoccum*).

Study location

This study was conducted in southwestern PA, U.S.A (39°43'-42°16' N; 74°41'-80°31' W). This region is part of the Appalachian Plateau physiographic province and is dominated by oak-hickory forests (Pennsylvania Natural Heritage Program, 2019). The climate in PA consists of two major climatic zones, southwestern PA, is classified as, “humid subtropical” (The Pennsylvania State Climatologist, 2021). Mean annual precipitation is between 32 in./81 cm and 47 in./119 cm (The Pennsylvania State Climatologist, 2021).

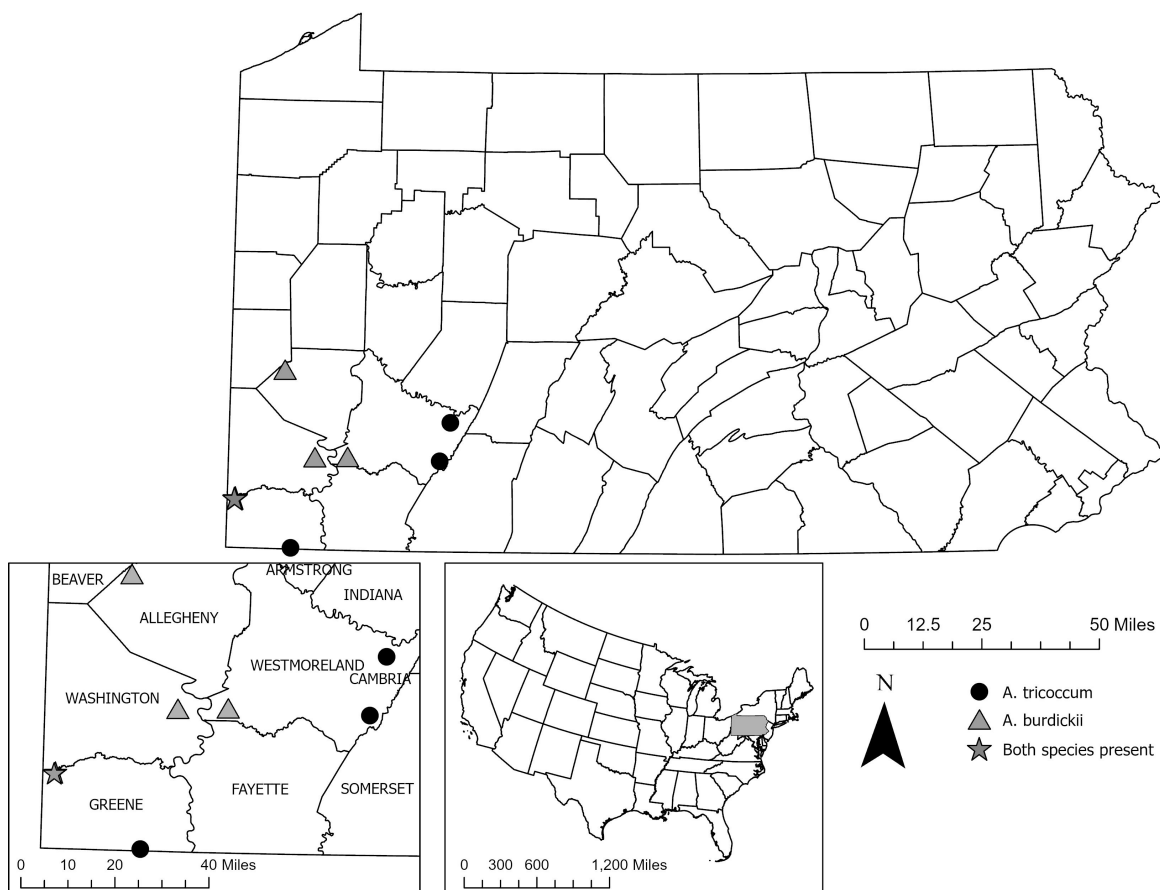


Figure 3-2: *Allium burdickii* (n=4) and *A. tricoccum* (n=4) study populations in Pennsylvania. Soil moisture data was collected where *A. tricoccum* and *A. burdickii* co-occur at the same site, this is denoted by the grey star on the map. Other *A. tricoccum* populations are denoted by a black circle and *A. burdickii* by a grey triangle. All points are larger than scale to obscure locations

Site factor data collection and analysis

Topographic data collection and analysis

At each study location, plots were located subjectively (e.g., visually) within populations with a goal of capturing the breadth of the site with five plots. In most cases, this meant that plots transected a slope or were spread upon a floodplain. Topographic position was recorded at each plot as the position on the slope (upper, middle-upper, middle, middle-lower, lower, toe-slope) or “bottom/flat” if the plot was on a floodplain. Elevation and aspect were recorded for each plot. Global Position System (GPS) coordinates taken at each plot allowed for calculation and comparison of aspect, slope in degrees, and elevation using ArcGIS Pro (ArcGIS pro v. 29, Environmental Systems Research Institute (ESRI) Redlands, CA). These calculations were compared alongside field collected data for accuracy and consistency. Soil drainage class and hydrologic soil group were compiled using Web Soil Survey (Web Soil Survey, 2022).

Soil moisture data collection and analysis

Soil moisture measurements were taken at one AB population and one AT population at a single study site in southwest PA were both occurred in proximity. These populations co-occurred at the same site with AB on a southwest aspect and AT across a stream on a north aspect (Figure 3-3). This site will hereafter be referred to as BSP (both species present). Five moisture sampling plots were overlain on floristic sampling plots and 30 measurements were taken with a ML3 Theta Soil Moisture Probe (Dynamax Inc. Houston, TX). To take readings, the soil moisture probe was inserted to bulb depth or about 6 in./15 cm deep into the soil (Bernatchez et al., 2013; Bretreger et al., 2021; Tenenbaum et al., 2006). Soil moisture measurements were taken from April through December 2021 at 8-week intervals (April 23, June 16, August 21, October 8, and December 10). Soil moisture data were averaged across the entire site for each sampling date. Because populations of both species occurred in the same area, both were exposed to similar weather conditions in 2021 while data was collected.

Unexpectedly, between the first visit in April and second visit in June, the forested slope where two out of five AT plots occurred were logged and could no longer be used in the data set

due to site disturbance. Therefore, two replacement plots were placed on the mid and toe-slope, slightly altering the upper elevation limit of plots.

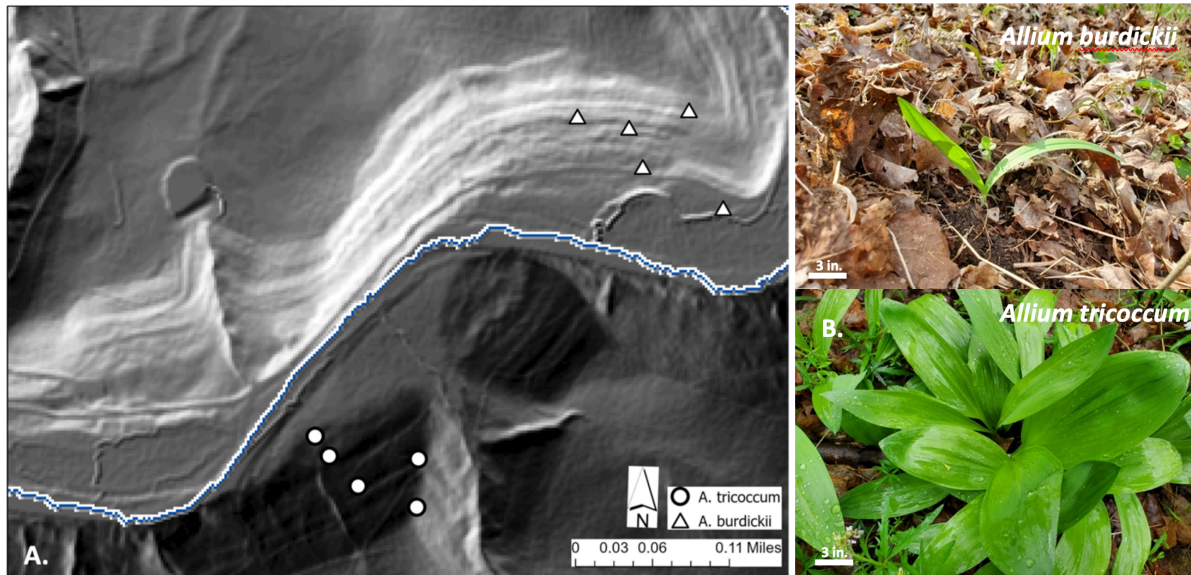


Figure 3-3: (A) Hill shade map where soil moisture data was collected in Pennsylvania and (B) ramp species. ArcGIS Pro was used to calculate hill shade with default settings (315° azimuth, 45° altitude). Top right image is *Allium burdickii* and bottom right is *A. tricoccum*. White circles denote *A. tricoccum* populations and white triangles denote *A. burdickii*.

Canopy density data collection and analysis

To examine tree canopy openness throughout the ramp growing season, hemispherical light photographs were taken and averaged in BSP plots when soil moisture data was being collected. This was done using a Nikon D90 digital camera with a Nikon 10.5 mm Fisheye lens mounted on a tripod. Gap Light Analyzer (Gap Light Analyzer, Version 2.0) was used to calculate Global Site Factor (GSF), which is the percent of canopy openness (Hemiview Manual 2.1,1998)

Hydrological properties

Topographic wetness indices (TWI) were calculated to determine if there was a difference between AT and AB sites. TWI is used to measure the amount of moisture in the soil using digital elevation models (DEMs) (Tenenbaum et al., 2006). TWI, is calculated by

$\ln(\alpha/\tan(\beta))$ where alpha is local upslope catchment area divided by contour length and beta is slope. TWI accounts for local slope and gravitational forces on water processes (Hojati and Mokarram, 2016). TWI was calculated for BSP site using ArcGIS pro (ArcGIS pro v. 29, Environmental Systems Research Institute (ESRI) Redlands, CA) with an extension toolbox through “Whitebox Geospatial Inc” (The Whitebox Geospatial Analysis tools project, University of Glasgow).

One-meter DEMS resampled into three-meter DEMs were downloaded from Pennsylvania Spatial Data Access (PASDA). DEMs were clipped and merged to contain the entire upslope drainage area for both populations. This area was determined by following streams upslope using national hydrography datasets (NHD) until they came to an end. Hydrologic unit code 12s (HUC12), which contained the entirety of these streams, were used to determine the size of the clipped raster. “Breach depressions” was used on the merged DEM. Breach was used instead of fill to create the most accurate flow path (Lidberg et al., 2017). The watershed was delineated using D8 flow direction, D8 flow accumulation, and a stream threshold was set of 140,000. This threshold was determined by selecting multiple stream heads, recording the values, and determining which value for flow accumulation encompassed the entirety of the stream section that needed to be included. After this, slope was calculated on the breached DEM. TWI was calculated using the breached DEM and slope file. Data on soil drainage class and hydrologic soil group of sites was gathered using Web Soil Survey (Web Soil Survey, 2022).

Soil chemistry data collection and analysis

At each site, five soil samples were collected. In each understory floristic sampling plot, one sample was collected from the top 8 in./20 cm of soil (A horizon) and within 6 in./15 cm proximity to ramp bulbs and roots. Each sample was therefore a single rather than composite soil sample. This sampling method was used to ensure that samples (1) accurately represented only

the localized soil from the rhizosphere; and (2) to examine any fine scale rooting zone variation between plots within each site.

Soil samples were submitted to the Pennsylvania State Agricultural Analytical Services Laboratory, University Park, PA for chemical analysis. The following protocol was used to analyze samples: soil pH was determined using the Water method (Eckert and Sims, 1995) and macro-nutrient content (available P, K, Ca, Mg) of samples was determined using the Melich 3 (ICP) method (Wolf and Beegle, 1995).

A total of 40 soil samples were collected and analyzed. SPSS (IMB Statistics for Macintosh, v. 28, IMB Corp., Armonk, New York) was used to run a Mann-Whitney U to determine if there was a difference in soil characteristics (pH, Ca, K, P, Mg) between AT and AB. To run this statistical test, soil characteristics were put in as scale, continuous variables and grouped based on ramp species present.

Floristic sampling and analysis

Over and understory flora associated with ramps were documented using a combination of plot and plot-less sampling methods. The overstory layer included dominant or co-dominant tree species while, understory included resident woody species (e.g., small trees, shrubs, vines) and herbaceous plants (Gilliam, 2014).

Sites were visited for sampling purposes between 2018 and 2021. Multiple visits were made to sites to ensure documentation of seasonal transitions in flora and to confirm identification of some taxa. Visits were timed to document the spring and early summer flora at each site (April-May) and then mid and late summer flora (July-August). If the abundance of a floristic associate changed over time the greatest abundance value was used. Herbarium voucher specimens were collected for all ramp populations and deposited at the Carnegie Museum of Natural History (CM), The Morris Arboretum of the University of Pennsylvania (MOAR), and

the Pennsylvania State University Herbarium (PAC). All plant nomenclature follows “Flora of the Southeastern U.S.: Pennsylvania” (Weakley, 2020).

For overstory documentation, each plot was divided into four quarters using the Point-Centered Quarter-Method (Causton, 1987; Kent and Coker, 1992). Using this method, only the nearest dominant or co-dominant canopy tree (stems ≥ 3 in./7.6 cm diameter at breast-height (4.5 ft/1.4 m) and height ≥ 4.5 ft/1.4 m) within each quarter was recorded, yielding one tree per quarter and four trees per plot. Diameter at breast-height (dbh) was recorded for each tree species to calculate importance values (IV) (Curtis and McIntosh, 1951; McCune and Grace, 2002). IVs were calculated for all overstory tree species recorded using relative frequency, relative density, and relative dominance (Curtis and McIntosh, 1951).

For understory documentation, five circular plots, 628 m²/687 yards² (d=40 m/ 44 yards, r=20 m/ 22 yards), were established at each site throughout the population using a stratified nonrandom approach. Plot size was based on the goal that only “nearest neighbors” were to be recorded and to examine microvariability in associates by topographic position. In addition to noting presence, the local abundance of each floristic element was recorded within the plot and the immediate vicinity (i.e., within vision) using the following scale: (1) one plant observed; (2) 2-10 plants observed; (3) 11-49 plants observed; (4) 50 or more observed.

Sorenson coefficients (S_s) (also known as Bray-Curtis) were calculated for both vegetation layers to determine percent similarity between floristic associates at plots. Sorenson's coefficients are reported as percentages with 0% being no shared species and 100% being identical species composition (McCune and Grace, 2002). A Sorenson coefficient is calculated using $S_s = 2a/(2a+b+c)$, where “a” is the number of species in both samples and “b” and “c” are the number of species unique to each sample. Binary, presence/absence data was used with a Sorenson (Bray-Curtis) distance measure and city block geometry.

Indicator species analysis (ISA) was used to assess the degree to which a species is correlated with ramp occurrence. An indicator value is the product of the relative abundance and frequency of a given species (Dufrêne and Legendre, 1997; Peck, 2016). Dufrêne and Legendre methodology with a Monte Carlo randomization test were done to determine significance (Peck, 2016). Abundance data per plot was analyzed with the following factors of interest: species (AT or AB), soil chemistry (calcium and magnesium content), aspect, and topographic position. However, aspect and topographic position yielded no significant results and thus were excluded. Calcium thresholds were: 0-3,000, 3,000-6,000, and >6,000. Magnesium thresholds were: 0-450, 450-650 and 650-1,100. Calcium and magnesium content were included because literature suggests AB and AT differ in these nutrient requirements (Bernatchez et al., 2013). The given thresholds chosen were due to the distribution of the data. A significance level of $p < 0.05$ was used for overstory trees and woody understory species as no species had significant values less than 0.01 whereas a significance level of $p < 0.01$ was used for herbaceous plants as most species were highly significant indicators.

Nonmetric multidimensional scaling (NMS), also known as NMDS, is used to detect patterns within data sets (Peck, 2016). In this study, it was used to confirm if site factors, and floristic associates differed between AB and AT sites. Additionally, NMS was used to strengthen ISA results by suggesting which floristic associates were more correlated with which ramp species. NMS distances are constructed based on rank ordering of ordination scores with axes that represent a summary of redundant responses (Peck, 2016). Herbaceous abundance data with a Sorenson (Bray-Curtis) distance matrix was used to calculate ordination scores. NMS was only calculated for herbaceous data; overstory and woody understory data sets were too small for NMS to detect a pattern. A significant (randomization test $p = 0.008$) two-dimensional NMS solution with a final stress of 2.9 was chosen after verifying consistency of interpretation among several

NMS solutions. A correlation coefficient (r) of greater than $|0.4|$ was determined for species to be considered “correlated”.

ISA, similarity indices (Sorenson’s coefficient), and NMS were calculated using PC-ORD (Multivariate Analysis of Ecological Data, v. 7.0, MJM software design, Gleneden Beach, Oregon).

Results

This is the first scientific study on AT and AB habitat in PA, and the first to document AB populations and habitat within the state. The primary objective was to determine differences in habitat and floristic associates between AT and AB. Due to the stratified, nonrandom approach in which ramp sites were located using informants, targeted plot placement for sampling and the lack of replication due to restricted knowledge on AB populations, conclusions of this study should be regarded as suggestive. As true random vegetative sampling is rare due to practical difficulties and paired “control” plots without ramp populations were not included, this methodology can result in bias (Kent and Coker, 1992; McGraw et al., 2003). Nevertheless, the results obtained in this study help to highlight and identify key characteristics associated with AB habitat for further research and conservation purposes.

Site factors

Topographic results

Recorded aspect of AT and AB populations differed with 15 out of 20 AT plots on north aspects, and AB plots distributed across varying aspects (Figure 3-4). Both AB and AT plots were most frequently found on “middle slope”. Average AT elevation was greater at 1,434 ft compared to AB at 931 ft (Figure 3-4). The NMS verifies these results as the elevation vector is more correlated with AT (Figure 3-6). ArcGIS pro calculations indicate median aspect for AB populations was south and for AT was north, average slope was 20 degrees for AB and 22 degrees for AT, average elevation was 917 ft for AB and 1,414 ft for AT.

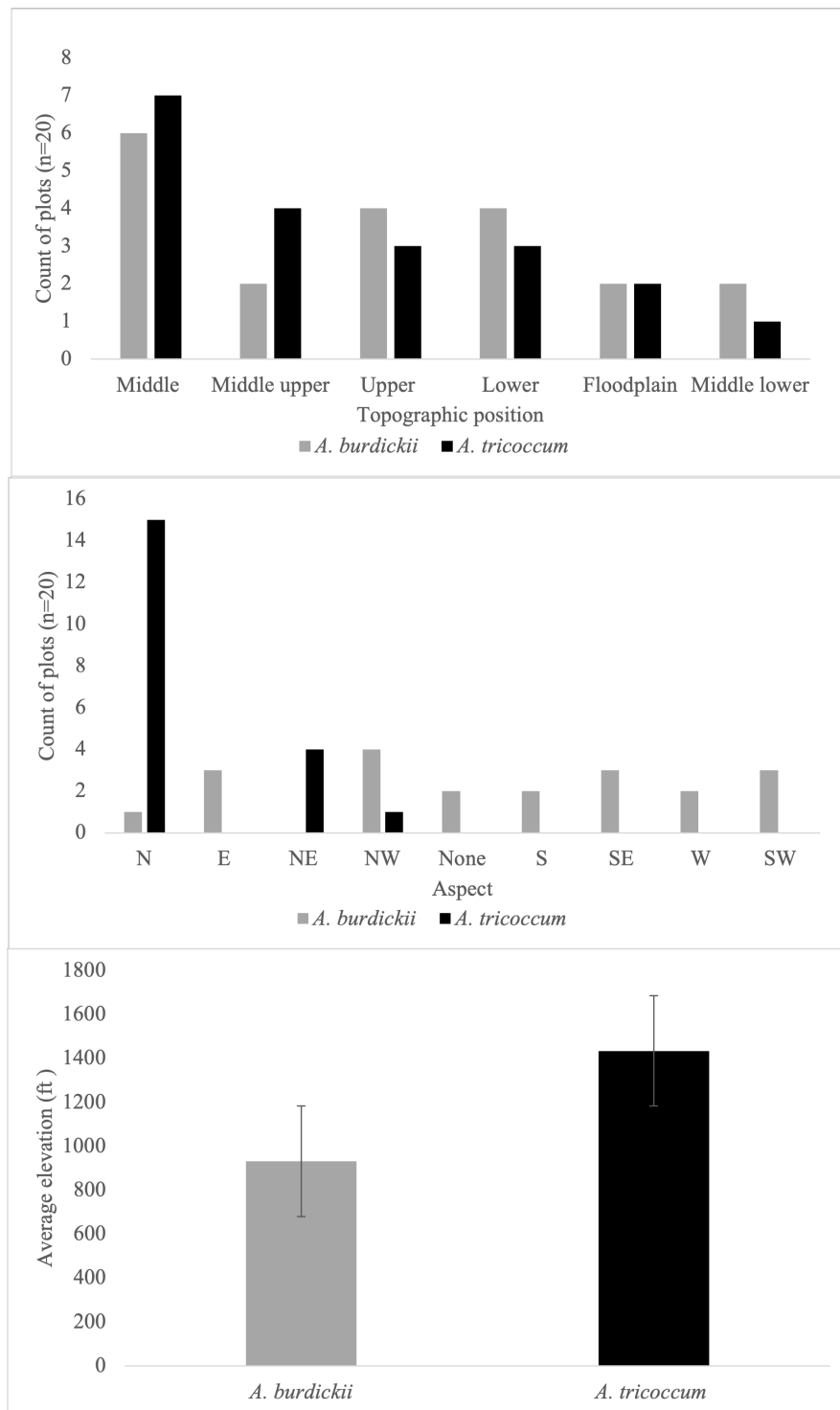


Figure 3-4: Topographic position (slope or floodplain), aspect, and elevation (ft) results from southwestern Pennsylvania *Allium tricoccum* and *A. burdickii* populations.

Hydrologic results (soil moisture, TWI, hydrologic soil group, and drainage class)

Soil moisture was consistently greater at AT populations compared to AB (Figure 3-5). In April, both populations had similar soil moisture contents with AB at 30% volume (% vol) and AT at 35% vol. Then values diverge with AT soil moisture increasing and peaking in August at 50% vol while AB decreased through October to 19% vol (Figure 3-5). In December soil moisture increases at both populations with AT at 46% vol and AB populations at 35% vol. Average percent canopy openness was the highest in April and December at 48% and the lowest in June at 5% (Figure 3-5).

Topographic wetness indices (TWI) were higher for AB (7.3) compared to AT (6.1). Drainage classes of AB and AT populations were “well drained” with one AT site being “poorly drained”. Hydrologic soil group results were inconsistent and produced a wide range of results.

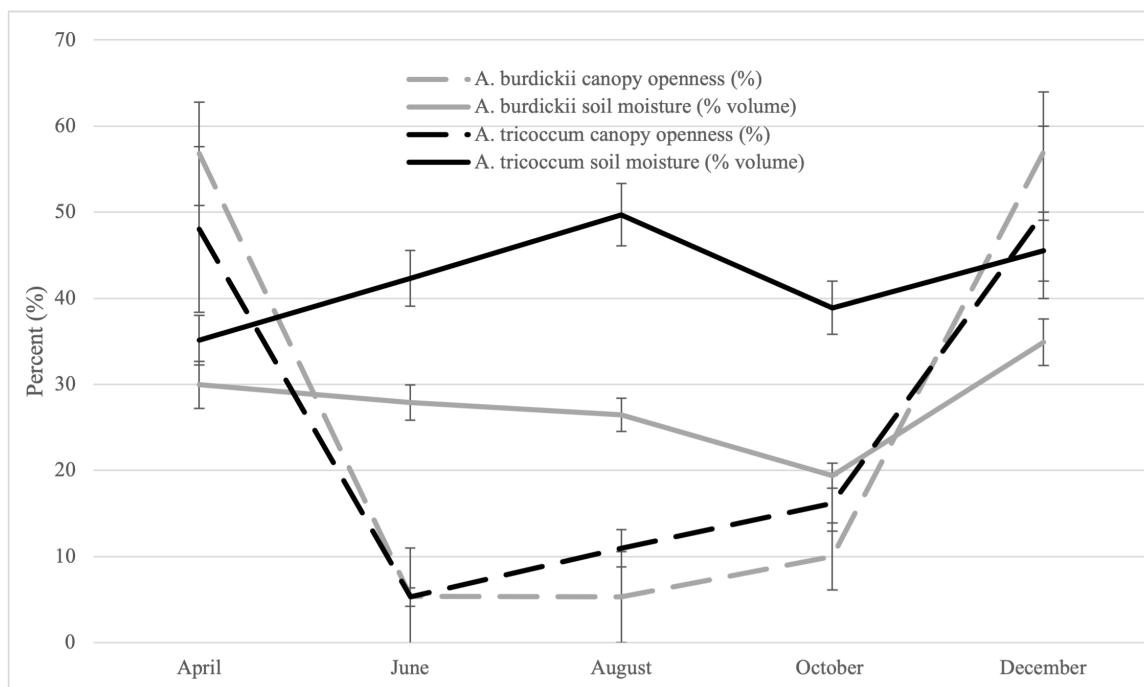


Figure 3-5: Soil moisture (% volume) and percent canopy openness at southwestern Pennsylvania *Allium burdickii* and *A. tricoccum* populations (n=2) from April through December. Bars represent standard error (σ/\sqrt{n}).

Soil chemistry

Mann Whitney-U results revealed pH, calcium, magnesium, and potassium content were statistically significantly greater at AB populations compare to AT (Table 3-1). These results are supported by the NMS which suggests pH, magnesium, calcium, and potassium content are more correlated with AB sites, whereas AT sites are more acidic (correlation coefficient ($r > |0.2|$)) (Figure 3-6). Phosphorus is more correlated with axis two which accounts for less than 1% of variation in this matrix, this suggests phosphorus is not correlated with either AT or AB sites (Figure 3-6).

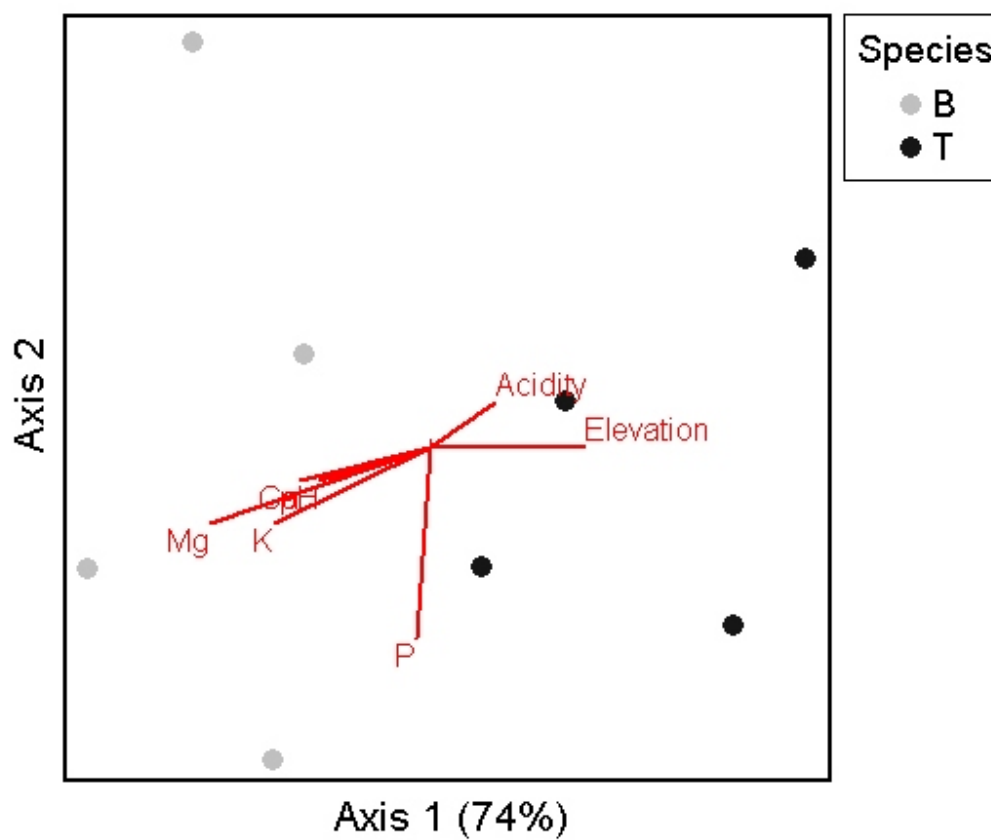


Figure 3-6: Nonmetric multidimensional analysis results from *Allium burdickii* (B) and *A. tricoccum* (T) populations located in southwestern Pennsylvania. Soil nutrients, pH, and elevation are overlaid on two-dimensional herbaceous abundance ordination.

Table 3-1: Mean and standard deviation (μ , s) of *Allium tricoccum* (n=20) and *A. burdickii* populations (n=20). Asterisk (*) denote significance from Mann-Whitney U analysis ($p < 0.05^*$, $p < 0.01^{**}$).

	<i>A. tricoccum</i>	<i>A. burdickii</i>
	μ , s	μ , s
pH	5.7, 0.6	6.1, 0.6*
Phosphorus ppm	85, 96	114, 90
Potassium ppm	301, 129	403, 121*
Magnesium ppm	389, 236	666, 195**
Calcium ppm	4053, 2834	5818, 1941*

Flora

A total of 170 species were documented in this study: 18 overstory tree species, 33 small trees, shrubs, lianas, or vines, and 119 herbaceous plants (Entire species lists located in Appendix B). All summary data can be found in tables: 3-2, 3-3, 3-4, and 3-5. The most frequent and dominant overstory tree species was sugar maple (*Acer saccharum* Marsh.) which was present at 85% of AT and AB plots (Table 3-2, Table 3-3). Sugar maple IV was greater at AB populations at 97 compared to AT at 87 (Table 3-3). The second most frequent tree species at AT plots was American basswood (*Tilia americana* L.) and at AB plots was bitternut hickory (*Carya cordiformis* (Wang) K. Koch) (Table 3-2). Spicebush (*Lindera benzoin* L. Blume) was the most frequent understory woody species found at AB and AT plots. Spicebush was found on 75% of AB plots and 50% of AT plots (Table 3-4). Japanese barberry (*Berberis thunbergii* A.P. de Candolle) and multiflora rose (*Rosa multiflora* Thunb. Ex. Murr.) were the second most frequently occurring understory woody species (Table 3-4). The most frequently occurring herbaceous species with AT was blue cohosh (*Caulophyllum thalictroides* (L.) Michx.) and great white trillium (*Trillium grandiflorum* (Michx.) Salis.) which occurred in 90% of plots (Table 3-

5). The most frequently occurring herbaceous species at AB plots was cut-leaf toothwort (*Cardamine concatenata* (Michx.) O. Schwarz) at 85% of plots and mayapple (*Podophyllum peltatum* L.) at 80% of plots (Table 3-5). Cut-leaf toothwort was also present at 85% of AT plots (Table 3-5).

Table 3-2: Overstory tree frequency table for southwestern Pennsylvania *Allium tricoccum* and *A. burdickii* study populations.

Common name	Scientific name	Percentage of plots and (n) for <i>A. tricoccum</i>	Percentage of plots and (n) for <i>A. burdickii</i>
Sugar maple	<i>Acer saccharum</i> Marsh.	85 (17)	85 (17)
Bitternut hickory	<i>Carya cordiformis</i> (Wang) K. Koch	30 (6)	40 (8)
Tulip poplar	<i>Liriodendron tulipifera</i> L.	30 (6)	
Northern red oak	<i>Quercus rubra</i> L.	25 (5)	35 (7)
Slippery elm	<i>Ulmus rubra</i> Muhl.	10 (2)	25 (5)
American basswood	<i>Tilia americana</i> L.	45 (9)	20 (4)
American beech	<i>Fagus grandifolia</i> Ehrh.	15 (3)	
Black cherry	<i>Prunus serotina</i> Ehrh.	5 (1)	15 (3)
White oak	<i>Quercus alba</i> L.		15 (3)
Shagbark hickory	<i>Carya ovata</i> (P. Miller) K. Koch		10 (2)
Pignut hickory	<i>Carya glabra</i> (P. Miller) Sweet		5 (1)
Northern hackberry	<i>Celtis occidentalis</i> L.		5 (1)
Black walnut	<i>Juglans nigra</i> L.	10 (2)	5 (1)
Sycamore	<i>Platanus occidentalis</i> L.	10 (2)	5 (1)
Shingle oak	<i>Quercus imbricaria</i> Michx.		5 (1)
Yellow oak	<i>Quercus muehlenbergii</i> Enge.		5 (1)
American elm	<i>Ulmus americana</i> L.		5 (1)
Black birch	<i>Betula lenta</i> L.	5 (1)	

Table 3-3: Importance values (IV) for overstory dominant and co-dominant species at southwestern Pennsylvania *Allium tricoccum* and *A. burdickii* populations.

Species		IV	
Common name	Scientific name	<i>A. tricoccum</i>	<i>A. burdickii</i>
Sugar maple	<i>Acer saccharum</i> Marsh.	87	97
Sweet birch	<i>Betula lenta</i> L.	4	
Bitternut hickory	<i>Carya cordiformis</i> (Wang) K. Koch	28	31
Pignut hickory	<i>Carya glabra</i> (P. Miller) Sweet		4
Shagbark hickory	<i>Carya ovata</i> (P. Miller) K. Koch		7
Northern hackberry	<i>Celtis occidentalis</i> L.		5
American beech	<i>Fagus grandifolia</i> Ehrh.	12	
Black walnut	<i>Juglans nigra</i> L.	7	7
Tulip poplar	<i>Liriodendron tulipifera</i> L.	30	
Sycamore	<i>Platanus occidentalis</i> L.	18	6
Black cherry	<i>Prunus serotina</i> Ehrh.	3	11
White oak	<i>Quercus alba</i> L.		13
Shingle oak	<i>Quercus imbricaria</i> Michx.		5
Yellow oak	<i>Quercus muehlenbergii</i> Enge.		6
Northern red oak	<i>Quercus rubra</i> L.	28	36
American basswood	<i>Tilia americana</i> L.	43	19
American elm	<i>Ulmus americana</i> L.		3
Slippery elm	<i>Ulmus rubra</i> Muhl.	9	20

Table 3-4: The 10 most frequent understory woody species at southwestern Pennsylvania *Allium tricoccum* and *A. burdickii* study sites. Asterisks (*) denote non-native, exotic species.

Common name	Scientific name	Percentage of plots and (n) for <i>A. tricoccum</i>	Percentage of plots and (n) for <i>A. burdickii</i>
Spice bush	<i>Lindera benzoin</i> L. Blume	50 (10)	75 (15)
Grape vine	<i>Vitis</i> sp.		55 (11)
Japanese barberry	<i>Berberis thunbergii</i> A.P. de Candolle*	40 (8)	35 (7)
Striped Maple Multiflora	<i>Acer pensylvanicum</i> L.	25 (5)	
rose	<i>Rosa multiflora</i> Thunb. Ex. Murr. *	25 (5)	65 (13)
Gooseberry	<i>Ribes</i> sp.	20 (4)	
Red elderberry	<i>Sambucus racemosa</i> var. <i>pubens</i> (L.) Michx. Traut. & C.A. Meyer	20 (4)	
Yellow buckeye	<i>Aesculus flava</i> Sol.	15 (3)	
Elderberry	<i>Sambucus</i> sp.	10 (2)	
Witch hazel	<i>Hamamelis virginiana</i> L.	5 (1)	30 (6)
Amur honeysuckle	<i>Lonicera maackii</i> (Rupr.) Herder*	5 (1)	
American hornbeam	<i>Carpinus caroliniana</i> Walter		25 (5)
Virginia creeper	<i>Parthenocissus quinquefolia</i> (L.) Planch.		25 (5)
Bladdernut	<i>Staphylea trifolia</i> L.		25 (5)
Poison ivy	<i>Toxicodendron radicans</i> L. Kuntze		25 (5)

Table 3-5: The 25 most frequent herbaceous species at southwestern Pennsylvania *Allium tricoccum* and *A. burdickii* populations. Asterisks (*) denote non-native, exotic species.

Common name	Scientific name	Percentage of plots and (n) for <i>A. tricoccum</i>	Percentage of plots and (n) for <i>A. burdickii</i>
Blue cohosh	<i>Caulophyllum thalictroides</i> (L.) Michx.	90 (18)	45 (9)
Great white trillium	<i>Trillium grandiflorum</i> (Michx.) Salis.	90 (18)	
Cut-leaf toothwort	<i>Cardamine concatenata</i> (Michx.) O. Schwarz	85 (17)	85 (17)
Mayapple	<i>Podophyllum peltatum</i> L.		80 (16)
Christmas fern	<i>Polystichum acrostichoides</i> (Michx.) Schott	80 (16)	75 (15)
Intermediate woodfern	<i>Dryopteris intermedia</i> (Muhl. Ex Willd.) A. Gray	75 (15)	
Violet species	<i>Viola spp.</i>	75 (15)	70 (14)
Spring beauty	<i>Claytonia virginica</i> L.	50 (10)	70 (14)
Stonecrop	<i>Sedum ternatum</i> Michx.		70 (14)
Wild geranium	<i>Geranium maculatum</i> L.		65 (13)
False Solomon's seal	<i>Maianthemum racemosum</i> (L.) Link		65 (13)
False mermaid	<i>Floerkea proserpinacoides</i> Willde.	35 (7)	60 (12)
Wood-nettle	<i>Laportea canadensis</i> (L.) Wedd.	60 (12)	
Jumpseed	<i>Persicaria virginiana</i> (L.) Gaer.	60 (12)	50 (10)
White wood aster	<i>Eurybia divaricata</i> (L.) Nesom		55 (11)
Bedstraw	<i>Galium sp.</i>		55 (11)
Clearweed	<i>Pilea pumila</i> (L.) A. Grey	35 (7)	55 (11)
Hairy sweet cicely	<i>Osmorhiza claytonii</i> (Michx.) C.B. Clarke	50 (10)	
Garlic mustard	<i>Alliaria petiolata</i> (Berb.) Cav. & Gran. *	45 (9)	
Sweet scented bedstraw	<i>Galium triflorum</i> Michx.	45 (9)	60 (12)
Canada waterleaf	<i>Hydrophyllum canadense</i> L.	45 (9)	
Long bristled smartweed	<i>Persicaria longiseta</i> (de Bruijn) Kitagawa *	45 (9)	
Broadleaf toothwort	<i>Cardamine diphylla</i> (Michx.) Alph. Wood	40 (8)	
Squirrel corn	<i>Dicentra canadensis</i> (Goldie) Walpers	40 (8)	
Eastern blue phlox	<i>Phlox divaricata</i> L.	40 (8)	50 (10)
Hairy Solomon's Seal	<i>Polygonatum pubescens</i> (Willde.) Pursh.	40 (8)	50 (10)
Zip zag goldenrod	<i>Solidago flexicaulis</i> L.		50 (10)

Enchanter's- nightshade	<i>Circaea canadensis</i> (L.) Hill		45 (9)
White avens	<i>Geum canadense</i> Jacq.		45 (9)
Kidney leaf buttercup	<i>Ranunculus abortivus</i> L.		45 (9)
Sweet white violet	<i>Viola blanda</i> Willde.	40 (8)	
Spotted Joe-pye- weed	<i>Eutrochium maculatum</i> (L.) E.E. Lamont		40 (8)
Carolina spring beauty	<i>Claytonia caroliniana</i> Michx.	35 (7)	
Woodfern	<i>Dryopteris</i> sp.	35 (7)	
Red trillium	<i>Trillium erectum</i> L.	35 (7)	
Jack-in-the-pulpit	<i>Arisaema triphyllum</i> (L.) Schott	30 (6)	40 (8)
Honewort	<i>Cryptotaenia canadensis</i> (L.) A.P. de Candolle		35 (7)
Forest bedstraw	<i>Galium circaezans</i> Michx.		35 (7)

Sorenson coefficients for average overall similar species at AT plots was 38% (44-85%), at AB plots was 37% (45-84%), and between AT and AB plots was 44% (35-75%) (Table 3-6). Average Sorenson coefficients for overstory species at AT plots was 51% (65-95%), at AB plots was 42% (68-96%), and between AT and AB was 63% (51-87%) (Table 3-6). Average Sorenson coefficients for woody understory species at AT plots was 60% (45-92%), at AB plots was 48% (53-95%), between AT and AB plots was 58% (35-81%) (Table 3-6). Average Sorenson coefficients for herbaceous species at AT plots was 39% (49-89%), at AB plots was 39% (47-85%), and between AT and AB plots was 43% (39-81%) (Table 3-6).

For AB and AT populations, the ISA identified 23 indicator species with $p < 0.05$: two overstory tree species, five understory woody species, and 16 herbaceous species (Table 3-7, Table 3-8). The NMS confirmed herbaceous indicator species using a correlation coefficient (r) and tau of $> |0.4|$ (Figure 3-6). The proportion of variance represented by NMS ordination axis one, calculated as the proportion of variation in the reduced matrix relative to the original data set matrix, was 74% while axis two accounted for less than 1% (Figure 3-7). Therefore, the cut off value of $|0.4|$ was implicated for axis one as it accounted for almost all the variation. When comparing the ISA results with the NMS correlation coefficients, only 13 herbaceous species were identified indicators and had a correlation coefficient and tau $> |0.4|$ (Figure 3-7, Table 3-8). Wood nettle (*Laportea canadensis* (L.) Wedd.) ($r = -0.69$, $\tau = -0.62$) and blue cohosh ($r = -0.86$, $\tau = -0.68$) were both significant indicators for AT with a $p < 0.001$ and correlated with AT populations. Mayapple (*Podophyllum peltatum* L.) ($r = 0.86$, $\tau = 0.76$), stonecrop (*Sedum ternatum* Michx.) ($r = 0.90$, $\tau = 0.77$), false Solomon's seal (*Maianthemum racemosum* (L.) Link) ($r = 0.64$, $\tau = 0.59$), and lion's foot (*Nabalus* sp.) ($r = 0.725$, $\tau = 0.624$) were indicators for AB and highly correlated with AB sites (Figure 3-7, Table 3-8).

Table 3-6: Sørensen coefficient mean and standard deviation for *Allium tricoccum* plots (n=20), *A. burdickii* plots (n=20) and between *A. burdickii* and *A. tricoccum* plots (n=40).

	Sørensen coefficient (S_s)		<i>A. tricoccum</i> and <i>A. burdickii</i>
	<i>A. tricoccum</i>	<i>A. burdickii</i>	
Between plots			
Overstory tree species	51%, 26%	42%, 24%	63%, 18%
Understory woody species	60%, 22%	48%, 21%	58%, 18%
Herbaceous species	39%, 16%	39%, 16%	43%, 14%
Overall	38%, 15%	37%, 15%	44%, 13%

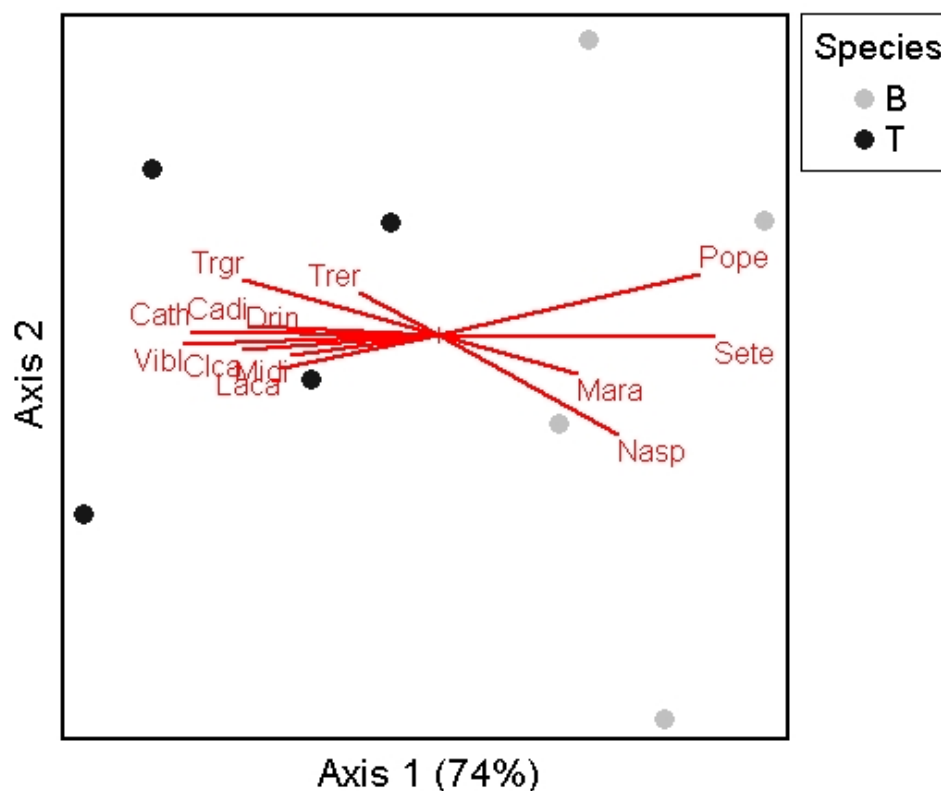


Figure 3-7: Nonmetric multidimensional analysis results with herbaceous indicator species overlaid on two-dimensional herbaceous abundance ordination ($r > |0.4|$, $\tau > |0.4|$). Species are denoted by the first two letters of their genus and specific epithet. Sites of *Allium burdickii* (B) and *A. tricoccum* (T) located in southwestern Pennsylvania

Table 3-7: Indicator species analysis (ISA) for overstory trees and understory woody species at southwestern Pennsylvania *Allium tricoccum* and *A. burdickii* populations. Significance denoted by $p < 0.5$ * and $p < 0.01$ **. Species grouped as *A. tricoccum* (T) or *A. burdickii* (B), and with varying calcium thresholds.

Species		ISA	
Common name	Scientific name	Species	Calcium
Tulip poplar	<i>Liriodendron tulipifera</i> L.	T*	
American basswood	<i>Tilia americana</i> L.		6,600ppm>*
Striped maple	<i>Acer pensylvanicum</i> L.	T*	
Musclewood	<i>Carpinus caroliniana</i> Walter	B*	
Multiflora rose	<i>Rosa multiflora</i> Thunb. Ex. Murr. *	B*	
Bladdernut	<i>Staphylea trifolia</i> L.	B*	
Grape vine	<i>Vitis</i> sp.	B**	

Table 3-8: Indicator species analysis (ISA) for herbaceous species at southwestern Pennsylvania *Allium tricoccum* and *A. burdickii* populations. Significance denoted by $p < 0.01$ ** and $p < 0.001$ ***. Species grouped as *A. tricoccum* (T) or *A. burdickii* (B) and with varying calcium and magnesium thresholds.

Species		ISA		
Common name	Scientific	Species	Calcium	Magnesium
Cut-leaf toothwort	<i>Cardamine diphylla</i> Michx. <i>Caulophyllum thalictroides</i> (L.)	T**		
Blue cohosh	Michx.	T***		
Carolina spring beauty	<i>Claytonia caroliniana</i> Michx.	T**		0-450**
Intermediate woodfern	<i>Dryopteris intermedia</i> (Muhl. Ex Willd.) A. Gray	T**	0-3000**	0-450**
Big leaved aster	<i>Eurybia macrophylla</i> (L.) Cassini	B**		
Forest bedstraw	<i>Galium circaezans</i> Michx.	B**		
Wood nettle	<i>Laportea canadensis</i> (L.) Wedd.	T***	0-3000***	0-450**
False Solomon's seal	<i>Maianthemum racemosum</i> L.	B**		
Two-leaved mitterwort	<i>Mitella diphylla</i> L.		0-3000**	0-450**
Mayapple	<i>Podophyllum peltatum</i> L.	B**		
Blue phlox	<i>Phlox divaricata</i> L.		0-3000**	
Lion's foot	<i>Nabalus sp.</i>	B**		650-1100**
Stonecrop	<i>Sedum ternatum</i> Michx.	B**		
Red trillium	<i>Trillium erectum</i> L.	T**		
Great white trillium	<i>Trillium grandiflorum</i> Michx. Salis.	T**		
Sweet white violet	<i>Viola blanda</i> (Willde.)	T**	0-3000***	

Discussion

The goal of this study was to identify site factors and flora associated with both *A. tricoccum* and *A. burdickii* through data collection at wild ramp populations in southwestern PA. Results suggest both site factors and flora differ between AB and AT populations.

Site factors

AT was more frequently found on north facing slopes which are exposed to less insolation and are therefore cooler and moister in the northern hemisphere when compared with south facing slopes which are warmer and drier (Figure 3-4) (Nevo et al., 1999). AB was found on

a wide range of aspects, including south (Figure 3-4). AT populations were found at higher elevations compared to AB, which is consistent with previous work that found altitude at AT sites to be greater than at AB (Figure 3-4) (Sitepu, 2018). However, contradictory observational reports suggest AB is found at more upland and higher elevations compared to AT (Hanes, 1953; NatureServe, 2022; Weakley, 2020). This could be due to the nature of the observations or small sample size in this study.

Soil moisture

AT soil moisture was greater than AB from April to December, suggesting AT requires a consistently moist soil throughout the year (Figure 3-5). This may be attributed to AT having a consistently shallower bulb depth when compared to AB (Sitepu, 2018) and these results are supported by horticultural results suggesting soil moisture as an influential factor on AT growth and survival (Bernatchez et al., 2013; Vassuer and Gagnon, 1993). These soil moisture results are impacted by corresponding topography, AT plots were on the floodplain and up a northern facing slope whereas AB populations were on a southern facing slope. Thus, the microhabitats in which these species occur differs and may result in ecological differentiation. Corresponding canopy openness results reveal canopy openness was the highest in April before the canopy leaves out and in December once the canopy has lost all its leaves (Figure 3-5). When ramps emerge in the spring (April), they take advantage of this high of light and conduct all their photosynthesis during this time before leaves senesce and plants transition to dormancy or flowering (Baumflek and Chamberlain, 2019).

Other hydrologic factors such as drainage class, hydrologic soil group, and topographic wetness index (TWI) proved to be inconclusive. Drainage class refers to how long the soil remains wet after being exposed to water, and hydrologic soil group is group is based off runoff potential and consists of four groups from A through D (Soil Survey Division, 1993). While drainage class of all ramp populations were predominately “well drained”, hydrologic soil group

results were inconsistent. Topographic wetness index (TWI) results proved to be the opposite of what field data results exhibited, with average TWI higher at AB plots compared to AT. AB habitat has been described as “upland” and “dry” and field data moisture content readings are lower at AB plots; therefore, TWI results are contradicting (Figure 3-4) (Hanes and Ownbey, 1946; Jones 1979). However, perhaps this data implies TWI is not a useful metric to use when applying it to ramp site selection. Causes for inconsistency could be that a three-meter DEM is too large to capture the microsite variation where ramps reside. Previous work suggests TWI results extracted from DEMs are sensitive to grid cell resolution (Tenenbaum et al., 2006). TWI is a relative measurement that is correlated with soil moisture over a long period of time and this field data was collected over a period of a couple of months and therefore, may not be comparable (Kopecký and Čížková, 2010). Lastly, D8 methodology was used to derive TWI and future attempts using Dinfinity flow algorithms may result in more useful results.

Soil chemistry

Soil nutrients, including calcium, magnesium, and potassium were greater at AB populations (Table 3-1; Figure 3-5). Calcium has proven to be a nutrient of interest as application of lime and gypsum have increased ramp growth and survival rates (Bernatchez et. al., 2013; Ritchey and Schumann, 2005). Both AT and AB are often regarded as “calciphytes,” meaning their growth is positively correlated with calcium rich soil (Ritchey and Schumann, 2005). When comparing AB and AT, higher calcium concentrations were found in AB leaves after gypsum application, suggesting AB has a greater calcium need (Bernatchez et al., 2013). This study confirms this claim as calcium content was significantly greater at AB sites (Bernatchez et al., 2013).

AT was found on more acidic soils (5.7) compared to AB (6.1) (Table 3-1; Figure 3-5). It is thought soils with a lower pH support greater ramp growth (Bernatchez et al., 2013; Davis and Greenfield, 2002). In a North Carolina study, average pH of wild AT populations was 5.5

(Davis and Greenfield, 2002). However, in cultivation trials optimal survival rates were observed at a pH of 4.9 and when pH was raised from 4.5 to 6.5, percent survival decreased almost 10% (Davis and Greenfield, 2002). It has been recorded that AT growth rates were higher at sites with a lower pH compared to sites with a higher pH and greater calcium content (Bernatchez et al., 2013). Therefore, it may be that a lower pH is more influential for AT whereas AB relies more heavily on higher calcium content.

Floristic results

Although there were 170 species documented in this study, flora tended to be more similar between plots of the two species, compared to at only AT or AB plots. This is likely due to a small sample size which resulted in a low species diversity. When comparing AT and AB the sample is larger (n=40) compared to within plots (n=20) this likely also contributes to this difference.

AT and AB were most frequently found under sugar maple (Table 3-2). Sugar maple is found in areas with calcium rich soil; as their leaves decompose, they deposit calcium into the soil through their leaf litter (Moore et al., 2015; Ott and Watmough, 2021). In the ISA, American basswood was significantly associated with sites where calcium content was the greatest in the study, this is likely because basswood leaves are also high in calcium (Table 3-7) (Kallio and Godman, 1973). Ramps found under basswood and sugar maple were found to have greater growth rates due to increased sunlight exposure (Bernatchez et al., 2013; Dion et al., 2017).

Multiflora rose and Japanese barberry are both non-native, exotic species that were frequently found growing with ramps. This is important to note as these species could eventually pose a threat to ramp habitat. Multiflora rose was identified as an indicator species for AB, however, as invasive species can tolerate a wide range of habitats, they are not good indicator species (Table 3-5) (Hager, 1998).

Blue cohosh was the most frequent herbaceous species, a significant ISA indicator, and correlated with AT populations (Table 3-5, Figure 3-7, Table 3-8). At sites where blue cohosh was present in the spring, wood nettle was observed later in the season. Wood nettle was also identified as an indicator species for AT, high calcium, and high magnesium content and correlated with AT populations (Figure 3-7, Table 3-8). Blue cohosh and wood nettle may be good plant indicators for AT site selection as they are easy to see at both ends of the season. In a study on identifying two mesic forest community types, "*Acer saccharum- Allium tricoccum- Caulophyllum thalictroides*" was identified as main vegetative group, suggesting these species are frequently found in similar habitats (Bellemare et al., 2005). This vegetation type was most correlated with solar insolation, suggesting aspect and soil moisture are important factors governing the habitat conditions where these species are found (Bellemare et al., 2005).

Mayapple, stonecrop, and false Solomon's seal were significant indicator species for AB and correlated with AB populations (Figure 3-6, Table 3-8). Recent floristic guides note mayapple grows on a variety of landscapes from bottom lands to upslope and is found on rich soils (Weakley, 2020). False Solomon's seal is recorded as growing in moist to dry forests yet was only found among AB populations (Table 3-5) (Weakley, 2020). Stonecrop is geographically restricted and only occurs in southern PA (BONAP, 2021). This species was likely an indicator due to the small sample size and study site locations. An assortment of species that can tolerate a wide range of habitats were indicators and correlated with AB compared to indicators of AT habitat require cooler, moist habitats. This is likely because AB can tolerate drier soil, and thus a wider range of habitats compared to AT.

In conclusion, habitat differences between AB and AT include soil moisture content, fertility, pH, associated species, aspect, and elevation. Differences in local site factors have a large impact on the microhabitats in which these species are found and provide supporting evidence for potential ecological differentiation between AT and AB. For example, AT requires

a higher soil moisture content compared to AB and this difference in need for soil moisture coincides with why these species occur on differing aspects. AB may rely more heavily on fertile soil, specifically that is rich in calcium, whereas AT prefers more acidic soils. Associated species with AT are those that require moist, mesic habitats, such as wood nettle or blue cohosh, whereas AB is found with a wide range of genera with varying habitat preferences. This information on AB habitat can be used to locate more populations and identify more key habitat attributes. Additionally, this work may shed light on populations that have been previously incorrectly identified as AT, yet their habitat profile matches AB. Further population discovery can be used to implement appropriate conservation and stewardship practices.

Chapter 4

Conclusion

The goal of this study was to identify site factors and flora associated with both *A. tricoccum* and *A. burdickii* through data collection at wild ramp populations in Pennsylvania (PA). This was an observational study done to provide guidance for forest farming, population discovery, and future research. In the broader study, consisting of 30 wild populations throughout PA, *A. tricoccum* was most frequently found on moist, lower slopes or floodplains and east and north aspects. Ramps were found on nutrient rich soil, especially with respect to calcium content, with neutral to slightly acidic pH. In prior research, ramps were recognized to be associated with soil moisture. The present study results demonstrate soil moisture content at *A. tricoccum* populations remains high throughout the year not just during the growing season. Fifty percent of flora found at plots throughout the PA were the same. This flora can be used to designate ideal ramp habitat through “indicator species”. Key indicator species associated with *A. tricoccum* were sugar maple (*Acer saccharum.*), bitternut hickory (*Carya cordiformis*), spice bush (*Lindera benzoin*), blue cohosh (*Caulophyllum thalictroides*), wood nettle (*Laportea canadensis*), yellow trout lily (*Erythronium americanum*), mayapple (*Podophyllum peltatum*), and jack-in-the-pulpit (*Arisaema triphyllum*) depending on state locality, province, aspect, and topographic position. Presence of indicator species should be viewed as suggestive rather than definitive of ramp habitat as all other site characteristic should also be considered.

Conclusions from the *A. burdickii* and *A. tricoccum* case study in southwestern PA revealed that *A. tricoccum* grows in areas with a higher soil moisture content compared to *A. burdickii* and *A. tricoccum* is found in soils that more acidic. *A. burdickii* by contrasts, grows in areas that are alkaline and nutrient rich in magnesium, calcium, and phosphorus. It has been suggested *A. burdickii* grows in drier areas compared to *A. tricoccum* and this study supports this

claim. Species accompanying *A. tricoccum* are associated with moist, mesic habitat conditions such as blue cohosh and wood nettle whereas species associated with *A. burdickii* can tolerate drier habitats such as false Solomons seal (*Maianthemum racemosum*), mayapple, and stonecrop (*Sedum ternatum*).

The following study limitations should be considered when applying these results in the field or in future modeling:

- *A. burdickii* had not been discovered in PA until this study and therefore there was limited replication of plots for this species when compared with *A. tricoccum*.
- Soil moisture data was collected at only one *A. burdickii* and *A. tricoccum* field site where both populations were known to occur.
- Sampling was biased as plots were intentionally located within ramp populations with no corresponding “absence” plots. Therefore, caution is required when extrapolating results beyond this study.

While these limitations exist, this first scientific study of ramp habitat associations in PA, and the first of its kind within the range of the species (*A. tricoccum* and *A. burdickii*), therefore the results remain valuable and can be used to guide further investigation.

As this study was conducted in PA, results should be carefully extrapolated. Research involving additional ramp populations throughout the eastern U.S. might be used to expand this study for habitat modeling. In this process, study results provide potential important factors that could be used as predictor variables in a future habitat modeling. A habitat suitability model (Rottenberry et al., 2006; Zuiderveen et al., 2019). could be used to predict ramp presence and where ramps could be successfully forest farmed. Additionally, extended research with increased replication is needed to further elucidate soil moisture content requirements for *A. tricoccum*.

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Appendix A

Chapter 2 Appendices

Appendix A-1: Complete list of dominant and co-dominant overstory tree species associated with ramp populations in Pennsylvania (n=25). Species are ranked greatest to least by site abundance.

Common name	Scientific name	Percentage of sites and (n)	Percentage of plots and (n)
Sugar maple	<i>Acer saccharum</i> Marsh.	90 (27)	77 (116)
American basswood	<i>Tilia americana</i> L.	67 (20)	33 (50)
Black cherry	<i>Prunus serotina</i> Ehrh.	57 (17)	26 (39)
Tulip poplar	<i>Liriodendron tulipifera</i> L.	50 (15)	23 (34)
Bitternut hickory	<i>Carya cordiformis</i> (Wang) K. Koch	50 (15)	21 (31)
Northern red oak	<i>Quercus rubra</i> L.	40 (12)	17 (26)
White ash	<i>Fraxinus americana</i> L.	40 (12)	13 (19)
American beech	<i>Fagus grandifolia</i> Ehrh.	30 (9)	10 (15)
Shagbark hickory	<i>Carya ovata</i> (P. Miller) K. Koch	30 (9)	8 (12)
Slippery elm	<i>Ulmus rubra</i> Muhl.	30 (9)	8 (12)
Black walnut	<i>Juglans nigra</i> L.	23 (7)	5 (8)
Yellow birch	<i>Betula alleghaniensis</i> Britt.	17 (5)	5 (7)
Black birch	<i>Betula lenta</i> L.	17 (5)	4 (6)
White oak	<i>Quercus alba</i> L.	13 (4)	4 (6)
Red maple	<i>Acer rubrum</i> L.	10 (3)	3 (5)
Sycamore	<i>Platanus occidentalis</i> L.	10 (3)	3 (4)
Mockernut hickory	<i>Carya tomentosa</i> (Lam.) Nutt	10 (3)	2 (3)
Pignut hickory	<i>Carya glabra</i> (P. Miller) Sweet	7 (2)	1 (2)
Eastern hemlock	<i>Tsuga canadensis</i> L.	7 (2)	1 (2)
Black locust	<i>Robinia pseudoacacia</i> L.	3 (1)	1 (2)
Hickory species	<i>Carya sp.</i>	3 (1)	1 (1)
Cucumber tree	<i>Magnolia acuminata</i> L.	3 (1)	1 (1)
Chestnut oak	<i>Quercus prinus</i> Willd.	3 (1)	1 (1)
Sassafras	<i>Sassafras albidum</i> (Nutt.) Nees	3 (1)	1 (1)
American elm	<i>Ulmus americana</i> L.	3 (1)	1 (1)

Appendix A-2: Complete list of woody species at ramp populations in Pennsylvania. Species are ranked greatest to least by site abundance (n= 41). Asterisk (*) denote exotic, non-native plants.

Common name	Scientific name	Percentage of sites and (n)	Percentage of plots and (n)
Multiflora rose	<i>Rosa multiflora</i> Thunb. Ex.Murr.*	80 (24)	43 (64)
Japanese barberry	<i>Berberis thunbergii</i> A.P. de Candolle*	63 (19)	34 (51)
Spicebush	<i>Lindera benzoin</i> L. Blume	50 (15)	35 (52)
Gooseberry	<i>Ribes sp.</i>	47 (14)	20 (30)
Blackberry	<i>Rubus sp.</i>	47 (14)	16 (24)
Red elderberry	<i>Sambucus racemosa</i> L. var. <i>pubens</i>	43 (13)	15 (22)
Witch hazel	<i>Hamamelis virginiana</i> L.	37 (11)	11 (16)
Choke cherry	<i>Prunus virginiana</i> L.	33 (10)	12 (18)
Grape vine	<i>Vitis sp.</i>	33 (10)	11 (17)
Poison ivy	<i>Toxicodendron radicans</i> L. Kuntze	27 (8)	12 (18)
Musclewood	<i>Carpinus caroliniana</i> Walter	27 (8)	9 (13)
Virginia creeper	<i>Parthenocissus quinquefolia</i> (L.) Planch.	23 (7)	13 (20)
American hophornbeam	<i>Ostrya virginiana</i> (P. Miller) K. Koch	23 (7)	11 (17)
Wineberry	<i>Rubus phoenicolasius</i> (Maxim.)*	20 (6)	11 (16)
Black haw	<i>Viburnum prunifolium</i> L.	20 (6)	7 (11)
Oriental bittersweet	<i>Celastrus orbiculatus</i> Thunb.*	17 (5)	9 (14)
Hawthorn	<i>Crataegus sp.</i>	17 (5)	5 (8)
Morrow or bell's honeysuckle	<i>Lonicera morrowii</i> A. Gray or <i>bella</i> Zabel *	17 (5)	5 (8)
Amur honeysuckle	<i>Lonicera maackii</i> (Rupr.) Herder*	13 (4)	5 (8)
Autumn olive	<i>Elaeagnus umbellata</i> Thunb.*	13 (4)	5 (7)
Japanese honeysuckle	<i>Lonicera japonica</i> Thunb.*	10 (3)	8 (12)
Obtuse leaved privet	<i>Ligustrum obtusifolium</i> Siebold & Zucc.*	10 (3)	4 (6)
Striped maple	<i>Acer pensylvanicum</i> L.	7 (2)	5 (8)
Running strawberry bush	<i>Euonymus obovatus</i> Nutt.	7 (2)	3 (5)
Beech root sprouts	<i>Fagus grandifolia</i> (root-sprouts) Ehrh.	7 (2)	1 (2)

Purple flowering raspberry	<i>Rubus odoratum</i> L.	7 (2)	1 (2)
Greenbrier	<i>Smilax</i> sp.	7 (2)	1 (2)
Yellow buckeye	<i>Aesculus flava</i> Sol.	3 (1)	2 (3)
American bladdernut	<i>Staphylea trifolia</i> L.	3 (1)	2 (3)
Viburnum	<i>Viburnum</i> sp.	3 (1)	2 (3)
Common paw paw	<i>Asimina triloba</i> (L.) Dunal	3 (1)	1 (2)
Sambucus species	<i>Sambucus</i> sp.	3 (1)	1 (2)
Eastern Hemlock	<i>Tsuga canadensis</i> (saplings) L.	3 (1)	1 (2)
Maple leaf viburnum	<i>Viburnum acerifolium</i> L.	3 (1)	1 (2)
Alternate dogwood	<i>Cornus alternifolia</i> L. f.	3 (1)	1 (1)
Eastern leatherwood	<i>Dirca palustris</i> L.	3 (1)	1 (1)
Burning bush	<i>Euonymus alatus</i> (Thunb.) Siebold*	3 (1)	1 (1)
Smooth hydrangea	<i>Hydrangea arborescens</i> L.	3 (1)	1 (1)
Black raspberry	<i>Rubus occidentalis</i> L.	3 (1)	1 (1)
Common greenbrier	<i>Smilax rotundifolia</i> L.	3 (1)	1 (1)

Appendix A-3: Complete list of herbaceous species at ramp populations in Pennsylvania. Species are ranked greatest to least by site abundance (n= 186). Asterisk (*) denote exotic, non-native plants.

Common name	Scientific name	Percentage of sites and (n)	Percentage of plots and (n)
Blue cohosh	<i>Caulophyllum thalictroides</i> (L.) Michx.	83 (25)	66 (100)
Yellow trout lily	<i>Erythronium americanum</i> Ker-Gawl.	83 (25)	51 (77)
Mayapple	<i>Podophyllum peltatum</i> L.	80 (24)	51 (76)
Christmas fern	<i>Polystichum acrostichoides</i> (Michx.) Schott	77 (23)	59 (88)
Violet	<i>Viola</i> sp.	77 (23)	53 (80)
White wood aster	<i>Eurybia divaricata</i> (L.) G.L. Nesom	73 (22)	45 (67)
Enchanter's nightshade	<i>Circaea canadensis</i> L. Hill	70 (21)	39 (58)
Intermediate woodfern	<i>Dryopteris intermedia</i> (Muhl. Ex Willd.) A. Gray	70 (21)	47 (71)
Bedstraw	<i>Galium</i> sp.	70 (21)	42 (63)
Hairy sweet cicely	<i>Osmorhiza claytonii</i> (Michx.) C. B. Clarke	70 (21)	41 (61)
Hairy Solomon's seal	<i>Polygonatum pubescens</i> (Willd.) Pursh.	70 (21)	37 (56)
Garlic mustard	<i>Alliaria petiolata</i> (Bieb.) Cavara & Grande *	67 (20)	48 (72)
Jack-in-the-pulipit	<i>Arisaema triphyllum</i> (L.) Schott	67 (20)	45 (67)
Broadleaf toothwort	<i>Cardamine diphylla</i> (Michx.) Alph. Wood	67 (20)	44 (66)
White avens	<i>Geum canadense</i> Jacquin	67 (20)	29 (43)
False Solomon's seal	<i>Maianthemum racemosum</i> (L.) Link	67 (20)	25 (38)
Jumpseed	<i>Persicaria virginiana</i> (L.) Gaert.	67 (20)	41 (61)
Jewelweed	<i>Impatiens</i> sp.	66 (20)	42 (63)
Cut-leaf toothwort	<i>Cardamine concatenata</i> (Michx.) O. Schwarz	63 (19)	46 (69)
Common blue violet	<i>Viola sororia</i> Willde.	63 (19)	29 (44)
Wood nettle	<i>Laportea canadensis</i> (L.) Wedd.	60 (18)	38 (57)
Red trillium	<i>Trillium erectum</i> L.	60 (18)	41 (62)
Bedstraw	<i>Galium triflorum</i> Michx.	57 (17)	39 (59)
Wild geranium	<i>Geranium maculatum</i> L.	53 (16)	22 (33)
Virginia waterleaf	<i>Hydrophyllum virginianum</i> L.	53 (16)	24 (36)
Lion's foot	<i>Nabalus</i> sp.	53 (16)	26 (39)
Virginia spring beauty	<i>Claytonia virginica</i> L.	50 (15)	33 (50)
Clearweed	<i>Pilea pumila</i> (L.) A. Grey	50 (15)	30 (45)

Goldenrod	<i>Solidago sp.</i>	50 (15)	16 (24)
Carolina spring beauty	<i>Claytonia caroliniana</i> Michx.	47 (14)	26 (39)
Squirrel corn	<i>Dicentra canadensis</i> (Goldie) Walp.	47 (14)	33 (49)
Two-leaved mitterwort	<i>Mitella diphylla</i> L.	47 (14)	20 (30)
Long bristled smartweed	<i>Persicaria longiseta</i> (de Bruijin) Kitagawa *	47 (14)	25 (37)
Kidneyleaf buttercup	<i>Ranunculus abortivus</i> L.	47 (14)	24 (36)
Snakeroot	<i>Sanicula sp.</i>	47 (14)	15 (22)
Sharp lobed hepatica	<i>Hepatica acutiloba</i> A.P. de Candolle	43 (13)	24 (36)
Woodfern	<i>Dryopteris sp.</i>	43 (13)	31 (46)
Smooth sweet cicely	<i>Osmorhiza longistylis</i> (Torrey) A.P. de Candolle	43 (13)	15 (22)
Downy yellow violet	<i>Viola pubescens</i> Ait.	43 (13)	27 (41)
Seersucker sedge	<i>Carex plantaginea</i> Lam.	40 (12)	24 (36)
Bloodroot	<i>Sanguinaria canadensis</i> L.	40 (12)	23 (34)
Japanese stilt grass	<i>Microstegium vimineum</i> (Trinius) A. Camus *	37 (11)	23 (34)
Common white snakeroot	<i>Ageratina altissima</i> (L.) R.M. King & H. Robinson	33 (10)	15 (23)
Hog-peanut	<i>Amphicarpa bracteata</i> L. Fernald	33 (10)	17 (26)
Honewort	<i>Cryptotaenia canadensis</i> (L.) A.P. de Candolle	33 (10)	11 (17)
Silvery spleenwort	<i>Deparia acrostichoides</i> (Swartz) M. Kato	33 (10)	13 (20)
Dwarf ginseng	<i>Nanopanax trifolius</i> (L.) A. Haines	33 (10)	10 (15)
Eastern blue phlox	<i>Phlox divaricata</i> L.	33 (10)	19 (28)
Great white trillium	<i>Trillium grandiflorum</i> (Michx.) Salisberry	33 (10)	23 (35)
Wild ginger	<i>Asarum canadense</i> L.	30 (9)	10 (15)
Rattlesnake fern	<i>Botrypus virginianus</i> (L.) Michx.	30 (9)	13 (19)
Skunk cabbage	<i>Symplocarpus foetidus</i> (L.) Salis. Ex. W.P.C. Bart.	30 (9)	13 (19)
Sweet white violet	<i>Viola blanda</i> (Willde.)	30 (9)	17 (25)
Agrimony	<i>Agrimonia sp.</i>	27 (8)	9 (13)
Wood anemone	<i>Anemone quinquefolia</i> L.	27 (8)	11 (16)
Zigzag goldenrod	<i>Solidago flexicaulis</i> L.	27 (8)	9 (14)
Foamflower	<i>Tiarella cordifolia</i> L.	27 (8)	11 (16)
Dolls'-eyes	<i>Actaea pachypoda</i> Elliot	23 (7)	11 (16)

Common black cohosh	<i>Actaea racemosa</i> L.	23 (7)	13 (19)
Dutchman's britches	<i>Dicentra cucullaria</i> (L.) Bernhadi	23 (7)	13 (20)
False mermaid	<i>Floerkea proserpinacoides</i> Willde.	23 (7)	16 (24)
Canada waterleaf	<i>Hydrophyllum canadense</i> L.	23 (7)	11 (16)
Canada mayflower	<i>Maianthemum canadense</i> Desfontaines	23 (7)	9 (14)
Sensitive fern	<i>Onoclea sensibilis</i> L.	23 (7)	7 (11)
Chickweed species	<i>Stellaria</i> sp.	23 (7)	11 (17)
Northern maidenhair fern	<i>Adiantum pedatum</i> L.	20 (6)	10 (15)
Lowland bladder fern	<i>Cystopteris protrusa</i> (Weatherby) Blasdell	20 (6)	6 (9)
Virginia stickseed	<i>Hackelia virginiana</i> (L.) I.M. Johnston	20 (6)	7 (11)
Orange jewelweed	<i>Impatiens capensis</i> Merrb.	20 (6)	12 (18)
Yellow fairy bells	<i>Prosartes lanuginosa</i> (Michx.) D. Don	20 (6)	9 (14)
New York fern	<i>Parathelypteris noveboracensis</i> (L.) Ching	20 (6)	12 (18)
Sessile bellwort	<i>Uvularia sessilifolia</i> L.	20 (6)	7 (10)
White hellebore	<i>Veratrum viride</i> Ait.	20 (6)	7 (10)
Tall white violet	<i>Viola canadensis</i> L.	20 (6)	7 (11)
Marginal woodfern	<i>Dryopteris marginalis</i> (L.) A. Grey	17 (5)	7 (10)
Interrupted fern	<i>Claytosmunda claytoniana</i> (L.) Metz & Rouh.	17 (5)	5 (7)
American ginseng	<i>Panax quinquefolius</i> L.	17 (5)	6 (9)
Smooth yellow forest violet	<i>Viola eriocarpa</i> Schweinitz	17 (5)	7 (11)
Creamy violet	<i>Viola striata</i> Ait.	17 (5)	11 (16)
Baneberry	<i>Actaea</i> sp.	13 (4)	3 (5)
Onion grass	<i>Allium vineale</i> L.	13 (4)	4 (6)
Richweed	<i>Collinsonia canadensis</i> L.	13 (4)	5 (7)
Hay scented fern	<i>Dennstaedtia punctilobula</i> (Michx.) T. Moore	13 (4)	4 (6)
Wild strawberry	<i>Fragaria virginiana</i> P. Miller	13 (4)	3 (5)
Hemp nettle	<i>Galeopsis tetrahit</i> L. *	13 (4)	3 (4)
Virginia bluebells	<i>Mertensia virginica</i> (L.) Persoon ex Link	13 (4)	7 (11)
Partridge berry	<i>Mitchella repens</i> L.	13 (4)	3 (4)
Wood sorrels	<i>Oxalis</i> sp.	13 (4)	7 (11)
Small Solomon's seal	<i>Polygonatum biflorum</i> (Walt.) Elliot	13 (4)	3 (5)
American aster species	<i>Symphyotrichum</i> spp.	13 (4)	3 (4)
Long spurred violet	<i>Viola rostrata</i> Pursh	13 (4)	5 (7)

Eastern slender toothwort	<i>Cardamine angustata</i> O.E. Schulz	10 (3)	4 (6)
Spinulose woodfern	<i>Dryopteris carthusiana</i> (Villars) H.P. Fuchs	10 (3)	3 (4)
White trout lily	<i>Erythronium albidum</i> Nutt.	10 (3)	3 (4)
Knotweed	<i>Reynoutria sp.</i> Houltuyn *	10 (3)	3 (4)
Lesser celandine	<i>Ficaria verna</i> Hudson *	10 (3)	2 (3)
Dame's rocket	<i>Hesperis matronalis</i> L. *	10 (3)	2 (3)
Goldenseal	<i>Hydrastis canadensis</i> L.	10 (3)	2 (3)
Lily	<i>Lilium sp.</i>	10 (3)	3 (5)
Ostrich fern	<i>Matteuccia struthiopteris</i> L. Todaro	10 (3)	2 (3)
American wood-sorrel	<i>Oxalis montana</i> Rafinesque	10 (3)	6 (9)
Mile-a-minute	<i>Persicaria perfoliata</i> (L.) H. Gross *	10 (3)	3 (5)
American lopseed	<i>Phryma leptostachya</i> L.	10 (3)	3 (5)
Indian strawberry	<i>Potentilla indica</i> (Andrews) T. Wolf *	10 (3)	6 (9)
Hooked buttercup	<i>Ranunculus recurvatus</i> Poiret	10 (3)	7 (10)
Stonecrop	<i>Sedum ternatum</i> Michx.	10 (3)	6 (9)
Zigzag aster	<i>Symphotrichum prenanthoides</i> (Muhl. Ex. Willde.) Nesom	10 (3)	3 (4)
Rue anemone	<i>Thalictrum thalictroides</i> (L.) A.J. Eames & B. Boivin	10 (3)	5 (8)
Round leaf yellow violet	<i>Viola rotundifolia</i> Michx.	10 (3)	3 (4)
Goutweed	<i>Aegopodium podagraria</i> L. *	7 (2)	3 (4)
Rockcress	<i>Arabis sp.</i>	7 (2)	1 (2)
Walking fern	<i>Asplenium rhizophyllum</i> L.	7 (2)	3 (5)
Lady fern	<i>Athyrium sp.</i>	7 (2)	3 (5)
Beggar's ticks	<i>Desmodium spp.</i>	7 (2)	1 (2)
Wild yam	<i>Dioscorea villosa</i> L.	7 (2)	2 (3)
Harbinger of spring	<i>Erigenia bulbosa</i> (Michx.) Nutt.	7 (2)	1 (2)
Showy orchis	<i>Galearis spectabilis</i> (L.) Rafinesque	7 (2)	3 (4)
Forest bedstraw	<i>Galium circaezans</i> Michx.	7 (2)	2 (3)
Robert's geranium	<i>Geranium robertianum</i> (L.) Herb. Robert	7 (2)	3 (5)
Glade fern	<i>Diplaziopsis pycnocarpa</i> (Sprengel) M.G. Price	7 (2)	1 (3)
Indian cucumber root	<i>Medeola virginiana</i> L.	7 (2)	1 (2)
Hispid buttercup	<i>Ranunculus hispidus</i> Michx.	7 (2)	2 (3)
Buttercup	<i>Ranunculus sp.</i> L.	7 (2)	1 (2)
Bitterdock	<i>Rumex obtusifolius</i> L.	7 (2)	2 (3)

Cut-leaf grape fern	<i>Sceptridium dissectum</i> (Sprengel) Lyon	7 (2)	1 (2)
Tall meadow rue	<i>Thalictrum pubescens</i> Pursh	7 (2)	4 (6)
Trillium	<i>Trillium sp.</i>	7 (2)	1 (2)
European stinging nettle	<i>Urtica dioica</i> L.*	7 (2)	3 (4)
Perfoliate bellwort	<i>Uvularia perfoliata</i> L.	7 (2)	3 (4)
Ivyleaf speedwell	<i>Veronica hederifolia</i> L. *	7 (2)	4 (6)
Mountain black cohosh	<i>Actaea podocarpa</i> A.P. de Candolle	3 (1)	1 (2)
Round-lobed hepatica	<i>Hepatica americana</i> (A.P. de Candolle) Ker-Gawl	3 (1)	1 (2)
Maidenhair spleenwort	<i>Asplenium trichomanes</i> L.	3 (1)	1 (1)
Downy woodmint	<i>Blephilia ciliata</i> (L.) Benth.	3 (1)	1 (1)
False nettle	<i>Boehmeria cylindrica</i> (L.) Schwartz	3 (1)	1 (2)
Tall bell flower	<i>Campanulastrum americanum</i> (L.) Small	3 (1)	1 (1)
Greater celandine	<i>Chelidonium majus</i> L.*	3 (1)	1 (1)
Pipsissewa	<i>Chimaphila maculata</i> (L.) Pursh	3 (1)	1 (1)
Alpine enchanter's nightshade	<i>Circaea alpina</i> L.	3 (1)	1 (1)
Eastern blue-eyed Mary	<i>Collinsia verna</i> Nutt.	3 (1)	1 (2)
Bear corn	<i>Conopholis americana</i> (L.) Wall.	3 (1)	1 (1)
Deer-tongue witchgrass	<i>Dichanthelium clandestinum</i> (L.) Gould	3 (1)	1 (1)
Wild cucumber	<i>Echinocystis lobata</i> (Michx.) Torrey & A. Gray	3 (1)	1 (1)
Bottlebrush grass	<i>Elymus hystrix</i> L.	3 (1)	2 (3)
Beech drops	<i>Epifagus virginiana</i> (L.) W. Barton	3 (1)	1 (1)
Broad-leafed helleborine	<i>Epipactis helleborine</i> (L.) Crantz *	3 (1)	1 (2)
Giant knotweed	<i>Reynoutria sachalinensis</i> (F. Schmidt ex Maximowicz) Nakai *	3 (1)	1 (1)
Ground ivy	<i>Glechoma hederacea</i> L. *	3 (1)	1 (1)
Northern oak fern	<i>Gymnocarpium dryopteris</i> (L.) Newman	3 (1)	1 (1)
Biennial waterleaf	<i>Hydrophyllum appendiculatum</i> Michx.	3 (1)	3 (4)
Waterleaf	<i>Hydrophyllum sp.</i> L.	3 (1)	1 (1)
Spotted St. John's wort	<i>Hypericum punctatum</i> Lamarck	3 (1)	1 (1)
Yellow jewelweed	<i>Impatiens pallida</i> Nutt.	3 (1)	1 (1)
Henbit dead nettle	<i>Lamium amplexicaule</i> L. *	3 (1)	1 (2)
Red dead nettle	<i>Lamium purpureum</i> L.	3 (1)	1 (2)
Nipplewort	<i>Lapsana communis</i> L. *	3 (1)	1 (1)

Bugleweed	<i>Lycopus sp.</i> L.	3 (1)	1 (1)
Fringed loosestrife	<i>Steironema ciliatum</i> (L.) Baudo	3 (1)	1 (1)
Pennywort	<i>Obolaria virginica</i> L.	3 (1)	2 (3)
Whorled aster	<i>Oclemena acuminata</i> (Michx.) Greene	3 (1)	1 (2)
Cinnamon fern	<i>Claytosmunda spp.</i> L.	3 (1)	1 (1)
Golden ragwort	<i>Packera aurea</i> (L.) Á. Löve & D. Löve	3 (1)	1 (1)
Ragwort	<i>Packera sp.</i> Á. & D. Löve	3 (1)	1 (1)
Perilla	<i>Perilla frutescens</i> (L.) Britt *	3 (1)	1 (1)
Northern beech fern	<i>Phegopteris connectilis</i> (Michx.) Watt	3 (1)	1 (2)
Beech fern	<i>Phegopteris sp.</i>	3 (1)	2 (3)
Pokeweed	<i>Phytolacca americana</i>	3 (1)	3 (5)
Spreading Jacob's latter	<i>Polemonium reptans</i> L.	3 (1)	1 (2)
Old field five fingers	<i>Potentilla simplex</i> Michx.	3 (1)	1 (1)
Common cut-lead coneflower	<i>Rudbeckia laciniata</i> L.	3 (1)	1 (1)
Black snakeroot	<i>Sanicula canadensis</i> L.	3 (1)	1 (2)
Common carrion flower	<i>Smilax herbacea</i> L.	3 (1)	1 (1)
Auxiliary goldenrod	<i>Solidago caesia</i> L.	3 (1)	1 (1)
Eastern twisted stalk	<i>Streptopus lanceolatus</i> (Ait.) Reveal	3 (1)	1 (2)
Canada yew	<i>Taxus canadensis</i> Marsh.	3 (1)	1 (1)
Meadow rue	<i>Thalictrum sp.</i> L.	3 (1)	1 (1)
Foamflower	<i>Tiarella cordifolia</i> L.	3 (1)	1 (1)
Snow trillium	<i>Trillium nivale</i> Riddell	3 (1)	11 (16)
Painted trillium	<i>Trillidium undulatum</i> Floden & E.E. Schilling	3 (1)	1 (2)
Corn-salad	<i>Valerianella chenopodiifolia</i> (Pursh) A.P. de Candolle	3 (1)	1 (2)
Common wingstem	<i>Verbesina alternifolia</i> (L.) Britt. Ex Kearney	3 (1)	2 (3)
Golden-Alexanders	<i>Zizia sp.</i> W.D.J. Koch	3 (1)	1 (1)

Appendix A-4: Herbaceous species full indicator species analysis (ISA) results.

Common name	Scientific name	ISA				Topographic position
		Lat.	Long.	Province	Aspect	
Northern maidenhair fern	<i>Adiantum pedatum</i> L.	N*	E**			
Common black cohosh	<i>Actaea racemosa</i> L.		E*	P***	None*	F*
Ground ivy	<i>Glechoma hederacea</i> L.			RV**		
Agrimonia	<i>Agrimonia</i> sp.				None* *	F**
Sharp lobed hepatica	<i>Hepatica americana</i> (A.P. de Candolle) Ker-Gawl	N***		AP*	N*	
Wood anemone	<i>Anemone quinquefolia</i> L.	N***	E*		None* *	F***
Onion grass	<i>Allium vineale</i> L.	S*		P*	S**	
Jack-in-the-pulpit	<i>Arisaema triphyllum</i> (L.) Schott	N**	E**		None*	F**
Rattlesnake fern	<i>Botrypus virginianus</i> (L.) Michx.		E*		None* *	F**
Eastern slender toothwort	<i>Cardamine angustata</i> O.E. Schulz				None*	F**
Cut-leaf toothwort	<i>Cardamine concatenata</i> (Michx.) O. Schwarz		W**	RV**		
Broad-leaf toothwort	<i>Cardamine diphylla</i> (Michx.) Alph. Wood	N***	W**	AP**		
Seersucker sedge	<i>Carex plantaginea</i> Lam.	N***				
Blue cohosh	<i>Caulophyllum thalictroides</i> . (L.) Michx.	S**	W***		N**	
Enchanter's nightshade	<i>Circaea canadensis</i> L. Hill		E***	P*	None* *	F***
Carolina spring beauty	<i>Claytonia caroliniana</i> Michx.		W***	AP*		

Virginia spring beauty	<i>Claytonia virginica</i> L.	S***				
Silvery spleenwort	<i>Deparia acrostichoides</i> (Swartz) M. Kato	N**	E*	AP*		
Squirrel corn	<i>Dicentra canadensis</i> (Goldie) Walp.	N**		AP*		
Dutchman's breeches	<i>Dicentra cucullaria</i> (L.) Bernhardi		W**		N**	
Wild yam	<i>Dioscorea villosa</i> L.			P*		
Intermediat e woodfern	<i>Dryopteris intermedia</i> (Muhl. Ex Willd.) A. Gray		W***	AP*		
Woodfern	<i>Dryopteris sp.</i>		W***	AP*		U*
Indian strawberry	<i>Potentilla indica</i> (Andrews) T. Wolf	S**		P**	S***	
Bottlebrush grass	<i>Elymus hystrix</i> L.					F*
Yellow trout lily	<i>Erythronium americanum</i> Ker Gawl.	N***				
White wood aster	<i>Eurybia divaricata</i> (L.) G. L. Nesom	N**	E***			
Snowy orchid	<i>Galearis spectabilis</i> (L.) Rafinesque					F*
Wild geranium	<i>Geranium maculatum</i> L.					F*
Forest bedstraw	<i>Galium circaezans</i> Michx.					F*
Bedstraw	<i>Galium sp.</i>					U*
Virginia stickseed	<i>Hackelia virginiana</i> (L.) I.M. Johnston		E**			
Orange jewelweed	<i>Impatiens capensis</i> Merrb.		E***	RV*	None* *	F**
Wood nettle	<i>Laportea canadensis</i> (L.) Wedd.			RV**		
Lily	<i>Lilium sp.</i>				None*	F*
Canada mayflower	<i>Maianthemum canadense</i> Desfontaines		E**		None* *	F**
False Solomon's seal	<i>Maianthemum racemosum</i> (L.) Link				None* *	F**
Ostrich fern	<i>Matteuccia struthiopteris</i> L. Todaro					
Virginia bluebells	<i>Mertensia virginica</i> (L.) Persoon ex Link			RV**	None*	F*
Two-leaved mitterwort	<i>Mitella diphylla</i> L.	N***		AP*		

Japanese stilt grass	<i>Microstegium vimineum</i> (Trinius) A. Camus		E**			
Pennywort	<i>Obolaria virginica</i> L.					F*
Sensitive fern	<i>Onoclea sensibilis</i> L.	N**				
Smooth sweet cicely	<i>Osmorhiza longistylis</i> (Torrey) A.P. de Candolle	S*	W**			
American wood sorrel	<i>Oxalis montana</i> Rafinesque	N**				L***
Wood sorrel spp.	<i>Oxalis</i> sp.	N***	E***		None*	F*
Dwarf ginseng	<i>Nanopanax trifolius</i> (L.) A. Haines	N**				
American ginseng	<i>Panax quinquefolius</i> L.		E*	P***	None*	F**
Long-bristled smartweed	<i>Persicaria virginiana</i> (L.) Gaertn.	S***				
Mile-a-minute	<i>Persicaria perfoliata</i> (L.) H. Gross			P**	S*	
Beech fern	<i>Phegopteris</i> sp.					F*
Pokeweed	<i>Phytolacca americana</i>			P***	S***	
American lopseed	<i>Phryma leptostachya</i> L.			P***	None*	F*
Canadian clearwater	<i>Pilea pumila</i> L.			AP*		
Christmas fern	<i>Polystichum acrostichoides</i> (Michx.) Schott		W*	AP**		L*
Mayapple	<i>Podophyllum peltatum</i> L.		E*		None*	F**
Yellow fairy bells	<i>Prosartes lanuginosa</i> (Michx.) D. Don	S***	E**		S**	
Lion's foot	<i>Nabalus</i> sp.		E*		None*	F**
Hooked buttercup	<i>Ranunculus recurvatus</i> Poiret	N**	E**			
Bloodroot	<i>Sanguinaria canadensis</i> L.				RV**	
Black snakeroot	<i>Sanicula canadensis</i> L.			P*	S*	
Stonecrop	<i>Sedum ternatum</i> Michx.	S**	W**			
Zigzag goldenrod	<i>Solidago flexicaulis</i> L.		W*	RV**		
Goldenrod	<i>Solidago</i> sp.	N*	E**			
Snakeroot	<i>Sanicula</i> sp.					F*

Chickweed	<i>Stellaria sp.</i>	S**		RV*		
Walking fern	<i>Asplenium rhizophyllum</i> L.			RV**		
Rue anemone	<i>Thalictrum thalictroides</i> (L.) A.J. Eames & B. Boivin	S**		P*	None*	F**
Red trillium	<i>Trillium erectum</i> L.	N**	W***	AP**	S*	
Great white trillium	<i>Trillium grandiflorum</i> (Michx.) Salis.		W***	AP**	S**	
Perfoliate bellwort	<i>Uvularia perfoliata</i> L.			P**	None*	F**
Sessile bellwort	<i>Uvularia sessilifolia</i> L.	N**				
Common wingstem	<i>Verbesina alternifolia</i> (L.) Britt. Ex Kearney					F**
Ivy leaf speedwell	<i>Veronica hederifolia</i> L.	S*	E*	P***		
White hellebore	<i>Veratrum viride</i> Ait.	N*	E*	RV*	None*	F**
Tall white violet	<i>Viola canadensis</i> L.	N*				
Common blue violet	<i>Viola sororia</i> Willde.					F**
Creamy violet	<i>Viola striata</i> Ait.	N***			None*	F*

Appendix B

Chapter 3 Appendices

Appendix B-1: Complete list of woody understory (small shrubs, vines, and lianas) species at *Allium tricoccum* and *A. burdickii* populations (n= 33). Asterisks (*) denote non-native, exotic species.

Common name	Scientific name	Percentage of plots and (n) for <i>A. tricoccum</i>	Percentage of plots and (n) for <i>A. burdickii</i>
Boxelder	<i>Acer negundo</i> L.		5 (1)
Striped maple	<i>Acer pensylvanicum</i> L.	25(5)	
Yellow buckeye	<i>Aesculus flava</i> Sol.	15(3)	15 (3)
Japanese barberry	<i>Berberis thunbergii</i> A.P. de Candolle *	40(8)	35 (7)
American hornbeam	<i>Carpinus caroliniana</i> Walter		25 (5)
Oriental bittersweet	<i>Celastrus orbiculatus</i> Thunb *		10 (2)
Alternate dogwood	<i>Cornus alternifolia</i> L.		15 (3)
Hawthorn	<i>Crataegus</i> sp.		10 (2)
Autumn olive	<i>Elaeagnus umbellata</i> Thunb *		5 (1)
Burning bush	<i>Euonymus alatus</i> (Thunb.) Siebold *		15 (3)
Running strawberry bush	<i>Euonymus obovatus</i> Nutt.		20 (4)
Witch hazel	<i>Hamamelis virginiana</i> L.	5(1)	30 (6)
Smooth hydrangea	<i>Hydrangea arborescens</i> L.		10 (2)
Obtuse leaved privet	<i>Ligustrum obtusifolium</i> Siebold & Zucc *		5 (1)
Spice bush	<i>Lindera benzoin</i> L. Blume	50(10)	75 (15)
Japanese honeysuckle	<i>Lonicera japonica</i> Thunb *	5(1)	5 (1)
Amur honeysuckle	<i>Lonicera maackii</i> (Rupr.) Herder *		10 (2)
Morrow or bell's honeysuckle	<i>Lonicera morrowii</i> A. Gray or <i>bella</i> Zabel *	5(1)	5 (1)
Hophornbeam	<i>Ostrya virginiana</i> (P. Miller) K. Koch		20 (4)
Virginia creeper	<i>Parthenocissus quinquefolia</i> (L.) Planch.		25 (5)
Choke cherry	<i>Prunus virginiana</i> L.		5 (1)
Wineberry	<i>Rubus phoenicolasius</i> Maxim. *	5 (1)	

Gooseberry	<i>Ribes rotundifolium</i> Michx.		15 (3)
Blackberry	<i>Rubus sp.</i>	5(1)	
Gooseberry	<i>Ribes sp.</i>	20(4)	10 (2)
Multiflora rose	<i>Rosa multiflora</i> Thunb. Ex. Murr *	25(5)	65 (13)
Red elderberry	<i>Sambucus racemosa var. pubens</i> (L.) Michx. Traut. & C.A. Meyer	20(4)	
Elderberry species	<i>Sambucus sp.</i>	10(2)	
Greenbrier	<i>Smilax sp.</i>	5(1)	
Bladdernut	<i>Staphylea trifolia</i> L.		25 (5)
Poison ivy	<i>Toxicodendron radicans</i> L. Kuntze		25 (5)
Black haw	<i>Viburnum prunifolium</i> L.		10 (2)
Grape vine	<i>Vitis sp.</i>	5(1)	55 (11)

Appendix B-2: Complete list of herbaceous species found at *Allium tricoccum* and *A. burdickii* populations in Pennsylvania (n= 119). Asterisk (*) denote exotic, non-native plants.

Common name	Scientific name	Percentage of plots and (n) for <i>A. tricoccum</i>	Percentage of plots and (n) for <i>A. burdickii</i>
Dolls'-eyes	<i>Actaea pachypoda</i> Elliot	20(4)	
Mountain black cohosh	<i>Actaea podocarpa</i> A.P. de Candolle	10(2)	
Common black cohosh	<i>Actaea racemosa</i> L.	15(3)	15 (3)
Baneberry species	<i>Actaea sp.</i>	15(3)	30 (6)
Northern maidenhair fern	<i>Adiantum pedatum</i> L.	5(1)	
Common white snakeroot	<i>Ageratina altissima</i> King & H.E. Robinson	5(1)	25 (5)
Agrimonia species	<i>Agrimonia sp.</i>	5(1)	25 (5)
Garlic mustard	<i>Alliaria petiolata</i> (Berb.) Cav. & Gran. *	45(9)	60 (12)
Hog-peanut	<i>Amphicarpa bracteata</i> L. Fernald	15(3)	10 (2)
Sharp lobed hepatica	<i>Hepatica acutiloba</i> A.P. de Candolle	10(2)	5 (1)
Rockcress	<i>Arabis sp.</i>	5(1)	
Jack-in-the-pulpit	<i>Arisaema triphyllum</i> (L.) Schott	30(6)	40 (8)
Common wild ginger	<i>Asarum canadense</i> L.	30(6)	25 (5)
Downy wood mint	<i>Blephilia ciliata</i> (L.) Benth.		15 (3)
Rattlesnake fern	<i>Botrypus virginianus</i>		15 (3)
Tall bell flower	<i>Campanulastrum americanum</i> L.	5(1)	
Cut-leaf toothwort	<i>Cardamine concatenata</i> (Michx.) O. Schwarz	85(17)	85 (17)
Broad-leaf toothwort	<i>Cardamine diphylla</i> (Michx.)	40(8)	
Seersucker sedge	<i>Carex plantaginea</i> Lam.		15 (3)
Blue cohosh	<i>Caulophyllum thalictroides</i> (L.) Michx.	90(18)	15 (3)
Enchanter's nightshade	<i>Circaea canadensis</i> L. Hill	10(2)	45 (9)
Carolina spring beauty	<i>Claytonia caroliniana</i> (Michx.)	35(7)	
Interrupted fern	<i>Claytosmunda claytoniana</i> L.	5(1)	5 (1)
Virginia spring beauty	<i>Claytonia virginica</i> L.	50(10)	70 (14)
Honewort	<i>Cryptotaenia canadensis</i> (L.) A.P. de Candolle	25(5)	35 (7)

Silvery spleenwort	<i>Deparia acrostichoides</i> (Swartz) M. Kato	15(3)	
Dwarf larkspur	<i>Delphinium tricornes</i> Michx.		10 (2)
Beggar's ticks	<i>Desmodium sp.</i>	10(2)	
Squirrel corn	<i>Dicentra canadensis</i> (Goldie) Walpers	40(8)	5 (1)
Dutchman's bitches	<i>Dicentra cucullaria</i> (L.) Bernhadi	25(5)	5 (1)
Spinulose woodfern	<i>Dryopteris carthusiana</i> (Villars) H.P. Fuchs		20 (4)
Evergreen woodfern	<i>Dryopteris intermedia</i> (Muhl. Ex Willd.) A. Gray	75(15)	5 (1)
Marginal woodfern	<i>Dryopteris marginalis</i> (L.) A. Grey	10(2)	
Wood-fern species	<i>Dryopteris sp.</i>	35(7)	
Turpentine root	<i>Endodeca serpentaria</i> (L.) Rafinesque		25 (5)
Yellow trout lily	<i>Erythronium americanum</i> Ker Gawl.	20(4)	10 (2)
White wood aster	<i>Eurybia divaricata</i> (L.) G. L. Nesom	25(5)	55 (11)
Big leaved aster	<i>Eurybia macrophylla</i> (L.) Cassini		30 (6)
Spotted Joe-pye- weed	<i>Eutrochium maculatum</i> (L.) E.E. Lamont		40 (8)
Lesser celandine	<i>Ficaria verna</i> Hudson *		20 (4)
False mermaid	<i>Floerkea proserpinacoides</i> Willde.	35(7)	60 (12)
Forest bedstraw	<i>Galium circaezans</i> Michx.		35 (7)
Bedstraw	<i>Galium sp.</i>	30(6)	55 (11)
Sweet scented bedstraw	<i>Galium triflorum</i> Michx.	45(9)	5 (1)
Wild geranium	<i>Geranium maculatum</i> L.	30(6)	65 (13)
White avens	<i>Geum canadense</i> Jacquin	20(4)	45 (9)
Ground ivy	<i>Glechoma hederacea</i> L. *		5 (1)
Sunflower	<i>Helianthus sp.</i> L.		35 (7)
Quaker ladies	<i>Houstonia caerulea</i> L.		5 (1)
Golden seal	<i>Hydrastis canadensis</i> L.		5 (1)
Biennial waterleaf	<i>Hydrophyllum appendiculatum</i> (Michx.)	20(4)	30 (6)
Canada waterleaf	<i>Hydrophyllum canadense</i> L.	45(9)	10 (2)
Virginia water leaf	<i>Hydrophyllum virginianum</i> L.	30(6)	25 (5)
Orange jewelweed	<i>Impatiens capensis</i> Merrb.	5(1)	5 (1)
Yellow jewelweed	<i>Impatiens pallida</i> Nutt.	5(1)	
Jewelweed	<i>Impatiens sp.</i>	10(2)	25 (5)
Twinleaf	<i>Jeffersonia diphylla</i> (L.) Persoon		10 (2)
Henbit dead nettle	<i>Lamium amplexicaule</i> L. *		5 (1)
Red dead nettle	<i>Lamium purpureum</i> L. *		25 (5)
Lily	<i>Lilium sp.</i>		10 (2)

Wood-nettle	<i>Laportea canadensis</i> (L.) Wedd.	60(12)	
Canada mayflower	<i>Maianthemum canadense</i> Desfont.		5 (1)
False Solomon's seal	<i>Maianthemum racemosum</i> L.	15(3)	65 (13)
Early saxifrage	<i>Micranthes virginiensis</i> Michx.		5(1)
Japanese stiltgrass	<i>Microstegium vimineum</i> (Trinius) A. Camus *	5(1)	20 (4)
Partridge berry	<i>Mitchella repens</i> L.	5(1)	
Two-leaved mitterwort	<i>Mitella diphylla</i> L.	25(5)	
Lion's foot	<i>Nabalus sp.</i>		35 (7)
Hairy sweet cicely	<i>Osmorhiza claytonii</i> (Michx.) C.B. Clarke	50(10)	15 (3)
Smooth sweet cicely	<i>Osmorhiza longistylis</i> (Torrey) A.P. de Candolle	25(5)	20 (4)
Roundleaf ragwort	<i>Packera obovata</i> (Muhl. ex Willde.) W.A. Weber & Á. Löve		10 (2)
Ragwort species	<i>Packera sp.</i> Á. & D. Löve		10 (2)
American ginseng	<i>Panax quinquefolius</i> L.		5 (1)
Dwarf ginseng	<i>Nanopanax trifolius</i> (L.) A. Haines	5(1)	
New York fern	<i>Parathelypteris noveboracensis</i> (Ching) L.	25(5)	
Smartweed	<i>Persicaria longiseta</i> (de Bruijn) Kitagawa *	45(9)	35 (7)
Jumpseed	<i>Persicaria virginiana</i> (L.) Gaer.	60(12)	50 (10)
Eastern blue phlox	<i>Phlox divaricata</i> L.	40(8)	50 (10)
Richweed	<i>Pilea pumila</i> (L.) A. Gray	35(7)	55 (11)
Mayapple	<i>Podophyllum peltatum</i> L.	25(5)	80 (16)
Hairy Solomon's Seal	<i>Polygonatum pubescens</i> (Willde.) Pursh.	40(8)	50 (10)
Christmas fern	<i>Polystichum acrostichoides</i> (Michx.) Schott	80(16)	75 (15)
Old field five fingers	<i>Potentilla simplex</i> Michx.		5 (1)
Yellow fairy bells	<i>Prosartes lanuginosa</i> (Michx.) D. Don	20(4)	
Kidney leaf buttercup	<i>Ranunculus abortivus</i> L.	20(4)	45 (9)
Hispid buttercup	<i>Ranunculus hispidus</i> Michx.	10(2)	5 (1)
Bloodroot	<i>Sanguinaria canadensis</i> L.	30(6)	35 (7)
Snakeroot	<i>Sanicula sp.</i>	10(2)	35 (7)
Cut-leaf grape fern	<i>Sceptridium dissectum</i> (Sprengel) Lyon		5 (1)
Stonecrop	<i>Sedum ternatum</i> Michx.	15(3)	70 (14)
Auxiliary goldenrod	<i>Solidago caesia</i> L.		25 (5)
Zigzag goldenrod	<i>Solidago flexicaulis</i> L.	15(3)	50 (10)

Goldenrod	<i>Solidago sp.</i>	10(2)	15 (3)
Chickweed	<i>Stellaria sp.</i>	5(1)	20 (4)
Zigzag aster	<i>Symphyotrichum prenanthoides</i> (Muhl. Ex. Willde.) G.L. Nesom	5(1)	
Aster	<i>Symphyotrichum sp.</i>	10(2)	15 (3)
Skunk cabbage	<i>Symplocarpus foetidus</i> (L.) Salis. Ex. W.P.C. Bart.	5(1)	
Foamflower	<i>Tiarella cordifolia</i> L.	10(2)	
Early meadow rue	<i>Thalictrum dioicum</i> L.		5 (1)
Rue anemone	<i>Thalictrum thalictroides</i> (L.) A.J. Eames & B. Boivin		5 (1)
Red trillium	<i>Trillium erectum</i> L.	35(7)	
Great white trillium	<i>Trillium grandiflorum</i> (Michx.) Salis.	90(18)	45 (9)
Snow trillium	<i>Trillium nivale</i> Riddell		10 (2)
Sessile trillium	<i>Trillium sessile</i> L.		25 (5)
Trillium	<i>Trillium sp.</i>		5 (1)
Large-flowered bellwort	<i>Uvularia grandiflora</i> J.E. Smith		5 (1)
Corn-salad	<i>Valerianella chenopodiifolia</i> (Pursh) A.P. de Candolle		25 (5)
Sweet white violet	<i>Viola blanda</i> Willde.	40(8)	
Tall white violet	<i>Viola canadensis</i> L.	5(1)	
Smooth yellow forest violet	<i>Viola eriocarpa</i> Schweinitz	10(2)	30 (6)
Downy yellow violet	<i>Viola pubescens</i> Ait.	20(4)	10 (2)
Round leaf yellow violet	<i>Viola rotundifolia</i> Michx.	10(2)	
Common blue violet	<i>Viola sororia</i> (Willde.)	10(2)	35 (7)
Creamy violet	<i>Viola striata</i> Aiton		10 (2)
Violet species	<i>Viola sp.</i>	75(15)	
Golden-Alexanders	<i>Zizia sp.</i> W.D.J. Koch		5 (1)
Wood anemone	<i>Anemone quinquefolia</i> L.		30 (6)
Common spreading Chervil	<i>Chaerophyllum procumbens</i> (L.) Crantz		5 (1)
