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Source: Natural Areas Journal, 43(3) : 185-195

Published By: Natural Areas Association

URL: https://doi.org/10.3375/22-30

Research Article

Two Ramp Taxa, *Allium tricoccum* and *A. burdickii*, Differ in Abiotic Habitat Characteristics and Floristic Associates in Pennsylvania

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Associate Editor: Sarah Hamman

ABSTRACT

The name ramp or wild leek refers to two taxa: *Allium tricoccum* and *A. burdickii*. The latter, named narrow-leaf ramp, has historically been recognized as a variety but recently as a distinct species. Habitat differences between these species have been reported, although distribution of *A. burdickii* in eastern North America is unresolved. A better understanding of *A. burdickii* habitat will aid population discovery and conservation as *A. burdickii* is of conservation concern in parts of the United States. Eight populations, four for each species, were identified in southwestern Pennsylvania. The associated flora, soil fertility and moisture, and site characteristics (e.g., topography) were documented. *A. tricoccum* was associated with northern aspects and higher soil moisture content throughout the growing season whereas *A. burdickii* was found on a variety of aspects. Soil pH and nutrient content were greater at *A. burdickii* sites than *A. tricoccum* sites and suggest the former may rely more heavily on base nutrients such as calcium. The most common overstory tree associate was sugar maple (*Acer saccharum*) for both species but understory flora differed. Wet-mesic preferring species, including blue cohosh (*Caulophyllum thalictroides*) and wood nettle (*Laportea canadensis*), were associated with *A. tricoccum*, whereas dry-mesic species, including mayapple (*Podophyllum peltatum*) and false Solomon's seal (*Maianthemum racemosum*), were associated with *A. burdickii*. Results are consistent with observations that these species may differ in mesoscale habitat conditions due to topographic position and its influence on soil moisture and fertility.

Index terms: indicator species; phytogeography; plant ecology; soil moisture; wild leek

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. Hanes and Ownbey (1946) were the first to formally recognize two "ramp" taxa and to suggest a variety *burdickii* (versus var. *tricoccum*) based on morphological, phenological, and habitat differences. Recent research and floristic treatments now refer to *A. burdickii* (Hanes) A.G. Jones, narrow-leaf ramp, as a separate species rather than a variety of *A. tricoccum* (Voss and Reznicek 2012; Sitepu 2018; Weakley 2022). Due to the frequent references to *A. burdickii* and *A. tricoccum* throughout this paper they will be referred to as AB (*Allium burdickii*) and AT (*Allium tricoccum*).

Despite recognition of two ramp taxa, the geographic distribution of AB is unclear. Anecdotal observations suggest sporadic and overlapping occurrences between the two taxa. The Biota of North America Program (BONAP 2021) does not recognize AB and therefore no maps have been produced from its database. While AT can be found throughout the northeastern United States and adjacent regions of eastern Canada (Figure 1), the distribution of AB has been suggested to occur from North Dakota in the west to Maine in the east and as far south as Alabama and Georgia (Figure 1) (BONAP 2021; FNA 2022; NatureServe 2022; Weakley 2022). However, distribution maps for AB contradict one another regarding its presence in Virginia and North Carolina (NatureServe 2022; USDA 2022; Weakley 2022).

AT has two different color morphologies with either red/purple or green/white stems (often on the same growing site) whereas AB only has green/white stems. Misidentification of AB as green/white stemmed AT may contribute to uncertainty surrounding the distribution of AB. This confusion is likely due to frequent references of AT only having red/purple stems and AB as having green/white stems (Bernatchez et al. 2013). Other studies have referred to AB as "whites" and AT as "reds" (Bell 2007). The neglect of mentioning that AT has a white/green color morphology is likely contributing to confusion surrounding identification of AB and leading to misidentification of both species.

Nineteen states currently list AB's conservation status as vulnerable, imperiled, extinct, or unknown. Until this study, AB had not been officially documented in Pennsylvania (PA) (Rhoads and Klein 1993; Rhoads and Block 2007; Pennsylvania Flora Project 2022); therefore, its status in PA is still largely unknown. Harvesting may be impacting AB populations since AT is a well-known edible non-timber forest product, but it is not known if AB is incidentally harvested in regions where the

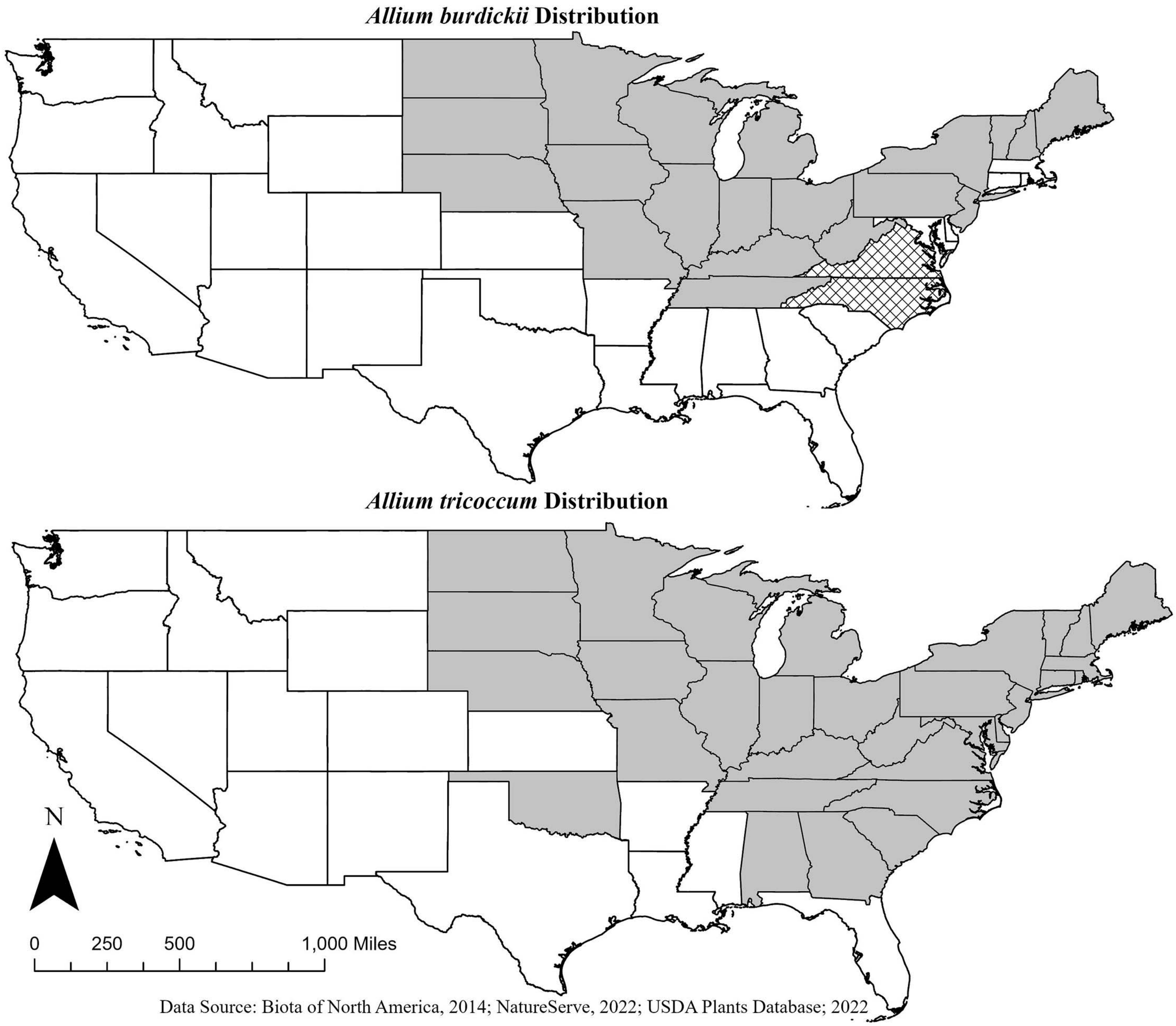

Figure 1.—*Allium burdickii* (top) and *A. tricoccum* (bottom) distribution throughout the United States. Crosshatched section on *A. burdickii* distribution map represents contradicting data on *A. burdickii* presence or absence.

two species co-occur. AT is a slow-growing species that can take 7–10 y to reach reproductive maturity, and the same is assumed for AB (Nantel et al. 1996; Dion et al. 2015). This slow growth makes them potentially vulnerable to overharvesting (Rock et al. 2003; Dion et al. 2015); as a result, ramp harvesting has been restricted in some areas of eastern North America (Dion et al. 2015; Patterson 2020).

Ramp leaves emerge in the early spring prior to canopy development. After or concurrent with canopy leaf out, ramp leaves senesce, and a stalk with an umbel inflorescence is produced that will persist throughout the summer months (Dion et al. 2015). Each flower will produce up to three hard, black seeds in August (Dion et al. 2015). Ramps also reproduce asexually via bulb division which typically occurs after 5–8 y (Nault and Gagnon 1993). Therefore, although ramps flower and reproduce later in the summer, their short-lived photosynthetic phase is like that of "spring ephemerals" since they leaf out before the overstory canopy to take advantage of high levels of sunlight.

Spring ephemeral abundance is associated with fertile soil (Host and Pregitzer 1991), perhaps because their short photosynthetic phases require a surplus of nutrients (Rothstein and Zak 2001). Ramps may also require fertile soil. Nault and Gagnon (1988) reported high levels of calcium in ramp reproductive structures at the end of the growing season. However, when comparing growth habits between the two ramp species, Bernatchez et al. (2013) noted that when 3000 kg/ha of gypsum was applied to both AB and AT forested plots, AB had greater calcium leaf concentration and invested more resources into reproduction (i.e., ramet production) and had a higher root:shoot ratio than AT. This calcium increase was also correlated with a greater seed set (Bernatchez et al. 2013).

Soil moisture content has been implicated as important for ramp growth and survival (Vasseur and Gagnon 1993; Bernatchez et al. 2013; Dion et. al. 2017). *Allium* species are vulnerable to water stress because they have short roots with bulbs that grow close to the soil surface. Due to these short root systems, alliums can only draw moisture from the upper 30 cm of the soil profile (Geries et al. 2020). AT bulb depth has been described as "very shallow and partially exposed" compared to AB bulbs that are "deeply set and fully submerged in the soil" (Sitepu 2018). This difference in bulb depth may contribute to differences in moisture tolerances. Vasseur and Gagnon (1993) suggested soil moisture was the most influential variable on AT as sites with greater soil moisture content had higher growth and survival rates. Bernatchez et al. (2013) found that AT growing at wetter sites with less nutrient availability had greater growth rates than drier sites with more nutrients available, suggesting soil moisture is more important for AT growth than is soil fertility.

Additionally, anecdotal observations suggest that AT may require soils that are moister than AB. Early descriptions of AB suggested it grew in drier, more upland areas than AT (Hanes 1953; Jones 1979). Sitepu (2018) noted that populations of AT and AB are often found at the same sites but in different microhabitats. If the two ramp species are found in different mesoscale habitats, indicator species, which are used to assess habitat suitability and characterize habitats (Dufrêne and Legendre 1997; Peck 2016), may differ for AT and AB.

In this study, the habitat characteristics associated with AT and AB populations occurring in southwest PA were documented and compared. The following data were collected and analyzed:

1) site factors: aspect, elevation, topographic position, and soil moisture with AT and AB populations
2) soil chemistry: pH and fertility associated with AT and AB populations
3) associated flora: most frequent over and understory species, dominant tree species, indicator species, and flora correlated with AT and AB populations

These results can be used by botanists and land managers to locate AB occurrences throughout the geographic range and to confirm site factors that explain why these two closely related taxa appear to differ in habitat. This, in turn, could aid in the discovery and conservation of AB populations.

METHODS

This study was conducted in southwestern PA, USA (39°43′–42°16′ N; 74°41′–80°31′ W). This region is part of the unglaciated Appalachian Plateau physiographic province and is dominated by oak-hickory forests (Pennsylvania Natural Heritage Program 2019). The climate is humid subtropical with a mean annual precipitation of 81–119 cm (Pennsylvania State Climatologist 2021).

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. A total of eight sites (four AB sites and four AT sites) were included in this study, with each site containing five plots for a total of 40 understory plots (20 understory plots per species) (Figure 2). Due to clonal growth, the number of genets present within a population was difficult to discern; therefore, estimates were made using ramets. Across the research sites, the population of AB ranged from 500 to 3,000 ramets and the population of AT ranged from 2,000 to 50,000 ramets. Inclusion of ramp populations were based on the following criteria: (1) Each population occupied at least an acre in size and consisted 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).

Floristic Sampling 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 through the placement of five plots. Plots and plot centers were established at AT and AB sites using a stratified but nonrandom approach in which the goal was to document only the vegetation within "patches" or populations of ramps, while still attempting to capture all floristic and/or site features. The intent was to ensure that only the nearest neighbors to ramps at each location were recorded; no attempt was made to inventory the entire flora at each site or account for any vegetation differences associated with areas of each site where ramps did not occur.

Overstory and understory flora associated with ramps was documented using a combination of plot and plot-less sampling methods. Overstory documentation was plot-less, using the Point-Centered Quarter-Method (PCQM; Causton 1987; Kent and Coker 1992) and for understory documentation, five 191 m^2 ($d = 12$ m, $r = 6$ m), circular plots were established. The plots were nonrandomly placed throughout the site to capture the extent of the vegetation present and the plots did not overlap. The overstory layer included dominant or co-dominant tree species while the understory layer included "resident" (Gilliam 2014) woody species (e.g., small trees, shrubs, vines) and herbaceous plants. Sites were visited 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. All plant nomenclature follows *Flora of the Southeastern U.S.: Pennsylvania* (Weakley 2022). Herbarium voucher specimens were collected at each ramp population and deposited at the Carnegie Museum of Natural History, the Morris Arboretum of the University of Pennsylvania, and the Pennsylvania State University Herbarium.

When using the PCQM method (Causton 1987; Kent and Coker 1992) for overstory documentation, plots were roughly divided into four quarters and one dominant or co-dominant tree (stems $\geq$7.6 cm diameter at breast height [1.4 m] and height

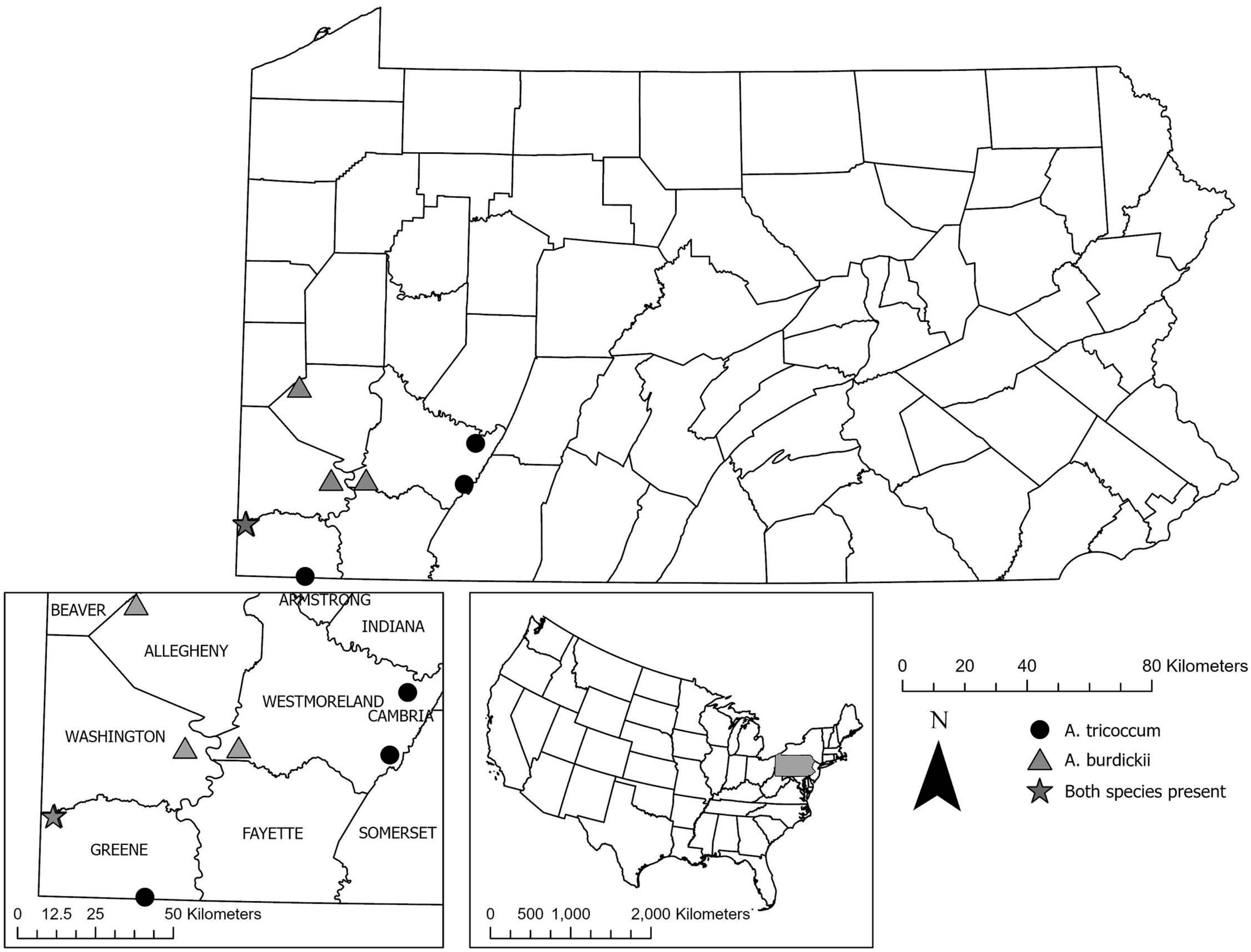

Figure 2.—*Allium burdickii* ($n = 4$) and *A. tricoccum* ($n = 4$) study populations in Pennsylvania. Soil moisture data were collected where *A. tricoccum* and *A. burdickii* co-occur at the same site, this is denoted by the gray star on the map. Other *A. tricoccum* populations are denoted by a black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

≥1.4 m) within or closest to that quarter was recorded. This yielded 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). For understory documentation, presence and 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.

PC-ORD (Multivariate Analysis of Ecological Data v. 7.0, MJM software design, Gleneden Beach, Oregon, USA) was used for indicator species analysis (ISA) and nonmetric multidimensional scaling (NMS). ISA was used to assess the degree to which a species is correlated with ramp occurrence. Dufrêne and Legendre methodology with a Monte Carlo randomization test were performed to determine significance (Peck 2016). For the ISA, abundance data per plot were analyzed based on species (AT or AB) and calcium content. Calcium (ppm) thresholds were <1500, 1500–3000, and >3000. Calcium was chosen as a nutrient of interest due to preexisting work that supported differences in calcium content between AB and AT (Bernatchez et al. 2013). Due to the small sample size, an alpha of 0.01 was selected; therefore, only results with a $P < 0.01$ are denoted as significant.

NMS was used to confirm if floristic associates differed between AB and AT sites. NMS was used to strengthen ISA results by suggesting what floristic associates were more correlated with which ramp species. Average herbaceous abundance data per site was used with a Sorenson (Bray-Curtis) distance matrix 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

(Peck 2016). A correlation coefficient (*r*) and tau greater than 0.4 or less than −0.4 was determined for species to be considered correlated.

Site Factor Data Collection and Analysis

Elevation, aspect, and topographic position were recorded for each plot. Soil moisture measurements were taken at one AB population and one AT population at a single study site in southwest PA where both occurred in proximity within the same watershed (Figure 2). We were limited to this single location because it was not possible to visit all sites within the region on the same day, and spring and summer rain events frequently occurred on localized scales complicating comparisons. The soil profile where soil moisture readings were taken ranged from silt loam to clay silt loam (USDA NRCS 2023).

The soil moisture sample collection site is hereinafter 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, Texas, USA). The soil moisture probe was inserted to bulb depth of approximately 15 cm into the soil (Tenenbaum et al. 2006; Bernatchez et al. 2013; Bretreger et al. 2021). Soil moisture measurements were taken from April through December 2021 at 8-week intervals. To examine tree canopy openness in relation to soil moisture throughout the growing season, hemispherical light photographs were taken and averaged in BSP plots when soil moisture data were collected.

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

A total of 40 soil samples were collected and analyzed from AB and AT plots. 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). SPSS (IBM Statistics for Macintosh v. 28, IBM Corp., Armonk, New York, USA) was used to run a Mann-Whitney *U* as data were nonnormal to determine if there was a difference in soil characteristics (pH, Ca, K, P, Mg) between AT and AB sites.

RESULTS

Site Factors

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). Both AB and AT plots were most frequently found on the topographic position of "middle slope" (Figure 3). Average AT elevation was greater at 437 m compared to AB at 284 m (Figure 3).

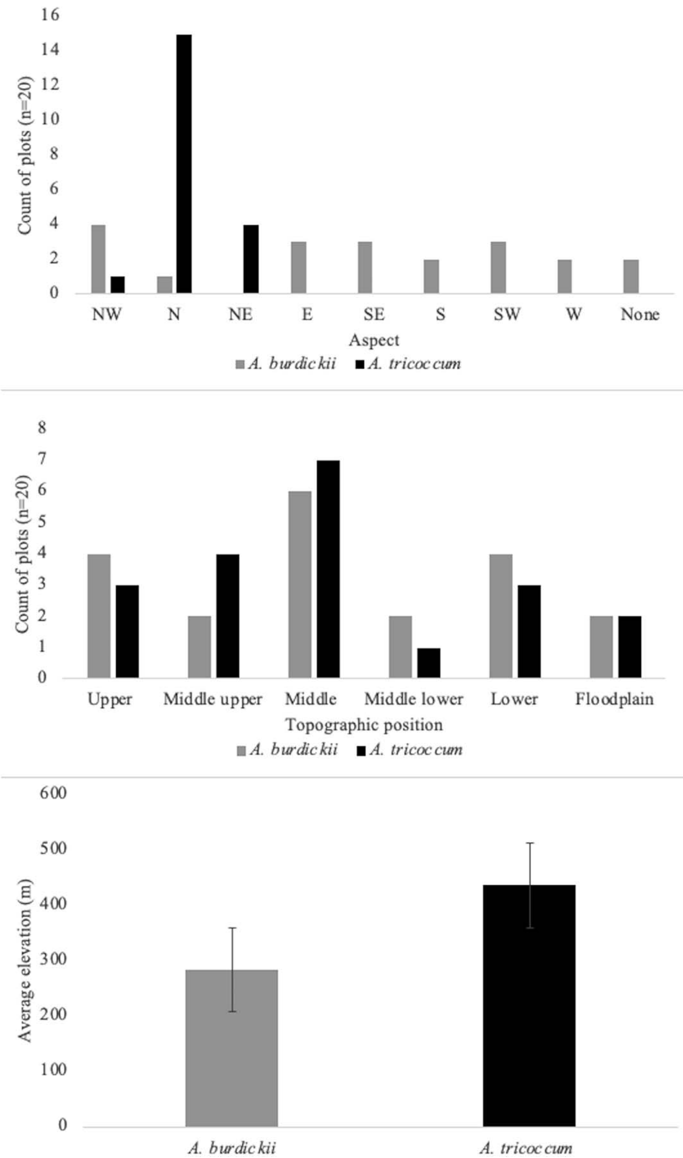

Figure 3.—Aspect, topographic position (slope or floodplain), and elevation (m) results from southwestern Pennsylvania *Allium tricoccum* and *A. burdickii* populations.

At BSP site, soil moisture was consistently greater at AT plots compared to AB plots (Figure 4). In April, both populations had similar soil moisture contents, then values diverge with AT soil moisture increasing and peaking in August at 50% volume (% vol) while AB decreased through October to 19% vol (Figure 4). Average percent canopy openness was the highest in April and December at 48% for AT and 57% for AB and the lowest in June at 5% for both ramp species (Figure 4).

Average pH at AT sites was 5.7 (4.7–7.2) and at AB sites was 6.1 (4.9–6.9). Mann-Whitney *U* results revealed pH ($P = 0.041$) was significantly more basic at AB populations compared to AT. Average calcium content at AB sites was 2909 ppm and at AT sites was 2027 ppm. Average magnesium content at AB sites was 333 ppm and at AT sites was 195 ppm. Average potassium content at AB sites was 202 ppm and at AT sites was 152 ppm. Calcium ($P = 0.033$), magnesium ($P = 0.0003$), and potassium

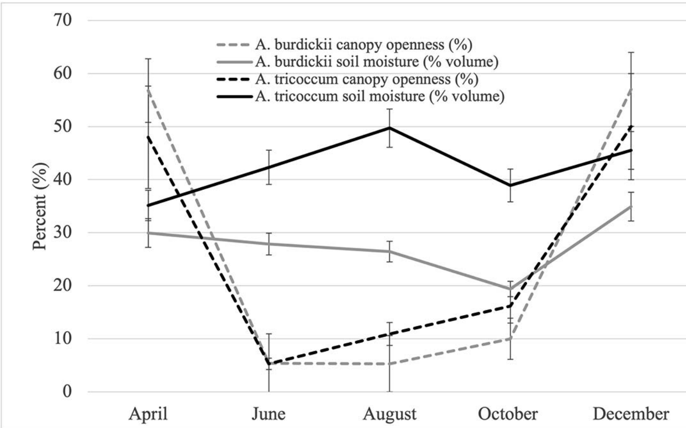

Figure 4.—Soil moisture (% volume) and percent canopy openness at southwestern Pennsylvania *Allium burdickii* and *A. tricoccum* populations ($n = 2$) from April through December. Bars represent standard error.

($P = 0.014$) content were significantly greater at AB populations compared to AT populations. Phosphorus content was not significantly different between species averaging at 57 ppm at AB sites and 43 ppm at AT sites.

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. The most frequent and dominant overstory tree species was sugar maple (*Acer saccharum* Marsh.), which was present at 85% of AT and AB plots (Appendix 1, Table 1). 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) (Appendix 1, Table 1). Spicebush (*Lindera benzoin* L. Blume) was the most frequent understory woody species found at AB and AT plots (Appendix 2, Table 2). 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 (Appendix 3, Table 3). 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).

The ISA identified 17 indicator species within AB and AT populations with a $P < 0.01$. Most of these species were herbaceous as only one over/understory woody species was a significant indicator (Table 4). When comparing the ISA results with the NMS correlation coefficients, only 13 herbaceous species were identified as indicator species and had a correlation coefficient and tau > 0.4 or < −0.4 (Table 5, Figure 5). The proportion of variance represented by NMS ordination axis 1, calculated as the proportion of variation in the reduced matrix relative to the original data set matrix, was 74% while axis 2 accounted for less than 1% (Figure 5). Therefore, the cutoff value of 0.4 was selected for axis 1 as it accounted for almost all the variation. Wood nettle (*Laportea canadensis* (L.) Wedd.) ($r = -0.69$, tau $= -0.62$) and blue cohosh ($r = -0.86$, tau $= -0.68$) were both significant indictors for AT with a $P < 0.001$ and correlated with AT populations (Table 5, Figure 5). Mayapple (*Podophyllum peltatum* L.) ($r = 0.86$, tau $= 0.76$), stonecrop (*Sedum ternatum* Michx.) ($r = 0.90$, tau $= 0.77$), and false Solomon's seal (*Maianthemum racemosum* (L.) Link) ($r = 0.64$, tau $= 0.59$) were indicators for AB and correlated with AB populations (Table 5, Figure 5).

DISCUSSION

This is the first scientific study comparing AT and AB habitat in PA, and the first to document AB habitat within the literature. Our primary objective was to compare habitat and floristic associates between AT and AB since observations as reported in the literature suggest that there may be habitat differences. Due

Table 1.—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	*A. tricoccum*	*A. burdickii*
Sugar maple	*Acer saccharum* Marsh.	87	97
Sweet birch	*Betula lenta* L.	4	
Bitternut hickory	*Carya cordiformis* (Wang) K. Koch	28	31
Pignut hickory	*Carya glabra* (P. Miller) Sweet		4
Shagbark hickory	*Carya ovata* (P. Miller) K. Koch		7
Northern hackberry	*Celtis occidentalis* L.		5
American beech	*Fagus grandifolia* Ehrh.	12	
Black walnut	*Juglans nigra* L.	7	7
Tulip poplar	*Liriodendron tulipifera* L.	30	
Sycamore	*Platanus occidentalis* L.	18	6
Black cherry	*Prunus serotina* Ehrh.	3	11
White oak	*Quercus alba* L.		13
Shingle oak	*Quercus imbricaria* Michx.		5
Yellow oak	*Quercus muehlenbergii* Enge.		6
Northern red oak	*Quercus rubra* L.	28	36
American basswood	*Tilia americana* L.	43	19
American elm	*Ulmus americana* L.		3
Slippery elm	*Ulmus rubra* Muhl.	9	20

Table 2.—The 10 most frequent understory woody species at southwestern Pennsylvania *Allium tricoccum* and *A. burdickii* study sites. Asterisks (*) denote nonnative, exotic species.

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

to the stratified, nonrandom approach in which ramp sites were located, targeted plot placement for sampling, and the lack of replication due to restricted knowledge on AB populations, the findings of this study should be regarded as suggestive. Random sampling for uncommon species presents practical difficulties and, in this study, paired "control" plots without ramp populations were not included due to limited resources and known locations, which can result in habitat bias (Kent and Coker 1992; McGraw et al. 2003). Nevertheless, the results obtained in this study highlight and identify key characteristics associated with AB habitat for further research and population discovery purposes.

Early observations of AB from midwestern states such as Illinois, Wisconsin, and Michigan have suggested that this species occurs in more upland habitats than AT (Hanes 1953; Jones 1979). More recently, Sitepu (2018) found AT sites occurred at a greater elevation than AB in Ohio. In this study, AT populations were found at higher elevations and both species were most frequently found mid-slope (Figure 3). However, AT was found on north-facing aspects whereas AB was found on a wide range of aspects, including southern (Figure 3).

Soil moisture content is influenced by topography. Northern aspects are exposed to less solar insolation and are therefore cooler and moister in the northern hemisphere while south aspects are warmer and drier (Figure 3; Nevo et al. 1999). Soil moisture content was likely affected by AT plots occurring on floodplains and north-facing slopes whereas AB plots were located on south-facing slopes. Thus, the mesoscale habitat in which these species occur differs, and ecological differentiation may be underway. Similar ecological differentiation due to moisture availability has been observed in two sister *Costus* species (*Costus allenii* and *C. villosissmus*) in Panama (Chen and Schemske 2015). *C. allenii* is found in areas that receive more precipitation and have consistently greater soil moisture in both the wet and dry seasons compared to *C. villosissmus*, which is found in drier areas (Chen and Schemske 2015). Thus, these species have a parapatric distribution throughout the island due to different habitat conditions (Chen and Schemske 2015).

At the BSP site, AT soil moisture was greater than AB from April thru December, suggesting AT requires consistently moister soil over the growing season than AB (Figure 4). Horticultural experiments support that soil moisture is an influential factor on AT growth and survival (Vasseur and Gagnon 1993; Bernatchez et al. 2013). When comparing light availability, soil nutrients, and soil moisture content, Vasseur and Gagnon (1993) found that soil moisture had the greatest effect on ramp growth and survival. Similarly, AT growing on moist soils with fewer nutrients available had greater growth rates than drier sites with more nutrients available (Bernatchez et al. 2013). Both studies suggest soil moisture may be an important factor for ramp growth and this study suggests that AT is associated with wetter areas than AB and may be less tolerant of dry conditions.

One of the notable differences between these two species, consistent even in a common garden, is that the bulb of AT is generally shallower in the soil than AB (Hanes 1953; Sitepu 2018). While collecting herbarium specimens in the field, we observed that AB was indeed more deeply buried in the soil when compared with AT. This shallow bulb and root system may make AT more vulnerable to water stress and could contribute to different habitat requirements. The moisture results we obtained are unfortunately limited by lack of replication beyond this single site and therefore additional research is needed to determine if soil moisture content differs consistently through the range of the species.

Soils with a lower pH may support greater ramp growth (Davis and Greenfield 2002; Bernatchez et al. 2013). AT growth rates have been reported as being higher on more acidic soils when compared to basic sites with greater calcium content (Bernatchez et al. 2013). Research reports soil pH of both species to be similar with AT ranging from 4.5 to 7.7 and AB ranging from 4.5 to 7.6 (Sitepu 2018). In this study, AT occurred on more acidic soils (pH 5.7) when compared with AB (pH 6.1).

Table 3.—The 25 most frequent herbaceous species at southwestern Pennsylvania *Allium tricoccum* and *A. burdickii* populations. Asterisks (*) denote nonnative, exotic species.

Common name	Scientific name	Percentage of plots and (*n*) for *A. tricoccum*	Percentage of plots and (*n*) for *A. burdickii*
Blue cohosh	*Caulophyllum thalictroides* (L.) Michx.	90 (18)	45 (9)
Great white trillium	*Trillium grandiflorum* (Michx.) Salis.	90 (18)	
Cut-leaf toothwort	*Cardamine concatenata* (Michx.) O. Schwarz	85 (17)	85 (17)
Mayapple	*Podophyllum peltatum* L.		80 (16)
Christmas fern	*Polystichum acrostichoides* (Michx.) Schott	80 (16)	75 (15)
Intermediate woodfern	*Dryopteris intermedia* (Muhl. Ex Willd.) A. Gray	75 (15)	
Violet species	*Viola* spp.	75 (15)	70 (14)
Spring beauty	*Claytonia virginica* L.	50 (10)	70 (14)
Stonecrop	*Sedum ternatum* Michx.		70 (14)
Wild geranium	*Geranium maculatum* L.		65 (13)
False Solomon's seal	*Maianthemum racemosum* (L.) Link		65 (13)
False mermaid	*Floerkea proserpinacoides* Willde.	35 (7)	60 (12)
Wood-nettle	*Laportea canadensis* (L.) Wedd.	60 (12)	
Jumpseed	*Persicaria virginiana* (L.) Gaer.	60 (12)	50 (10)
White wood aster	*Eurybia divaricata* (L.) Nesom		55 (11)
Bedstraw	*Galium* sp.		55 (11)
Clearweed	*Pilea pumila* (L.) A. Grey	35 (7)	55 (11)
Hairy sweet cicely	*Osmorhiza claytonii* (Michx.) C.B. Clarke	50 (10)	
Garlic mustard	*Alliaria petiolata* (Berb.) Cav. & Gran.*	45 (9)	
Sweet scented bedstraw	*Galium triflorum* Michx.	45 (9)	60 (12)
Canada waterleaf	*Hydrophyllum canadense* L.	45 (9)	
Long bristled smartweed	*Persicaria longiseta* (de Bruijn) Kitagawa*	45 (9)	
Broadleaf toothwort	*Cardamine diphylla* (Michx.) Alph. Wood	40 (8)	
Squirrel corn	*Dicentra canadensis* (Goldie) Walpers	40 (8)	
Eastern blue phlox	*Phlox divaricata* L.	40 (8)	50 (10)
Hairy Solomon's seal	*Polygonatum pubescens* (Willde.) Pursh.	40 (8)	50 (10)
Zig zag goldenrod	*Solidago flexicaulis* L.		50 (10)
Enchanter's-nightshade	*Circaea canadensis* (L.) Hill		45 (9)
White avens	*Geum canadense* Jacq.		45 (9)
Kidney leaf buttercup	*Ranunculus abortivus* L.		45 (9)
Sweet white violet	*Viola blanda* Willde.	40 (8)	
Spotted Joe-pye-weed	*Eutrochium maculatum* (L.) E.E. Lamont		40 (8)
Carolina spring beauty	*Claytonia caroliniana* Michx.	35 (7)	
Woodfern	*Dryopteris* sp.	35 (7)	
Red trillium	*Trillium erectum* L.	35 (7)	
Jack-in-the-pulpit	*Arisaema triphyllum* (L.) Schott	30 (6)	40 (8)
Honewort	*Cryptotaenia canadensis* (L.) A.P. de Candolle		35 (7)
Forest bedstraw	*Galium circaezans* Michx.		35 (7)

Soil nutrients including calcium, magnesium, and potassium were greater at AB populations than AT.

Soil calcium may be an important nutrient for ramp growth as application of lime and gypsum have been found to increase ramp growth and survival rates in forest cultivation (Ritchey and Schumann 2005; Bernatchez et. al. 2013). Our findings that calcium content was significantly greater at AB sites may suggest a link between occurrence and soils with higher calcium content. Moreover, many of the top overstory tree associates of AB are regarded as calciphytes and may not only indicate such soil conditions but also play an important role in the cycling of this nutrient. For example, sugar maple was the most frequent and dominant tree species found at AT and AB sites (Appendix 1, Table 1). As the leaves from this species decompose, they can provide an annual calcium input (Dijkstra and Smits 2002; Moore et al. 2015; Ott and Watmough 2021).

The forest community type "*Acer saccharum-Allium tricoccum-Caulophyllum thalictroides*" has been identified suggesting that these species are frequently found in similar habitats (Bellemare et al. 2005). In this study, blue cohosh was the most frequently observed herbaceous species at AT sites and was found to be both a significant indicator species and correlated with AT populations (Tables 3 and 5, Figure 5). This vegetation type has been correlated with solar insolation, indicating aspect and soil moisture are important factors governing the habitat conditions where these species are found (Bellemare et al. 2005).

At sites where blue cohosh was present in the spring, wood nettle was often observed later in the season. Wood nettle was correlated and identified as an indicator species for AT (Table 5, Figure 5). 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. Mayapple, stonecrop, and false Solomon's seal were significant indicator species for AB and correlated with

Table 4.—Indicator species analysis (ISA) for overstory trees and understory woody species at southwestern Pennsylvania *Allium tricoccum* and *A. burdickii* populations. Significance denoted by an asterisk at $P < 0.01$; results without an asterisk were associated but not significantly. Species grouped as *A. tricoccum* (T) or *A. burdickii* (B), and in relation to calcium.

Species		ISA	
Common name	Scientific name	Species	Calcium (ppm)
Tulip poplar	*Liriodendron tulipifera* L.	T	
American basswood	*Tilia americana* L.		>3000
Striped maple	*Acer pensylvanicum* L.	T	
American hornbeam	*Carpinus caroliniana* Walter	B	
Multiflora rose	*Rosa multiflora* Thunb. Ex. Murr.	B	
Bladdernut	*Staphylea trifolia* L.	B	
Grape vine	*Vitis* sp.	B*	

AB populations (Table 5, Figure 5). According to Weakley (2022), mayapple grows on a variety of landscapes from bottomlands to upper slopes and is found on rich soils. False Solomon's seal is described as growing in moist to dry forests yet was only found with AB (Table 3; Weakley 2022). Stonecrop is geographically restricted to southern PA (BONAP 2021) and was likely an indicator due to sample size and site location restrictions. Species such as mayapple, stonecrop, and false Solomon's seal can tolerate a wide range of habitats and were indicators and correlated with AB, whereas species that were indicators and correlated with AT require cool, moist habitats. This is likely because AB was associated with dry-mesic soils, and thus may tolerate a wider range of habitats than AT.

The occurrence of nonnative, exotic species on research sites is notable since these invasive species have the potential to compete with ramp populations by creating early-season shade. Early shading could alter ramp's ability to photosynthesize during the critical time of year prior to tree canopy establishment (Maynard-Bean et al. 2020). Invasive, exotic shrub species such as multiflora rose (*Rosa multiflora* Thunb. Ex. Murr) and Japanese barberry (*Berberis thunbergii* A.P. de Candolle) were frequently found as ramp associates (Table 2) and multiflora rose was identified as an indicator species for AB (Table 4).

CONCLUSION

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

AT was associated with a higher soil moisture content than AB, which may explain why these species occur on differing aspects. Both AT and AB may be associated with soil calcium, however AB was significantly associated with higher Ca, Mg, and K levels and AT was associated with acidic soils. Understory flora associated with AT are those that require moist, wet-mesic habitats, such as wood nettle or blue cohosh, whereas AB is found with a wide range of genera with more dry-mesic habitat preferences.

These habitat differences may aid in species identification and can be used to locate more populations through fieldwork and

Table 5.—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 in relation to calcium.

Species		ISA	
Common name	Scientific name	Species	Calcium (ppm)
Broadleaf toothwort	*Cardamine diphylla* Michx.	T*	
Blue cohosh	*Caulophyllum thalictroides* (L.) Michx.	T**	
Carolina spring beauty	*Claytonia caroliniana* Michx.	T*	
Intermediate woodfern	*Dryopteris intermedia* (Muhl. Ex Willd.) A. Gray	T*	<1500*
Big leaved aster	*Eurybia macrophylla* (L.) Cassini	B*	
Forest bedstraw	*Galium circaezans* Michx.	B*	
Wood nettle	*Laportea canadensis* (L.) Wedd.	T**	<1500**
False Solomon's seal	*Maianthemum racemosum* L.	B*	
Two-leaved mitrewort	*Mitella diphylla* L.		<1500*
Mayapple	*Podophyllum peltatum* L.	B*	
Blue phlox	*Phlox divaricata* L.		<1500*
Lion's foot	*Nabalus* sp.	B*	
Stonecrop	*Sedum ternatum* Michx.	B*	
Red trillium	*Trillium erectum* L.	T*	
Great white trillium	*Trillium grandiflorum* Michx. Salis.	T*	
Sweet white violet	*Viola blanda* Willde.	T*	<1500**

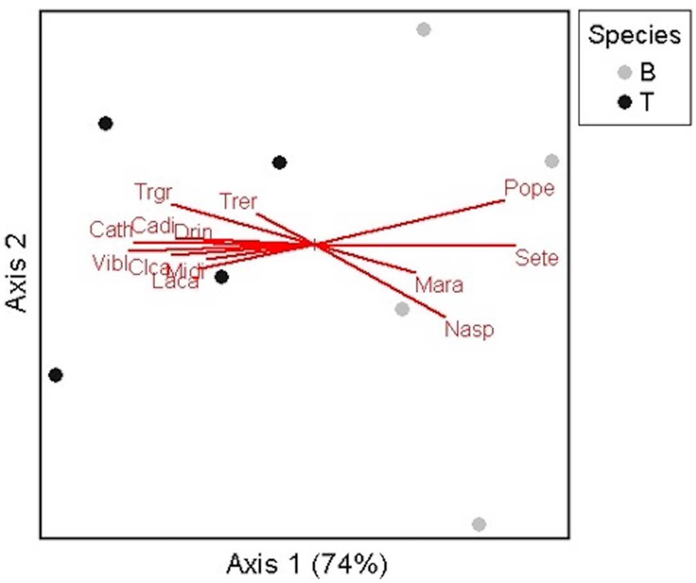

Figure 5.—Nonmetric multidimensional scaling (NMS) results with herbaceous indicator species overlayed on two-dimensional herbaceous abundance ordination ($r > 0.4$, tau > 0.4 or $r < -0.04$, tau < -0.4). Species are denoted by the first two letters of their genus and specific epithet. Sites of *Allium burdickii* (B) and *A. tricoccum* (T) located in southwestern Pennsylvania.

habitat modeling and further the status and any conservation needs for AB.

ACKNOWLEDGMENTS

This research was supported by Wild Resource Conservation Program grant 18585 administered by the Pennsylvania Department of Conservation and Natural Resources. We are thankful for the field assistance and botanical expertise provided Western Pennsylvania Conservancy (especially Steve Grund and Jessica McPherson) and Loree Speedy. We thank Dr. Harvey Ballard for confirming AB populations and the landowners and organizations that provided access. We thank Jeri Peck for her assistance with statistical analyses.

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