White-tailed deer (*Odocoileus virginianus*) herbivory in Northeastern Ohio riparian zones: A preference study

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ABSTRACT

The objective of this study was to determine white-tailed deer (*Odocoileus virginianus*) browsing preferences for tree and shrub species in riparian zones of Northeastern Ohio. A total of five sites were selected along the Grand River and Pymatuning Creek in Trumbull County, and along the Cuyahoga River in Geauga County. In autumn of 2012, three to five 12 x 20 m quadrats were established in a stratified random fashion at each site, and the canopy species composition was surveyed for each quadrat. For individual tree species that had foliage accessible to white-tailed, deer the following data were recorded quantitatively and/or categorically: total available browse, type of available browse, and severity of browsing. The shrub and sapling layer was also surveyed within two randomly placed 4x4 m nested plots per 12x20 m overstory quadrat. The Jacob's Electivity Index was used to assess browsing preferences for tree and shrub species. As determined by the Jacob's Electivity Index various tree and shrub species: 1) were consistently avoided at all quadrats when present (bitternut and shagbark hickories, swamp and black ashes, black cherry, American basswood, and American elm), 2) were consistently selected in all quadrats where present (American hornbeam and black willow), or 3) varied widely in their selection by deer (silver and sugar maples). Quadrats containing sugar and, especially, silver maple with epicormic sprouts had greatest total browsing impact. Results suggest that white-tailed deer herbivory may actually reflect a Marginal Value Theorem model dictated by patches abundant in such sprouts. Further research is needed to determine potential effects of white-tailed deer in hindering the regeneration of such flood and/or beaver damaged vegetation in Northeastern Ohio riparian zones.

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Introduction

Riparian Zones

Riparian zones are more than a link between aquatic and terrestrial ecosystems. Rather they are ecotones comprised of a complex patchwork of landforms and a diverse assemblage of communities. Riparian zones are influenced by a wide array of both abiotic (i.e., geomorphic and hydrologic) and biotic processes (e.g., nutrient cycling by plants and animals) that, coupled with frequent disturbance events, yield a heterogenous environment that can support a high level of plant and animal diversity (Gregory et al. 1991, Naiman et al. 1993). Riparian zones include the active stream channel up to the high water mark as well as surrounding landforms that are influenced by the stream, including floodplains and upper and lower terraces (Naiman et al. 1993, Naiman et al. 1997).

The type of riparian zone depends on the stream order, a hierarchal ranking system for streams and rivers. In lower order headwater streams the riparian zone is often quite small and indistinguishable from the surrounding forest. In mid-order streams (3rd to 5th) the riparian zone forms a distinct strip of diverse vegetation that influences the stream's aquatic ecosystem and is directly influenced by the stream through flooding activity, sediment deposition, and erosion (Gregory et al. 1991, Malanson 1993, Naiman et al. 1993). In large order streams (6th and larger) the riparian zone forms a vertical gradient of vegetation in multiple stages of succession (Malanson 1993, Naiman et al. 1993). Vegetation from the upper terraces, which is only affected during large-scale floods, does not directly interact with the river's aquatic ecosystem, although it does contribute allocthtonous carbon and nutrients, carbon and nutrients from outside of the stream or river, through leaf litter and woody debris (Gregory et al. 1991, Naiman and Decamps 1997).

Effects of Riparian Zone Vegetation on Stream Morphology and Hydrology

Riparian zone vegetation has considerable influence on both the morphology and hydrology of streams. Tree root networks stabilize stream banks and floodplains, reducing the mass wasting that cause channel widening (Gregory et al. 1991, Naiman and Decamps 1997). Root networks can further alter stream morphology by trapping sediments (Gregory et al. 1991, Muller et al. 2000). The roots can also affect stream hydrology by increasing the soil porosity via gaps within the root network allowing for greater ground water flow as opposed to graminoids (i.e. grasses and sedges), which form thick rhizome mats (Muller et al. 2000). Coarse woody debris from trees modifies in channel morphology by forming ramparts, which protect accumulating sediments, sometimes leading to the formation of islands (Keller and Swanson 1979). Coarse woody debris within streams can also alter flow patterns, thereby increasing residence time for dissolved and particulate matter (Gregory et al. 1991, Naiman and Decamps 1997).

Effects of Riparian Zone Vegetation on Stream Communities

Riparian zone vegetation affects aquatic communities by altering abiotic and biotic stream components. The amount of shade resulting from tree canopies depends on tree species composition. The degree of shade that a stream receives affects both the amount of available light for primary producers and the energy input in the form of heat by solar radiation (Gregory et al. 1991, Naiman et al. 1993). Riparian vegetation also affects water quality by buffering the stream from potentially deleterious inputs of nutrients, pesticides, and sediments from the surrounding watershed (Gregory et al. 1991, Naiman and Decamps 1997). It modifies the amount of nutrients and the timing of when nutrients enter the system directly through plant uptake, denitrification, and retention (Gregory et al. 1991, Hefting et al. 2005, Muller et al. 2000). Vegetation also inputs nutrients and allochthtonous carbon into the aquatic ecosystem through pulses of dissolved leachate, leaf litter, and woody debris (Gregory et al. 1991). The amount of time it takes to process plant matter depends on the leaf structure and chemical composition. Herbaceous plant material may only take a few weeks to breakdown, but leaves containing high concentrations of tannins (e.g. evergreen needles and oak leaves) take up to a year or longer to decompose (Gregory et al. 1991, Muller et al. 2000).

Effects of Herbivory on Riparian Zone Vegetation

Preferential browsing by large ungulates in the absence of predators can have a marked impact on the plant community composition and successional processes in riparian zones. In Olympic National Park, WA, Roosevelt elk (*Cervus elaphus*) have led to a decline in black cottonwood (*Populus trichocarpa*) and bigleaf maple (*Acer macrophyllum*) recruitment since the local extirpation of gray wolves (*Canis lupus*) in the 1920s (Beschta and Ripple 2008). Preferential browsing of palatable species has uncoupled the successional progression of black cottonwood to bigleaf maple and led to a shift to the unpalatable red alder (*Alnus rubra*) and Sitka spruce (*Picea sitchensis*). The reaches of the Hoh, Queets, and Quinault rivers within the park have wider active channels and increased braiding, (e.g., 37% inside the park as opposed to 2% outside of the park) due to mass wasting caused by over browsing by Roosevelt elk (Beschta and Ripple 2008).

In Zion National Park, UT, there is a (47 fold increase), of Freemont cottonwood (*Populus fremontii*) in North Creek, where cougars (*Puma concolor*), a primary predator of mule deer (*Odocoileus hemionus*), are common, compared to the Virgin River in Zion Canyon where they are scarce. Freemont cottonwood recruitment has been consistent in North Creek, whereas Zion Canyon has lacked recruitment since the increase of human activity that caused the local extirpation of cougars in the 1930s. The Virgin River also has a larger percentage of eroding banks as well as a greater channel width compared to North Creek, which is the north fork of this river (Ripple and Beschta 2006). Also preferential browsing by moose (*Alces alces*) along the Tanana River in Alaska accelerates the successional shift from a willow (*Salix* spp.) dominated community to one dominated by mountain alder (*Alnus tenuifolia*) (Keilland and Bryant 1998). Given the substantial effects that large ungulates can have on riparian zones it is surprising that relatively little research has been done on white-tailed deer (*Odocoileus virginianus*) herbivory in eastern riparian communities.

White- tailed Deer Overabundance

White-tailed deer populations in North America have increased to unprecedented numbers over the past century (Fuller and Gill 2001, McCabe and McCabe 1997, McShea et al. 1997), due in part to increased forage availability from agricultural and silvicultural activities coupled with fragmentation of native forests (Fuller and Gill 2001, Porter and Underwood 1999, Waller and Alverson 1997). Deer mortality has also significantly decreased over the last several decades due to diminishing populations of key predators such as gray wolves and cougars (Rooney and Waller 2003), in conjunction with increased regulations in sport hunting and shifts in public opinion towards hunting

(Brown et al. 2000). White-tailed deer fulfill all four of Caughley's (1981) criteria for an overabundant species. A species is overabundant if it: 1) threatens human life or livelihood, 2) reaches population levels that increase rates of starvation and spread of disease, 3) reduces abundance of economically or aesthetically important plant and animal species, or 4) negatively affects ecosystem function.

Effects of Preferential Browsing by White-tailed Deer at the Ecosystem Level

Preferential browsing by white-tailed deer can directly alter plant community composition and structure (Augustine and McNaughton 1998, Nuttle et al. 2013, Rooney 2001). There are a number of studies that demonstrate that overabundant deer populations shift canopy composition through preferential browsing of palatable seedlings and saplings (Augustine and McNaughton 1998, Nuttle et al. 2013, Potvin et al. 2003, Rooney et al. 2000, Waller and Alverson 1997). Intense browsing on juvenile woody species can lead to a reduction in tree species diversity (Gill and Beardall 2001), simplification of the vertical structure of the forest (Gill and Beardall 2001, Rooney and Waller 2003), and alter the rate of succession (Seagle and Liang 2001).

Persistent preferential browsing at high densities can also shift a forest ecosystem into an alternate steady state through biotic homogenization (Rooney 2009). High levels of preferential browsing on herbaceous and woody species by deer can lead to an overall decrease in palatable graze-intolerant species and an increase in unpalatable and graze-tolerant species (Augustine and McNaughton 1998, Nuttle et al. 2013, Rooney and Waller 2003). Unpalatable and graze-tolerant species benefit from reduced competition, which can lead to the creation of grazing lawns, which are productive graminoid and fern dominated areas that are perpetuated by grazing (Rooney 2009). Grazing lawns, an alternate steady state, differ from successional states because they are not readily reversed without significant human intervention even after deer densities are reduced (Scheffer et. al 2001).

Stand Attractiveness to Deer and Susceptibility to Damage

There are multiple landscape and stand-scale dependent factors that affect stand attractiveness and susceptibility to damage. At the landscape scale, white-tailed deer have a more pronounced impact on fragmented forest patches due to their small relative area in comparison to deer range size, their accessible forest interiors, and their large perimeters (Augustine and DeCalesta 2003, Kay 1993, Reimoser 2003). White-tailed deer browse fragmented forest patches surrounded by agriculture substantially more than those adjacent to other habitat types (Augustine and DeCalesta 2003, Reimoser 2003). They also have a greater impact on mid and late successional forests as opposed to forests in the early stage of succession, which could have implications for riparian zones (Augustine and DeCalesta 2003). At the stand scale, white-tailed deer prefer stands with hiding cover (Kay 1993), stands that were previously browsed (Bergqvist et al. 2003), and stands that have low productivity (Danell et al. 1991).

Effects of Browsing on Individual Trees

Browsing can alter tree morphology, reduce competitive ability, and/or directly kill individual trees (Bergqvist et al. 2003, Danell et al. 1994, Gill and Beardall 2001). Seedlings and saplings are the most susceptible to damage because they are within the browsing range of deer (Kay 1993). Browsing on seedlings reduce stem density.

Browsing on lead shoots of trees and saplings reduce height, while browsing on side shoots reduces foliage density (Gill and Beardall 2001). Changes in tree morphology due to herbivory can result in a feeding loop (Bergqvist et al. 2003) where in the herbivore will continue to revisit pre-browsed trees due to an increase in shoot size, availability, and palatability (Bergqvist et al. 2003, Danell et al. 1994).

Plant Tolerance to Herbivory

Browse-tolerant plant species are able to increase their relative growth rate to compensate for tissues lost to herbivory. In contrast, browse-intolerant species' relative growth rates will either decline or stay the same, as they are typically unable to replace lost tissue (Augustine and McNaughton 1998). Browse-intolerant species are often slow growing and shade-tolerant understory herbaceous plants, shrubs, and tree seedlings (Augustine and DeCalesta 2003, Augustine and McNaughton 1998).

A plant's capacity for compensatory growth depends on physical and morphological characteristics, environmental conditions, and timing of browsing (Augustine and McNaughton 1998, Hobbs 1996). The physical and morphological characteristics that have evolved over time to enable a plant to a resist or tolerate drought also confer tolerance to browsing. These traits include basal meristems, small stature, high shoot density, and deciduous shoots and leaves. Below ground nutrient reserves as well as rapid transpiration, photosynthesis, and growth that enable plants to capitalize on periodic influxes of water can also aid in replacing lost tissue from herbivory (Coughenour 1985).

A plant's ability to replace tissues lost during herbivory is heavily influenced by environmental conditions. Compensatory growth depends on the availability of light, water, and soil nutrients (Canham 1994, Hobbs 1996), as well as weather and climate (Hobbs 1996). The timing of browsing also plays a role in the plant's capacity to express its compensatory growth potential (Augustine and McNaughton 1998, Canham 1994). Seedlings are/can be capable of withstanding severe browsing during the winter months, although, they have an overall decrease in height and higher mortality rate from similar amounts of browsing during the summer months (Canham 1994).

Resistance to Herbivory, Stem Chemical Defenses and Palatability

Herbivore-resistant plant species have characteristics that deter herbivory (i.e. chemical defenses and low digestible content) or reduce plant tissue loss (i.e. leaf toughness and morphological defenses) (Bryant and Raffa 1995, Cote et. al 2004). Ungulates select which species to browse based on several factors, including plant chemical defenses, which effect palatability (Bryant et al. 1992). The amount of stem chemical defense varies both at the species level, which is influenced by adaptation to resource limitations and past regional levels of herbivory, and at the individual level, which is influenced by the plant's growth stage, time of year, and level of past herbivory (Bryant and Raffa 1995). Plant species that have adapted to resource-limited environments have a reduced ability to replace plant tissues destroyed by herbivores. Therefore, they often have evolved strong chemical defenses to deter herbivory. Plant species in resource-rich environments have evolved responses to frequent disturbances, and are able to utilize the pulse of resources that follow such disturbances to regrow above ground tissues. Those species are already adapted to tolerate herbivory and do not require chemical deterrents (Bryant et al. 1983). Several species that have evolved in regions of high levels of herbivory often have higher corresponding levels of chemical defense in comparison to species that have evolved in regions with less severe browsing (Bryant et al. 1994).

The amount of stem chemical defenses also varies during the stages of an individual plant's life, due to physiological competition for resources between chemical defenses and other plant functions such as growth (Bryant and Raffa 1995). Seedlings generally have a lower amount of chemical defenses than saplings due to a higher demand for carbon for growth. However, as the plant enters the adult stage of its life cycle it becomes limited more by nutrients than by carbon, so the production of secondary metabolites is less costly (Bryant et al. 1991). Juvenile woody plants are more prone to damage by herbivory than mature plants, and therefore have higher levels of chemical defenses in their stems than similar stems of adult woody plants of the same species (Bryant et al. 1983). The level of chemical defense in an individual corresponds to the time of year, with chemical defenses decreasing during periods of rapid growth and flowering (Bryant et al. 1991). Lastly trends show the levels of an individual's stem chemical defenses depends on the levels of past herbivory. Severe browsing on a juvenile can lead to carbon stress as the individual attempts to regrow tissue lost to herbivory, which results in a decline in chemical defenses. That reduction in chemical defenses leads to a positive feedback loop of increasing severity of herbivory coupled with further reductions in chemical defenses, which can ultimately result in the individual plant's death (Bryant et al. 1983).

White-tailed Deer Foraging and Marginal Value Theorem

Marginal Value Theorem (MVT) is an optimal foraging model that is used to predict the foraging behavior of animals in patchy environments. The MVT states that the rate of resource intake is maximized when the herbivore leaves the patch once the rate of intake of browse is less than the average rate of intake for the overall habitat (Charnov 1976). The rate of intake decreases within a patch over time due to diminishing bite size and difficulty finding and harvesting suitable plant matter. In a habitat with uneven patch quality, the herbivore will spend more time at patches of higher quality than at patches of average or lower quality. Additionally the herbivore will spend more time within a patch when the distance between patches increases in order to decrease the time between bites (Nonacs 2015, Shipley and Spalinger 1995).

White-tailed deer and other larger herbivores must take thousands of bites of plant matter to sustain themselves. Nutrient concentration is often inversely related to plant size, due to fibrous structural tissues, which leads to a tradeoff between nutrient concentration and high rate of intake. Larger bites result in a high rate of intake; however large bites often include fibrous structural tissue which reduces digestibility (Shipley and Spalinger 1995).

Objective

The purpose of this study was to assess the role that white-tail deer herbivory has on hydric and mesic woody plant community composition, by examining its effects on tree and shrub species in Northeastern Ohio riparian zones. The objective of this study was to determine white-tail deer grazing preferences of tree and shrub species in Northeastern riparian zones with the use of a Jacob's Electivity Index.

Methods

Site Description

Five sites were selected in riparian zones of 3rd to 5th order streams in state-managed public hunting and fishing areas located in the northern Ohio counties of Trumbull and Geauga. Site #1 was located along the banks of the Grand River in the Grand River Wildlife Area, which encompasses 7,453 acres in Trumbull County. Site #1 (41.396561,-80.9421) was located on a lower terrace with an estimated 100-120 year old stand comprised primarily of *Acer saccharum* Marshall (sugar maple), *Ulmus americana* L. (American elm), *Carya ovate* (Mill.) K. Koch (shagbark hickory), and *Carya cordiformis* (Wang.) K. Koch (bitternut hickory).

Site #2 and Site #3 were located along the Pymatuning Creek in the Shenango Wildlife Area, which encompasses 4,845 acres in Trumbull County. Site #2 (41.387805,-80.556586) was located on a lower terrace with an estimated 60-70 year old stand dominated by *Acer saccharinum* L. (silver maple). Site #3 (41.367034,-80.552466) was located on a floodplain with an estimated 60 year old stand also dominated by *A. saccharinum*.

Site #4 and Site #5 were located along the Cuyahoga River in the La Due Public Hunting Area, which encompasses 8,791 acres in Geauga County. Site #4 (41.426419,-81.155995) was located on an active floodplain dominated by *A. saccharinum*. Site #5 (41.37247,-81.158688) was an active floodplain with an estimated 100 year old stand comprised of *A. saccharinum*, *Quercus palustris* Müenchh. (pin oak), and *Fraxinus pennsylvanica* Marshall (swamp ash).

Table 1: Site and Corresponding Quadrats and Landforms.

Site	Number of Quadrats	Landform
Site #1 Grand River	3	Lower Terrace
Site #2 Northern Shenango	3	Lower Terrace
Site #3 Southern Shenango	5	Floodplain
Site #4 Northern La Due	3	Floodplain
Site #5 Southern La Due	3	Floodplain

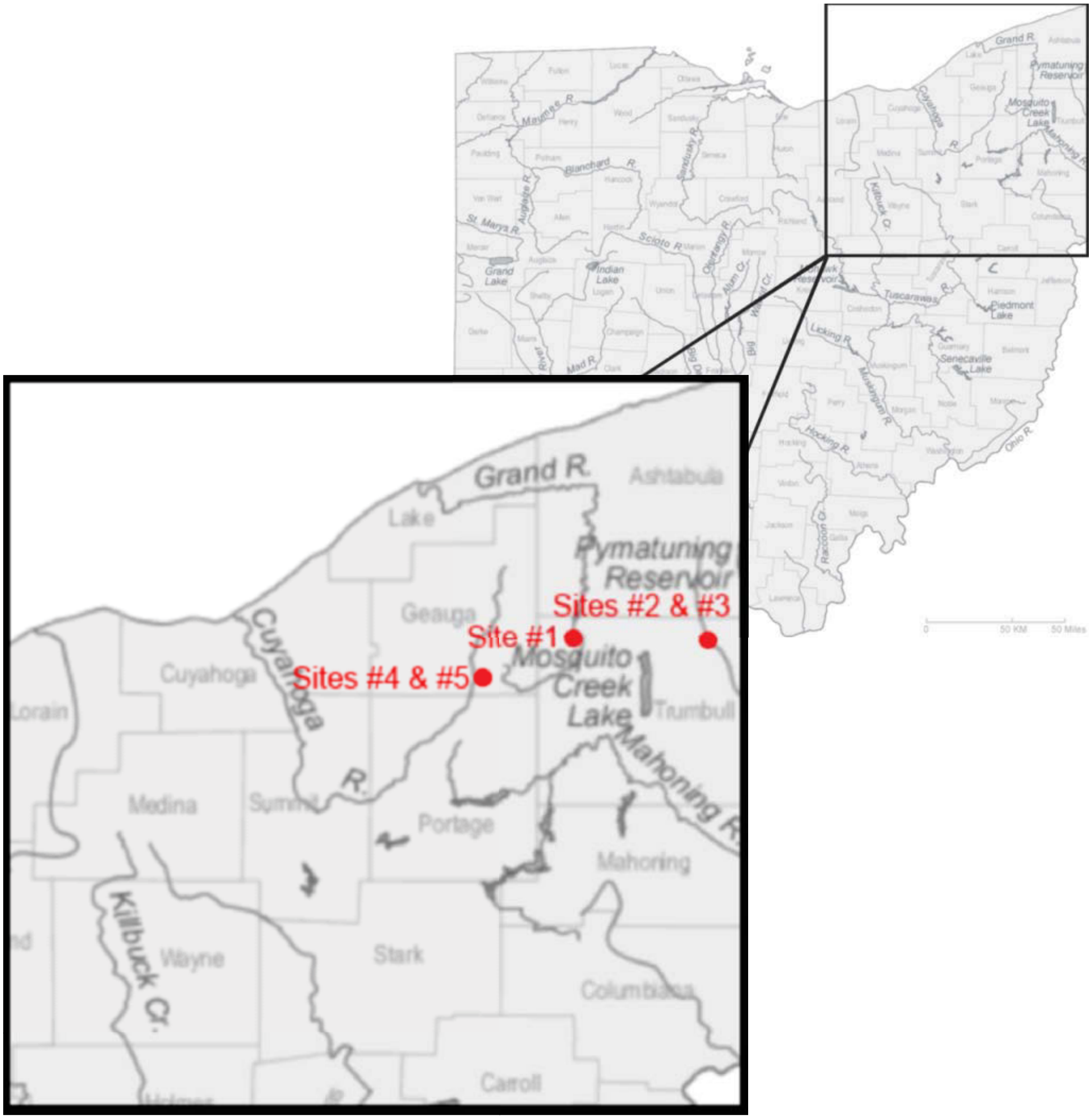


Figure 1: Regional site locations in Northeastern Ohio. Site #1 Grand River, Grand River Wildlife Area in Trumbull County. Site #2 & #3 Pymatuning Creek, Shenango Wildlife Area in Trumbull County. Site #4 & #5 Cuyahoga River, La Due Public Hunting Area in Geauga County.

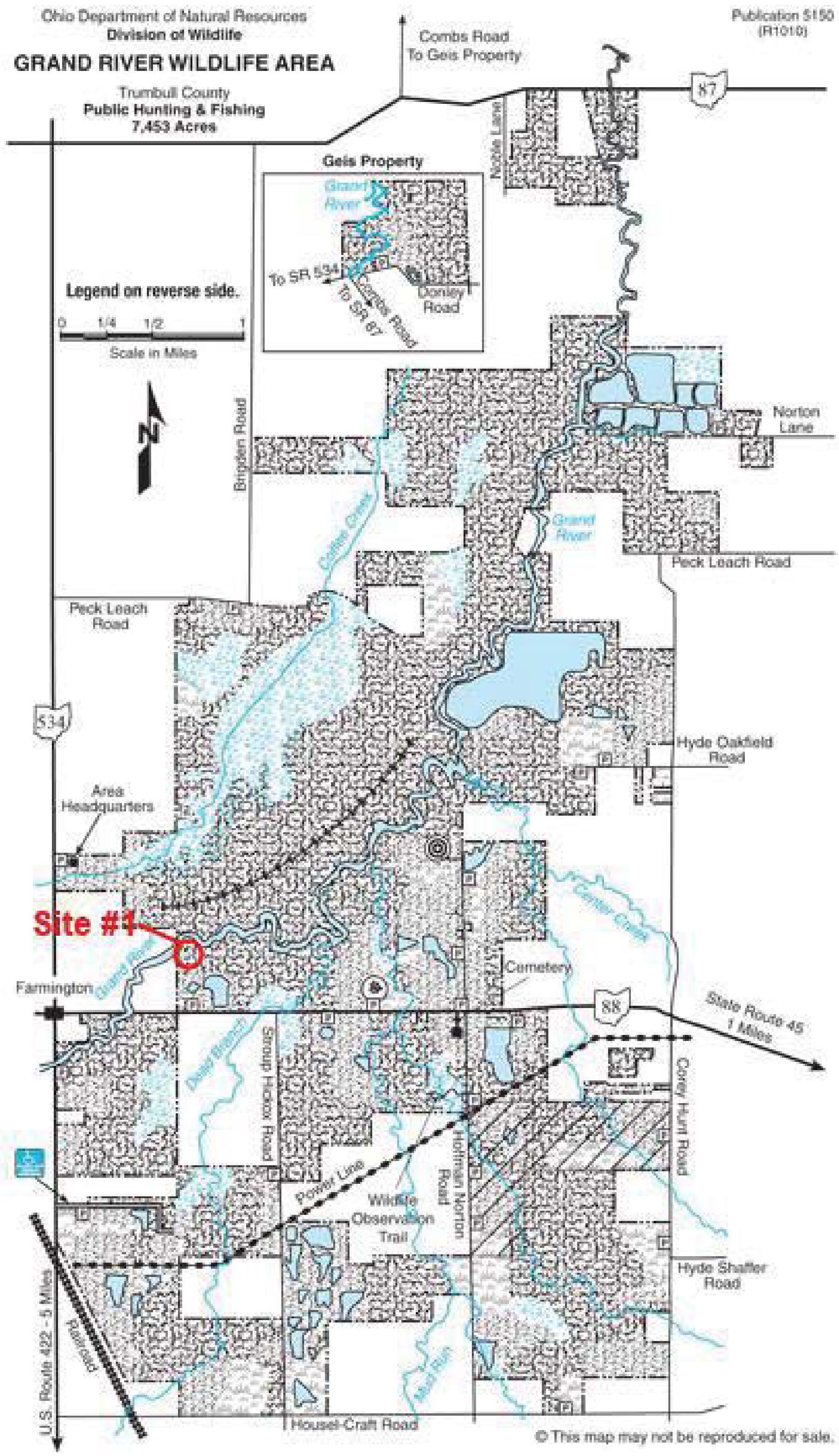


Figure 2: Details of Site #1 Grand River, Grand River Wildlife Area Trumbull County.

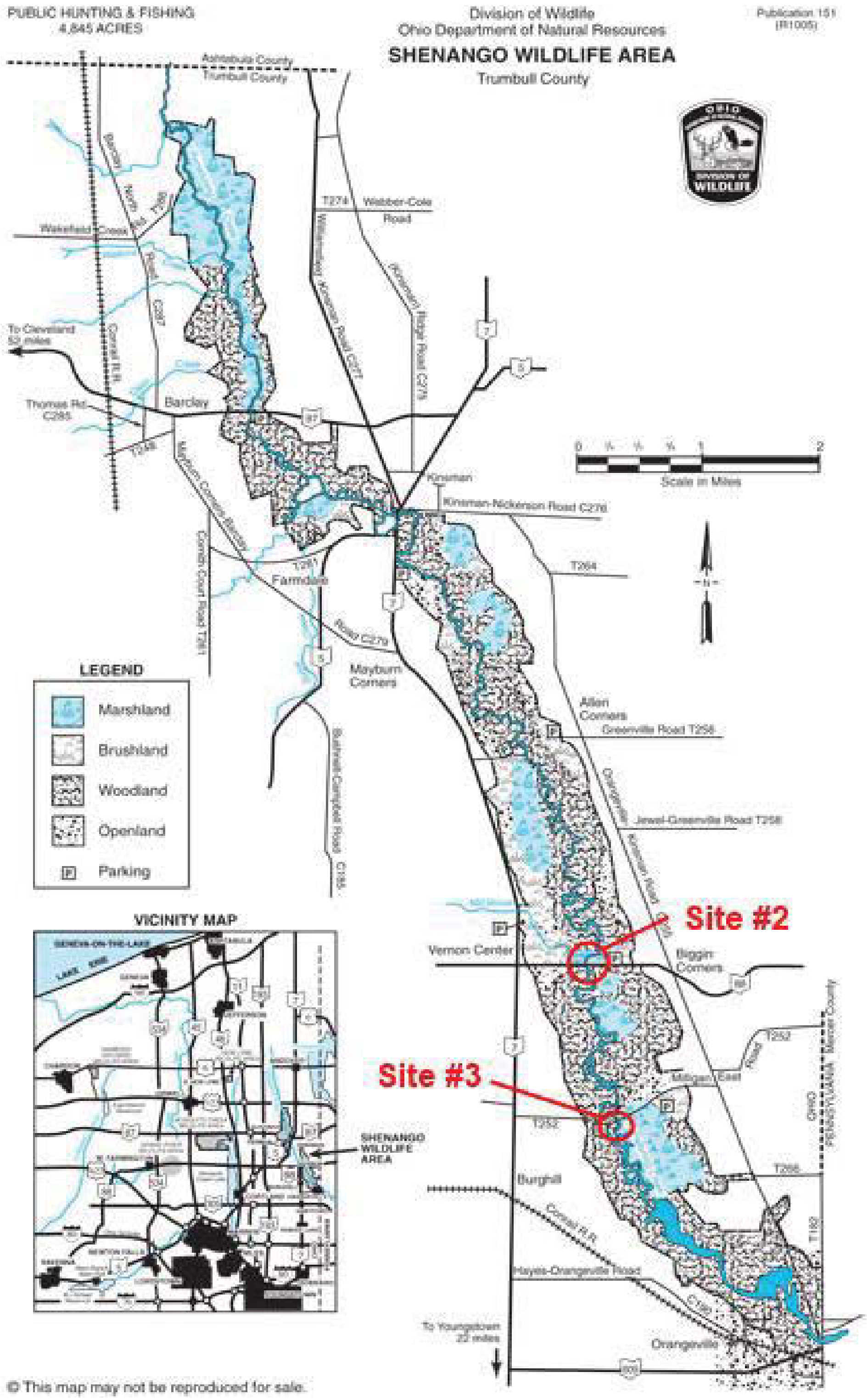


Figure 3: Details of Sites #2 and #3 Pymatuning Creek, Shenango Wildlife Area Trumbull County.

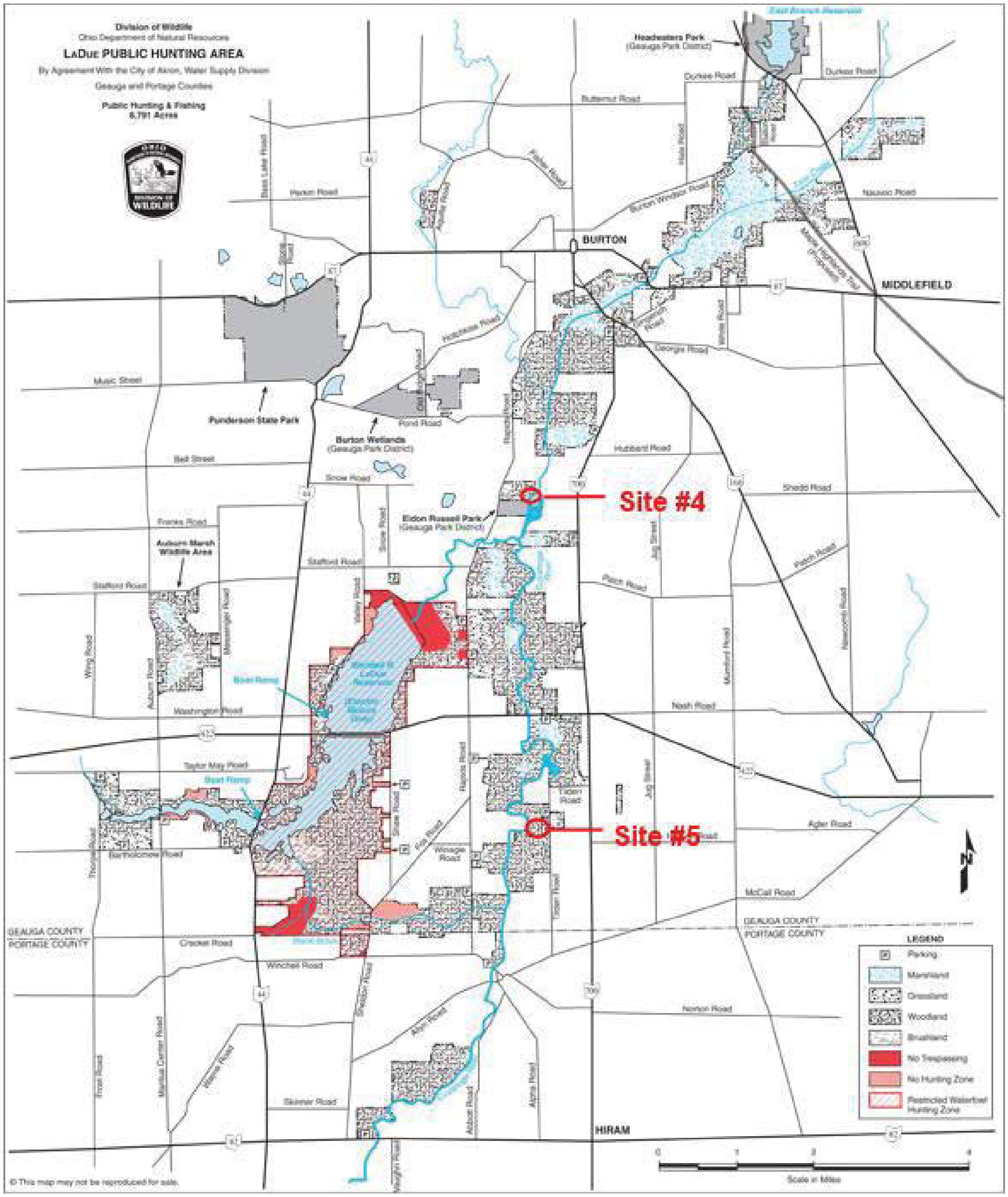


Figure 4: Details of Sites #4 and #5 Cuyahoga River, La Due Public Hunting Area Geauga County.

Canopy Composition Survey

In autumn/winter 2012 three 12 x 20m forest overstory survey quadrats were established in Sites # 1, 2, 4, and 5. Five quadrats were established in Site #3 to adequately survey this site given its larger area. The quadrats were distributed in a stratified random fashion in the riparian zones, which included active floodplains, floodplains, lower terraces, and alongside intermittent stream channels depending on the sites' landforms. Additional surveying was scheduled for spring/ summer 2013 in order to compare browsing preferences at the temporal scale. However sampling was hindered due to flooding and persistent inundation at Sites #3, 4, and 5. The canopy species composition was surveyed for each quadrat. For individual trees that had available browse, foliage within the browsing range, for white-tailed deer the following were recorded: species, total available browse (measured in browse units see Fig. 5), type of available browse (low branches or epicormic sprouts), severity of browsing (none, very light, light, moderate, heavy, and severe, as defined in Table 2), and if the tree had sustained beaver damage.

Shrub and Sapling Survey

The shrub and sapling (not included in canopy) layer was surveyed within two randomly placed 4x4 nested plots per 12x20 quadrat. In each 4x4 plot the following were recorded: species, height, severity of browsing, and if the shrub or sapling had sustained beaver damage.

Figure 5: Browse Unit. The browse unit is the unit of measurement for available browse. The browse unit is a rectangle of approximately 10 x 10 x 30.5 cm of browseable material, i.e. epicormic sprouts and branch tips.

Table 2: Browsing Note and Corresponding Numerical Category and Percentages.

Browsing Note	Numerical Category	Percentage of Available Branch Tips/ Epicormic Sprouts Browsed
None	0	0%
Very Light	1	0-10%
Light	2	10-30%
Moderate	3	30-60%
Heavy	4	60-90%
Severe	5	90-100%

"None" has no browsing on all foliage within the browse unit. "Very light" has light browsing on very little foliage within the browse unit. "Light" has light browsing on little foliage within the browse unit. "Moderate" has browsing on approximately half of the foliage within the browse unit. "Heavy" has heavy browsing on most foliage within the browse unit. "Severe" has heavy browsing on approximately all foliage within the browse unit.

Data Analysis

Floristic Composition

Non-metric Multidimensional Scaling (NMDS) Ordination was used to analyze the floristic composition of each quadrat. A separate NMDS Ordination Plot was computed for the total flora, the canopy layer flora, and the shrub layer flora. The shrub layer flora included all shrub and seedlings as well as flood and/or beaver damaged epicormic sprout producing trees. Spearman Rank Correlation was used to determine the relationship between the abundance of tree and shrub species and the floristic composition for the canopy layer and shrub layer flora. A separate Spearman Rank Correlation was not calculated for the total flora given the similarity to the canopy layer flora.

Browsing Preference for Tree and Shrub Species: Median Browse

The median deer browsing impact on each tree and shrub species was determined within quadrats with the following formula:

$M_{ij} = \sum(C_{ij} \times B_{ij}) / n$	
M_{ij}	Median browse of species i in quadrat j
C_{ij}	Total available vegetation for species i in quadrat j, measured in browsing units
B_{ij}	Severity of browsing of species i in quadrat j, designated by browsing note
n	Number of individual members of species i in quadrat j

In cases of Median Browsing that did not result in whole integers, both the greater and lesser Browsing Notes were used, i.e. A Median Browsing of 2.5 would have a corresponding Browsing Note of Light/Moderate.

Table 3: Median Browse and Corresponding Browsing Note.

Median Browse Numerical Category	Browsing Note
0	None
1	Very Light
2	Light
3	Moderate
4	Heavy
5	Severe

Browsing Preference for Tree and Shrub Species: Jacob's Electivity Index

The Jacob's Electivity Index, as described in Boulanger et al. (2009), was used to measure white-tailed deer browsing preferences for tree and shrub species. Electivity indexes are used when the amount of available food items are not equal for each forage or prey species. The index determines whether a food item is selected, avoided, or neutral by using the proportion of the food item consumed to total amount of all items consumed, and the proportion of the amount of the food item available to the total amount of all available food.

Step 1: Determine the total available vegetation for species i in quadrat j.

$A_{ij} = C_{ij} / \sum C_{ij}$	
A_{ij}	Proportion of species i in the total available vegetation of quadrat j
C_{ij}	Total available vegetation for species i in quadrat j, measured in browsing units

Step 2: Determine the contribution of species i to the total browsing in quadrat j.

$RC_{ij} = (C_{ij} \times B_{ij}) / \sum (C_{ij} \times B_{ij})$	
RC_{ij}	Contribution of species i to the total browsing in quadrat j
C_{ij}	Total available vegetation for species i in quadrat j
B_{ij}	Severity of browsing of species i in quadrat j, designated by browsing note

Step 3: Calculate electivity of species i in quadrat j with Jacob's Electivity Index.

$S_{ij} = (RC_{ij} - A_{ij}) / [RC_{ij} + A_{ij} - 2(RC_{ij} \times A_{ij})]$	
S_{ij}	Electivity of species i in quadrat j

Step 4: Calculate the standard error of electivity.

$SE = s/\sqrt{(n)}$	
SE	Standard Error
s	Sample standard deviation
n	Sample size

Step 5: Determine if species i in quadrat j is selected, avoided, or neutral. Electivity ranges from -1 to +1.

Selected	$S_{ij} > 0$	lower limit of standard error interval is above 0
Avoided	$S_{ij} < 0$	upper limit of standard error interval is below 0
Neutral		standard error interval intercepts 0

The total browse for each quadrat was calculated with the following formula:

$TB_j = [\sum(C_{i1j} \times B_{i1j})] + [\sum(C_{i2j} \times B_{i2j})] + [\sum(C_{i3j} \times B_{i3j})] + \ldots [\sum(C_{inj} \times B_{inj})]$	
TB_j	Total browse in quadrat j
C_{ij}	Total available vegetation for species i in quadrat j, measured in browsing units
B_{ij}	Severity of browsing of species i in quadrat j, designated by browsing note

The total browse for each species of each quadrat was calculated with the following formula:

$TB_{ij} = \sum(C_{ij} \times B_{ij})$	
TB_{ij}	Total browse for species i in quadrat j
C_{ij}	Total available vegetation for species i in quadrat j, measured in browsing units
B_{ij}	Severity of browsing of species i in quadrat j, designated by browsing note

The available browse for each species of each quadrat was calculated with the following formula:

$AB_{ij} = \sum C_{ij}$	
AB_{ij}	Available browse for species i in quadrat j
C_{ij}	Total available vegetation for species i in quadrat j, measured in browsing units

Results

Canopy Layer Floristic Composition

Canopy layer floristic composition varied among sites and quadrats (see Table 4). Grand River quadrats #1 and #2 both contained a high density of *Acer saccharum* (sugar maple) with 790 and 1040 trees per ha respectively. Quadrat #3 did not contain *A. saccharum*, but the quadrat had a higher range of diversity with *Carpinus caroliniana* (American hornbeam), *Ulmus americana* (American elm), *Prunus serotina* (black cherry), and *Crategus spp*. (Hawthorn spp.).

All three La Due North quadrats contained *Acer saccharinum* (silver maple) with 460, 330, and 170 trees per ha respectively. The quadrats differed with quadrat #2 and #3 containing *U. americana*. Quadrat #1 was the only quadrat at the site with *Fraxinus pennsyvania* (swamp ash). Quadrat #2 was the only quadrat at the site with *Salix nigra* (black willow). And Quadrat #3 was the only quadrat at the site with *Crategus spp*.

All three La Due South quadrats solely contained *A. saccharinum* with 330, 210, and 80 trees per ha respectively.

All three Shenango North quadrats solely contained *A. saccharinum* with 80, 40, and 80 trees per ha respectively.

All five of the Shenango South quadrats contained *A. saccharinum* with 80, 40, 40, 170, and 80 trees per ha respectively. Quadrat #1 and #2 both contained *Carya ovata* (shagbark hickory). Quadrat #1 was the only quadrat with *Tilia americana* (American basswood). Quadrat #2 was the only quadrat at the site with *Carya cordiformis* (bitternut hickory). Lastly quadrat #3 was the only quadrat at the site with *Fraxinus nigra* (black ash).

Table 4: Canopy Layer Floristic Composition. Tree density per ha. Empty blocks denote zero.

Site	Quadrat	*Ulmus americana*	*Tilia americana*	*Fraxinus nigra*	*Prunus serotina*	*Salix nigra*	*Carya cordiformis*
Grand River	1						
	2						40
	3	290			40		
La Due North	1						
	2	40				40	
	3	40					
La Due South	1						
	2						
	3						
Shenango North	1						
	2						
	3						
Shenango South	1		40				
	2						80
	3			40			
	4						
	5						

Figure 4: Canopy Layer Florisitic Composition cont. Tree density per ha. Empty blocks denote zero.

Site	Quadrat	*Crategus* spp.	*Carpinus caroliniana*	*Carya ovata*	*Acer saccharinum*	*Acer saccharum*	*Fraxinus pennsylvania*
Grand River	1	40				790	
	2					1040	
	3	80	40				
La Due North	1				460		130
	2				330		
	3	40			170		
La Due South	1				330		
	2				210		
	3				80		
Shenango North	1				80		
	2				40		
	3				80		
Shenango South	1			130	80		
	2	40		40	40		
	3				40		
	4				170		
	5				80		

Canopy Layer Floristic Composition: NMDS Ordination Plot

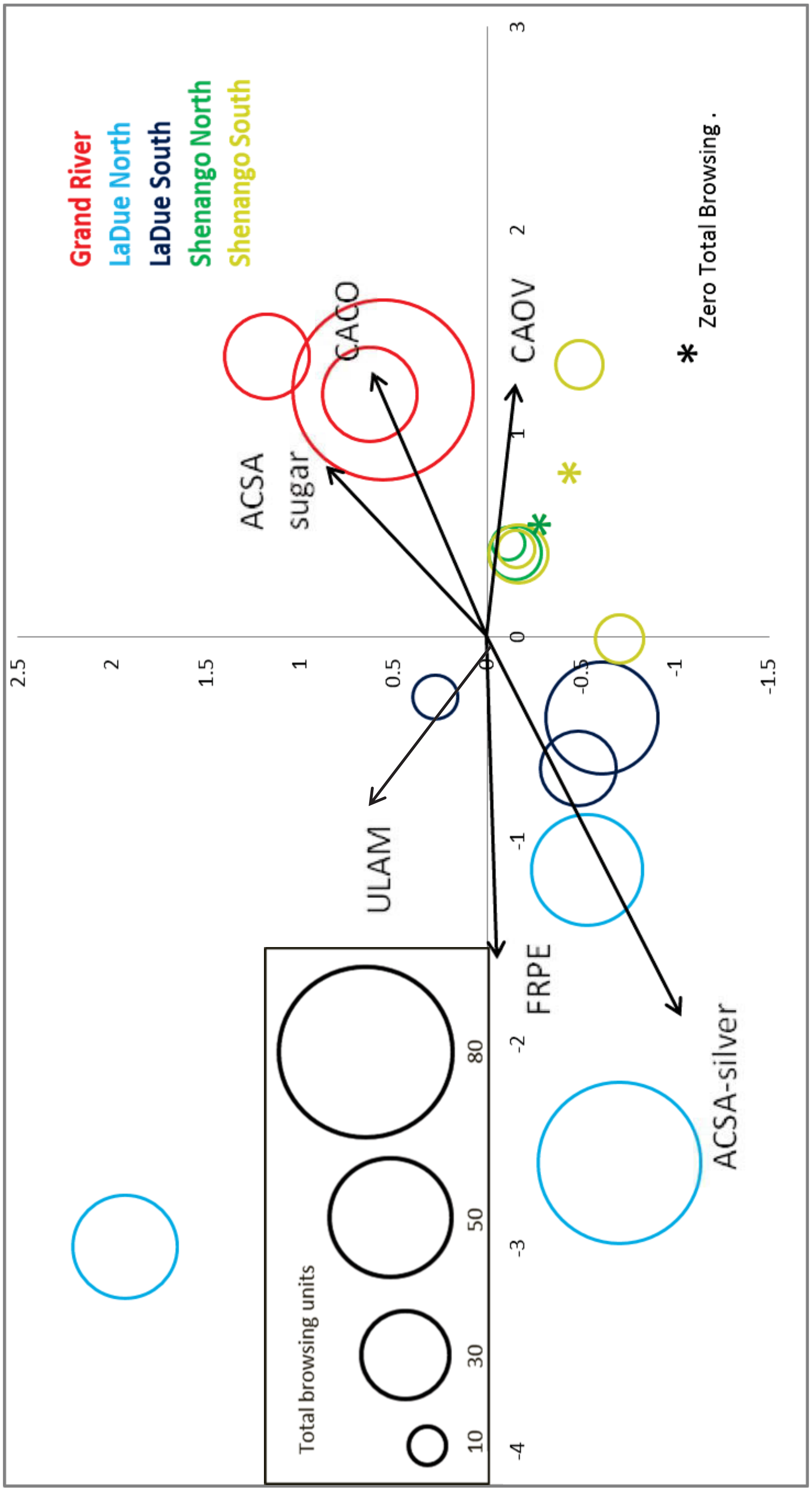
The three Grand River quadrats were clustered in (Figure 6), indicating similar canopy compositions. (NMDS Ordination Plots are unitless. However the distances between data points are proportional and represent the similarities/dissimilarities between the data points. The closer the data points are to each other, the greater the similarities. The farther the data points, the greater the dissimilarities.) The canopy composition was influenced by the abundance of *Acer saccharum* (sugar maple) and *Carya cordiformis* (bitternut hickory). (These species' abundances were strongly correlated with the NMDS axes. Strength of Spearman Rank correlation is represented by the length of the vector arrow.)

Two La Due North quadrats had somewhat similar canopy composition, being both located in the lower left quadrant of the ordination plot. The first quadrat of the pair was nearer to the origin suggesting a lesser influence of the abundance of *Fraxinus pennsylvania* (swamp ash) and *Acer saccharinum* (sliver maple) on the quadrat's canopy composition than the second quadrat. (Quadrats closer to the origin have a less distinct canopy composition. The further the quadrat is from the origin the more distinct the composition due to the abundance of specific species. Those species are determined by Spearman Rank Correlation.) The third quadrat differed from the other two, located in the upper left quadrant, and its canopy composition was influenced by the abundance of *Ulmus americana* (American elm).

Two La Due South quadrats were clustered closely together in the lower left quadrant near the origin suggesting similar canopy composition which was influenced somewhat by the abundance of *A. saccharinum* and *F. pennsylvania*. The third quadrat's, in the upper left quadrant near the origin, canopy composition was somewhat influenced by the abundance of *U. americana* and *F. pennsylvania*.

The three Shenango North quadrats and the five Shenango South quadrats were tightly clustered together near the origin, with two exceptions, suggesting markedly similar canopy composition that was not strongly influenced by a particular canopy species' abundance. Their canopy composition was minimally influenced by the abundance of *Carya ovata* (shagbark hickory), whereas the two separate quadrats' canopy compositions were more influenced by the abundance of *C. ovata*.

Figure 6: NMDS Ordination Plot: Canopy Floristic Composition with Spearman Rank Correlation. NMDS Ordination Plot axes represent the distribution of canopy trees in quadrats by stem count. Vector arrows represent Spearman Rank correlation coefficients of indicated tree species with dimension axes. The vector lengths were doubled for ease of reading. The diameter of plot circles corresponds to the total amount of browsing within the quadrat. Quadrats that had zero browsing units consumed are represented by an asterisk. Tree species are represented by their four letter designation: ACSA-silver *A. saccharinum*, ACSA-sugar *A. saccharum*, CACO *C. cordiformis*, CAOV *C. ovata*, FRPE *F. pennsylvania*, and ULAM *U. americana*.



Grand River
LaDue North
LaDue South
Shenango North
Shenango South
* Zero Total Browsing .
Total browsing units
10
30
50
80
ACSA sugar
CACO
CAOV
ULAM
FRPE
ACSA-silver
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-4
-3
-2
-1
0
1
2
3

Shrub and Sapling Layer Floristic Composition

The Grand River site had the most diverse shrub and sapling layer of the sites (seen in Table 5). However the quadrats have the most similar composition. All three quadrats contained *Cornus alternifolia* (alternate-leafed dogwood), *Fraxinus americana* (white ash), *Lindera benzoin* (spicebush), and *P. serotina*. Quadrat #1 was the only quadrat at the site with *C.ovata.* Quadrat #2 was the only quadrat at the site with *A. saccharum* and *Quercus bicolor* (swamp white oak).

All three quadrats at the La Due North site did not share a shrub/sapling species in common. Quadrats #1 and #2 both contained *Cephalanthus occidentali* (buttonbush) and *A. saccharinum*. Quadrat #1 was the only quadrat at the site with *U. americana* and *F. pennsylvania.* Quadrat #3 was the only quadrat at the site with *Crategus* spp.

All three quadrats at the La Due South site contained *F. pennsylvania* and *Quercus palustris* (pin oak). Quadrat #1 was the only quadrat at the site with *A. saccharinum* and *Vitis* spp (Grape spp.). Quadrat #3 was the only quadrat at the site with *L.benzoin, Rosa multiflora* (multiflora rose), and *U. americana*.

All three quadrats at the Shenango North site contained *C. ovata* and *L. benzoin*. Quadrats #1 and #2 both contained *Viburnum acerfolium* (maple-leafed viburnum). Quadrat #3 was the only quadrat at the site with *Crategus* spp. and *R. multiflora*.

All three quadrats at the Shenango South site did not share a species in common. Quadrats #2 through #5 all contained *Q. palustris*. Quadrats #1 and #3 both contained *A. saccharinum*. Quadrats #3 and #5 both contained *C. ovata*. Lastly quadrats #4 and #5 both contained *C. occidentali* and *U. americana*.

Table 5: Shrub and Sapling Layer Floristic Composition. Shrub and Sapling density per ha. Empty blocks denote zero.

Site	Quadrat	*Cornus alternifolia*	*Ulmus americana*	*Prunus serotina*	*Carya cordiformis*	*Cephalanthus occidentali*	*Crategus* spp.	*Carpinus caroliniana*
Grand River	1	940	1250	310			1250	4060
	2	310		310	2810			310
	3	310	310	940	1250		630	
La Due North	1		630			4690		
	2					310		
	3						310	
La Due South	1							
	2							
	3		310					
Shenango North	1							
	2							
	3						310	
Shenango South	1							
	2				630			
	3							
	4		630			630		
	5		310			3130		

Table 5: Shrub and Sapling Layer Floristic Composition cont. Shrub and Sapling density per ha. Empty blocks denote zero.

Site	Quadrat	*Viburnum acerfolium*	*Rosa multiflora*	*Quercus rubra*	*Quercus palustris*	*Carya ovata*	*Acer saccharinum*
Grand River	1			3440		2500	
	2			630			
	3						
La Due North	1						630
	2						310
	3						
La Due South	1				630		4380
	2				9380		
	3		940		310		
Shenango North	1	3440				630	
	2	310				8130	
	3		310			310	
Shenango South	1					2190	
	2				3750		310
	3				310	1560	
	4				3440		2500
	5				630	630	

Table 5: Shrub and Sapling Layer Floristic Composition cont. Shrub and Sapling density per ha. Empty blocks denote zero.

Site	Quadrat	*Lindera benzoin*	*Acer saccharum*	*Fraxinus pennsylvania*	*Quercus bicolor*	*Vitis* spp.	*Fraxinus americana*
Grand River	1	940					1250
	2	940	3750		310		630
	3	1560					310
La Due North	1			3440			
	2						
	3						
La Due South	1			5630	940	310	
	2			9060			
	3	3440		4690			
Shenango North	1	7500					
	2	4060					
	3	8750					
Shenango South	1						
	2						
	3						
	4						
	5						

Shrub and Sapling Layer Floristic Composition: **NMDS Ordination Plot**

Two Grand River quadrats (in Figure 7 and 8) were loosely clustered together in the lower right quadrant and had somewhat similar shrub and sapling layer composition that was strongly influenced by the abundance of *Carpinus caroliniana* (American hornbeam)*, Cornus alternifolia* (alternate-leafed dogwood)*, F. americana, A. saccharum, A. saccharum* (sapling), and less so by the abundance of *Quercus palustris* (pin oak) and *Crategus* spp (Hawthorn spp.). The third quadrat was close to the origin, which suggests that, its shrub and sapling layer composition was not influenced by a particular species' abundance.

Two La Due North quadrats were closely clustered on the origin, which suggests that they had similar shrub and sapling layer composition and that it was not influenced by any particular species' abundance. The third quadrat was near the origin in the left side of the ordination plot; however its shrub layer composition was somewhat influenced by the abundance of *Cephalanthus occidentali* (buttonbush).

The three La Due South quadrats were not clustered, which suggests that they had differing shrub and sapling layer composition. The quadrat in the left side of the ordination plot was closest to the origin and its shrub and sapling layer composition was marginally influenced by the abundance of *C. occidentali, F. pennsylvania, Quercus bicolor* (swamp white oak)*, A. saccharinum*, and *A. saccharinum* (sapling). The second quadrat, in the lower left quadrant, was further away from the origin and its shrub and sapling layer composition was influenced by the abundance of *F. pennsylvania, A. saccharinum*, and *A. saccharinum* (sapling). The third quadrat in the lower left quadrant was the furthest away from the origin and its shrub and sapling layer composition was also influenced by the abundance of *F. pennsylvania, A. saccharinum*, and *A. saccharinum* (sapling).

The three Shenango North quadrats were loosely clustered which suggests that their shrub and sapling layer composition was somewhat similar and it was influenced by the abundance of *Viburnum acerfolium* (maple-leafed viburnum)*, Quercus rubra* (Northern red oak)*, C. ovata*, and *Lindera benzoin* (spicebush).

The three Shenango South quadrats were clustered near the origin, which suggests similar canopy floristic composition that was not strongly influenced by any particular species' abundance. The fourth quadrat in the upper left quadrant was near the origin, but its shrub and sapling layer composition was marginally influenced by the abundance of *C. occidentali*. The last quadrat in the lower left quadrant was the furthest away from the origin and its shrub and sapling layer composition was influenced by the abundance of *F. pennsylvania* and *A. saccharinum*.

Figure 7: NMDS Ordination Plot: Shrub and Sapling Layer Floristic Composition with Spearman Rank Correlation. Tree and shrub species are represented by their four letter designation when available: BUTTON *C. occidentali*, CACA *C. caroliniana*, CORNUS *C. alternifolia*, CRAT *Crategus* spp., SPICE *L. benzoin*.

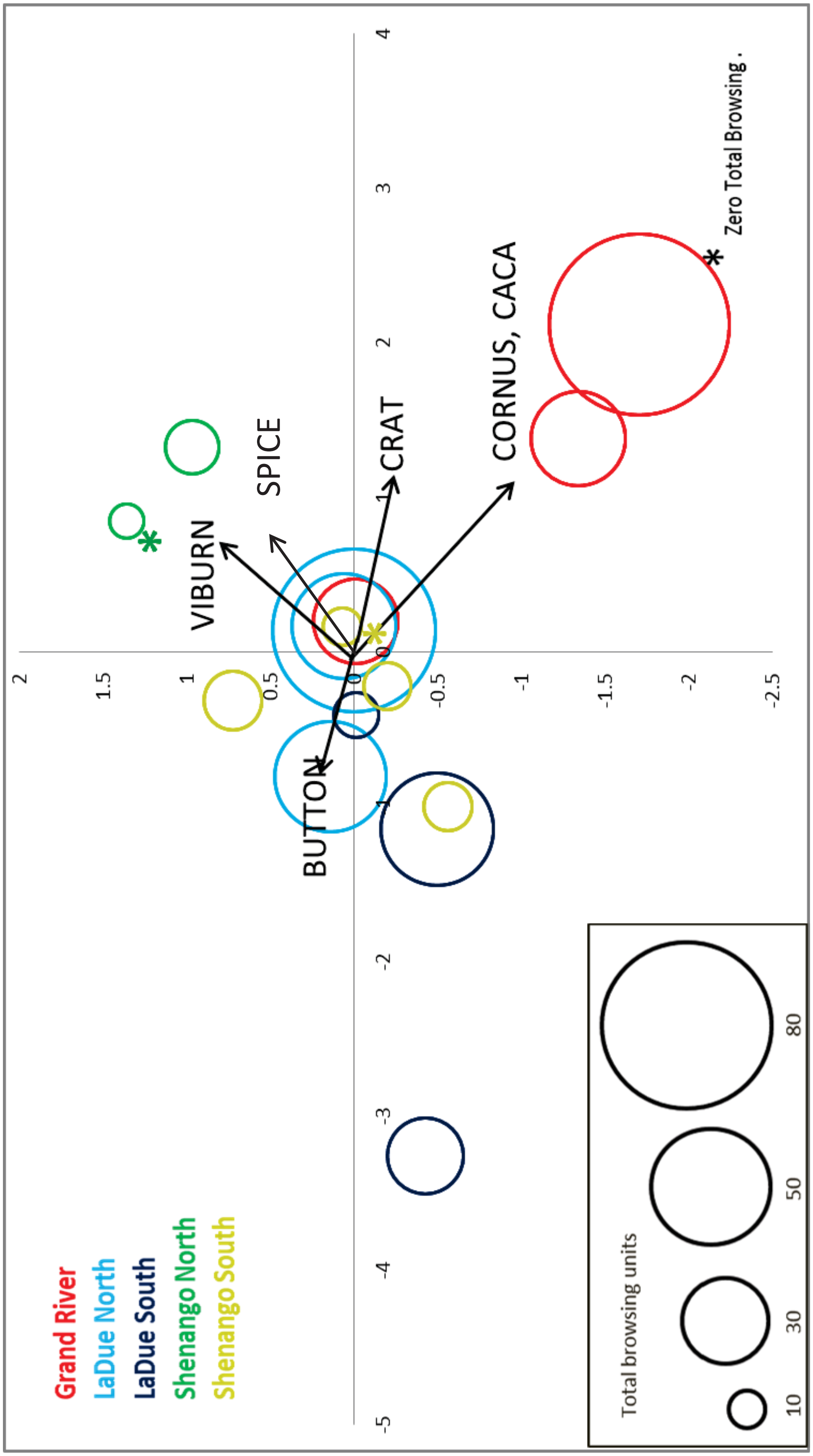
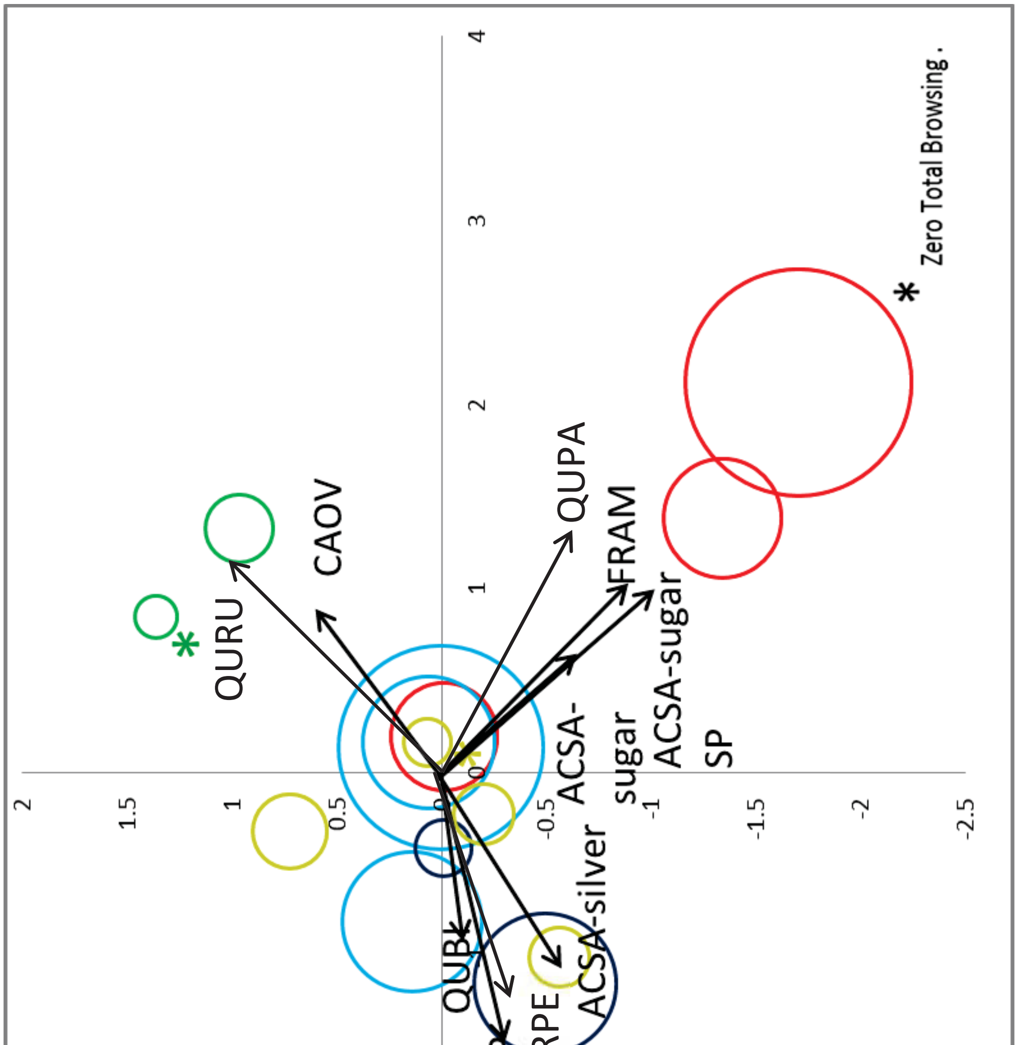

Grand River
LaDue North
LaDue South
Shenango North
Shenango South
VIBURN
SPICE
CRAT
CORNUS, CACA
BUTTON
Zero Total Browsing .
Total browsing units
10
30
50
80

Figure 8: NMDS Ordination Plot: Shrub and Sapling Layer Floristic Composition with Spearman Rank Correlation. Tree and shrub species are represented by their four letter designation when available: ACSA-silver *A. saccharinum*, ACSA-silver SP *A. saccharinum* sapling, ACSA-sugar *A. saccharum*, ACSA-sugar SP *A. saccharum* sapling, CAOV *C. ovata*, FRAM *F. americana*, FRPE *F. pennsylvania,* QUBI *Q. bicolor*, QUPA *Q. palustris*, and QURU *Q. rubra*.


Grand River
LaDue North
LaDue South
Shenango North
Shenango South
Total browsing units
10
30
50
80
Zero Total Browsing .
QURU
CAOV
QUPA
FRAM
ACSA-sugar
ACSA-sugar SP
ACSA-silver
ACSA-silver SP
FRPE
-5
-4
-3
-2
1
2
3
4
2
1.5
1
0.5
-0.5
-1
-1.5
-2
-2.5

Median Browsing for Canopy Layer Flora

In Table 6, the following species received no browsing in all quadrats present: *T. americana, F. nigra, C. cordiformis, C. ovata,* and *F. pennsylvania*. *P. serotina* received very light browsing in (Grand River #3). *C. caroliniana* received heavy browsing in (Grand River #3). *S. nigra* received severe browsing in (La Due North #2). *U. americana* received very light (Grand River #3) to no browsing (La Due North #2 and La Due North #3). *Crategus* spp. received light (Grand River #1 and Shenango South #2) and heavy browsing (La Due North #3). *A. saccharum* received moderate (Grand River #1) to no browsing (Grand River #2). *A. saccharinum* median browsing also varied widely within and among sites. *A. saccharinum* received no browsing in (Shenango North #1, Shenango South #1 , and Shenango South #2), very light in (Shenango North #3), light in (La Due North #1, La Due South #1 and, Shenango South #4), light/moderate in (La Due South #3 and Shenango South #3), moderate (La Due South #2), heavy in (La Due North #2 and Shenango South #5), heavy/severe in (La Due North #3), and severe in (Shenango North #2).

Electivity for Canopy Layer Flora

In Table 7, the following species were avoided in all quadrats present (*U. americana, T. americana, F. nigra, P. serotina, C. cordiformis, C. ovata, A. saccharum,* and *F. pennsylvania*). The species that were selected in all quadrats present are (*S. nigra* and *C. caroliniana*). *Crategus* spp. were avoided in (Grand River #1), however they were selected in (La Due North #3 and Shenango South #2). Electivity varied widely for *A. saccharinum* within and among sites. *A. saccharinum* was selected for in (La Due

North #1), neutral in (La Due North #2, La Due North #3, La Due South #1, La Due South #2, La Due South #3, Shenango North #2, Shenango North #3, Shenango South #3, Shenango South #4, and Shenango South #5), and avoided in (Shenango North #1, Shenango South #1, and Shenango South #2).

Table 6: Median Browsing for Canopy Layer Flora An empty block represents no available browse.

Site	Quadrat	*Ulmus americana*	*Tilia americana*	*Fraxinus nigra*	*Prunus serotina*	*Salix nigra*	*Carya cordiformis*
Grand River	1						
	2						
	3	very light			very light		
La Due North	1						
	2	none				severe	
	3	none					
La Due South	1						
	2						
	3						
Shenango North	1						
	2						
	3						
Shenango South	1		none				
	2						none
	3			none			
	4						
	5						

Table 6: Median Browsing for Canopy Layer Flora cont. An empty block represents no available browse.

Site	Quadrat	*Crategus* spp.	*Carpinus caroliniana*	*Carya ovata*	*Acer saccharinum*	*Acer saccharum*	*Fraxinus pennsylvania*
Grand River	1	light				moderate	
	2					none	
	3		heavy				
La Due North	1				light		none
	2				heavy		
	3	heavy			heavy/ severe		
La Due South	1				light		
	2				moderate		
	3				light/ moderate		
Shenango North	1				none		
	2				severe		
	3				very light		
Shenango South	1			none	none		
	2	light		none	none		
	3				light/ moderate		
	4				light		
	5				heavy		

Table 7: Electivity for Canopy Layer Flora. An empty block represents no available browse.

Site	Quadrat	*Ulmus americana*	*Tilia americana*	*Fraxinus nigra*	*Prunus serotina*	*Salix nigra*	*Carya cordiformis*
Grand River	1						
	2						
	3	avoided			avoided		
La Due North	1						
	2	avoided				selected	
	3	avoided					
La Due South	1						
	2						
	3						
Shenango North	1						
	2						
	3						
Shenango South	1		avoided				
	2						avoided
	3			avoided			
	4						
	5						

Table 7: Electivity for Canopy Layer Flora cont. An empty block represents no available browse.

Site	Quadrat	*Crategus* spp.	*Carpinus caroliniana*	*Carya ovata*	*Acer saccharinum*	*Acer saccharum*	*Fraxinus pennsylvania*
Grand River	1	avoided				avoided	
	2					avoided	
	3		selected				
La Due North	1				selected		avoided
	2				neutral		
	3	selected			neutral		
La Due South	1				neutral		
	2				neutral		
	3				neutral		
Shenango North	1				avoided		
	2				neutral		
	3				neutral		
Shenango South	1			avoided	avoided		
	2	selected		avoided	avoided		
	3				neutral		
	4				neutral		
	5				neutral		

Median Browsing for Shrub and Sapling Layer Flora

In Table 8, the species that received no browsing in all quadrats present are (*C. alternifolia, U. americana, P. serotina, C. cordiformis, C. occidentali, Crategus spp., C. caroliniana, R. multiflora, Q. rubra, Q. palustris, C. ovata, L. benzoin, A. saccharum, F. pennsylvania, Q. bicolor, Vitis spp.,* and *F. americana*). *V. acerfolium* received no browsing in (Shenango North #1) and light in (Shenango North #2). *A. saccharinum* received no browsing in (La Due South #1, Shenango South #2, and Shenango South #4), very light in (La Due North #1), and moderate in (La Due North #2).

Electivity for Shrub and Sapling Layer Flora

In Table 9, the species that were avoided in all quadrats present are (*C. alternifolia, U. americana, P. serotina, C. cordiformis, C. occidentali, C. caroliniana, R. multiflora, Q. rubra, Q. palustris, C. ovata, L. benzoin, A. saccharum, F. pennsylvania, Q. bicolor, Vitis spp.,* and *F. americana*). *Crategus* spp. were avoided in (Grand River #1, Grand River #3, and Shenango North #3), and neutral in (La Due North #3). *V. acerfolium* was avoided in (Shenango North #1) and selected in (Shenango North #2). *A. saccharinum* was avoided in (La Due South #1, Shenango South #2, and Shenango South #4), neutral in (La Due North #1), and selected in (La Due North #2).

Table 8: Median Browsing for Shrub and Sapling Layer Flora. An empty block represents no available browse.

Site	Quadrat	*Cornus alternifolia*	*Ulmus americana*	*Prunus serotina*	*Carya cordiformis*	*Cephalanthus occidentali*	*Crategus* spp.	*Carpinus caroliniana*
Grand River	1	none	none	none			none	none
	2	none		none	none			none
	3	none	none	none	none		none	
La Due North	1		none			none		
	2					none		
	3						none	
La Due South	1							
	2							
	3		none					
Shenango North	1							
	2							
	3						none	
Shenango South	1							
	2				none			
	3							
	4		none			none		
	5		none			none		

Table 8: Median Browsing for Shrub and Sapling Layer Flora cont. An empty block represents no available browse.

Site	Quadrat	*Viburnum acerfolium*	*Rosa multiflora*	*Quercus rubra*	*Quercus palustris*	*Carya ovata*	*Acer saccharinum*
Grand River	1			none		none	
	2			none			
	3						
La Due North	1						very light
	2						moderate
	3						
La Due South	1				none		none
	2				none		
	3		none		none		
Shenango North	1	none				none	
	2	light				none	
	3		none			none	
Shenango South	1					none	
	2				none		none
	3				none	none	
	4				none		none
	5				none	none	

Table 8: Median Browsing for Shrub and Sapling Layer Flora cont. An empty block represents no available browse.

Site	Quadrat	*Lindera benzoin*	*Acer saccharum*	*Fraxinus pennsylvania*	*Quercus bicolor*	*Vitis* spp.	*Fraxinus americana*
Grand River	1	none					none
	2	none	none		none		none
	3	none					none
La Due North	1			none			
	2						
	3						
La Due South	1			none	none	none	
	2			none			
	3	none		none			
Shenango North	1	none					
	2	none					
	3	none					
Shenango South	1						
	2						
	3						
	4						
	5						

Table 9: Electivity for Shrub and Sapling Layer Flora. An empty block represents no available browse.

Site	Quadrat	*Cornus alternifolia*	*Ulmus americana*	*Prunus serotina*	*Carya cordiformis*	*Cephalanthus occidentali*	*Crategus* spp.	*Carpinus caroliniana*
Grand River	1	avoided	avoided	avoided			avoided	avoided
	2	avoided		avoided	avoided			avoided
	3	avoided	avoided	avoided	avoided		avoided	
La Due North	1		avoided			avoided		
	2					avoided		
	3						neutral	
La Due South	1							
	2							
	3		avoided					
Shenango North	1							
	2							
	3						avoided	
Shenango South	1							
	2				avoided			
	3							
	4		avoided			avoided		
	5		avoided			avoided		

Table 9: Electivity for Shrub and Sapling Layer Flora cont. An empty block represents no available browse.

Site	Quadrat	*Viburnum acerfolium*	*Rosa multiflora*	*Quercus rubra*	*Quercus palustris*	*Carya ovata*	*Acer saccharinum*
Grand River	1			avoided		avoided	
	2			avoided			
	3						
La Due North	1						neutral
	2						selected
	3						
La Due South	1				avoided		avoided
	2				avoided		
	3		avoided		avoided		
Shenango North	1	avoided				avoided	
	2	selected				avoided	
	3		avoided			avoided	
Shenango South	1					avoided	
	2				avoided		avoided
	3				avoided	avoided	
	4				avoided		avoided
	5				avoided	avoided	

Table 9: Electivity for Shrub and Sapling Layer Flora cont. An empty block represents no available browse.

Site	Quadrat	*Lindera benzoin*	*Acer saccharum*	*Fraxinus pennsylvania*	*Quercus bicolor*	*Vitis* spp.	*Fraxinus americana*
Grand River	1	avoided					avoided
	2	avoided	avoided		avoided		avoided
	3	avoided					avoided
La Due North	1			avoided			
	2						
	3						
La Due South	1			avoided	avoided	avoided	
	2			avoided			
	3	avoided		avoided			
Shenango North	1	avoided					
	2	avoided					
	3	avoided					
Shenango South	1						
	2						
	3						
	4						
	5						

Total Browse for Canopy Layer Flora

In Figure 9, the amount of browsing on canopy species' epicormic sprouts varied within and among sites. (Grand River #1) received the most browsing with 113 total browsing units consumed. (La Due North #2) was second with 92 total browsing units consumed. The quadrats that received between 20 and 50 total browsing units consumed are (Grand River #2, Grand River #3, La Due North #1, La Due North #3, and La Due South #1). The quadrats that received 20 or less total browsing units consumed are (La Due South #2, La Due South #3, Shenango North #1, Shenango North #2, Shenango North #3, Shenango South #1, Shenango South #2, Shenango South #3, Shenango South #4, and Shenango South #5). (Shenango North #1 and Shenango South #1) had no browsing consumed.

Total Browse for Shrub and Sapling Layer Flora

In Figure 10, the amount of browsing on shrub and saplings varied within and among sites. (Shenango North #1) received the most browsing with 24 total browsing units consumed. (Shenango North #2) was second with 7 total browsing units consumed. (La Due North #1, La Due North #2, and La Due North #3) received two or less total browsing units consumed. (Grand River #1, Grand River #2, Grand River #3, La Due South #1, La Due South #2, La Due South #3, Shenango North #3, Shenango South #1, Shenango South #2, Shenango South #3, Shenango South #4, and Shenango South #5) had no browsing units consumed.

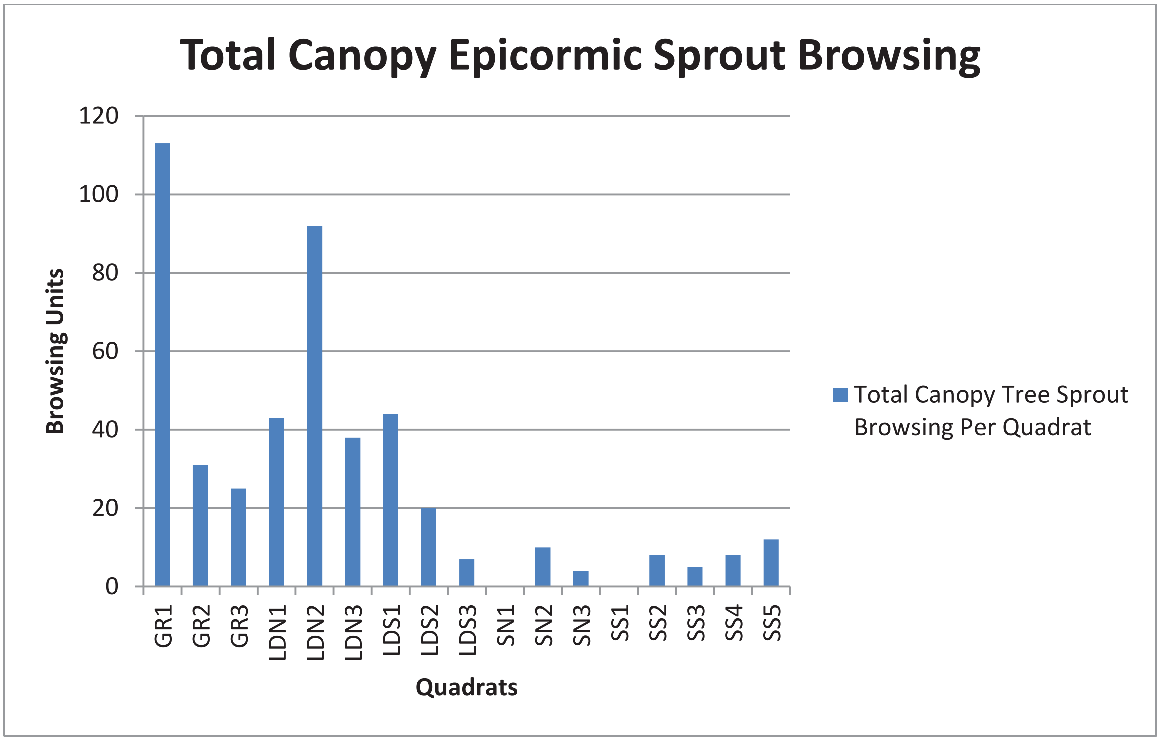


Figure 9: Total Canopy Epicormic Tree Sprout Browsing Per Quadrat

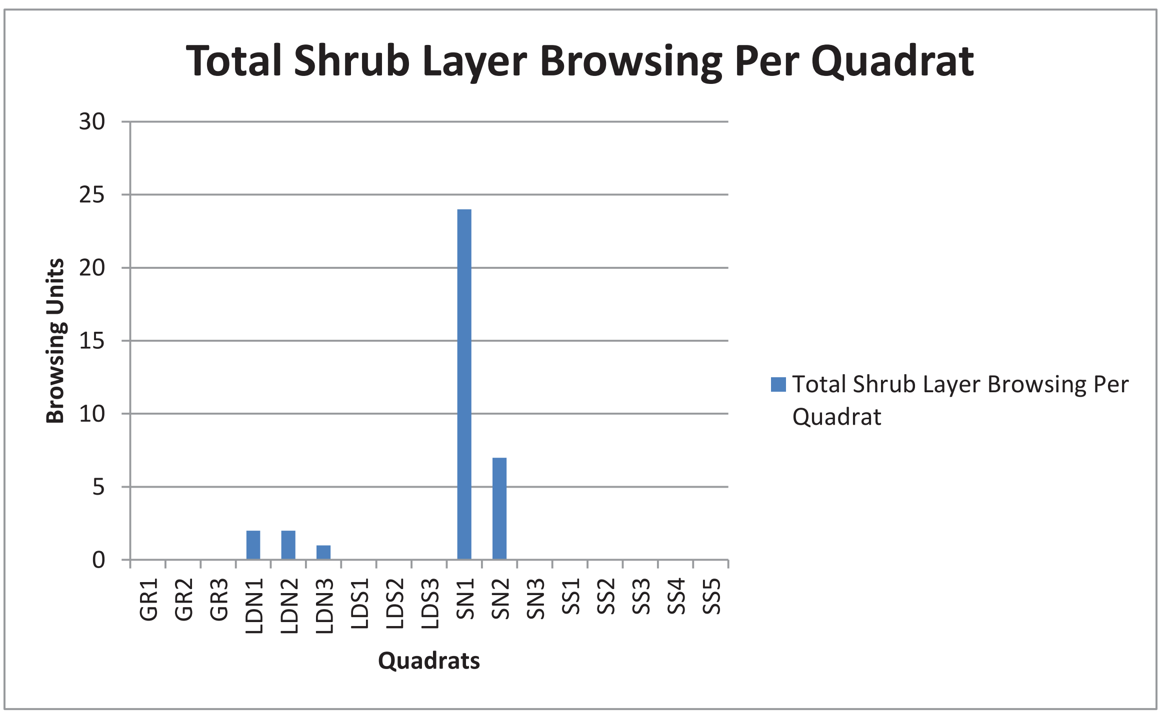


Figure 10: Total Shrub and Sapling Layer Browsing Per Quadrat

Discussion

Research on white-tailed deer herbivory since the late 1950s has primarily focused on economically important hardwood and evergreen species in mesic upland forests. Those studies consisted of man-made exclosures, natural exclusion, comparisons of plant community composition among sites with different deer densities, and comparisons of current species distribution versus historical abundance (Russell et al. 2001). Such studies were not possible in riparian zones given their heterogeneous nature, intermittent flooding, time constraints, and lack of historical plant community composition data. The challenge of the present study was to discover a method that would work to assess white-tailed deer browsing preferences in riparian zones. An Electivity Index was used to determine browsing preferences because the amount of available browse would not be equal for each species. The Jacob's Electivity Index, a modified Ivlev's Electivity Index, was chosen due to its low sensitivity to sampling errors and its ability to handle variations in abundances of species (Lechowitz 1982). Browsing notes and the corresponding percentages were borrowed from Boulanger et al. (2009), and ranked categories of available browse were determined in the field. The stratified random 12x20 m quadrats, for canopy layer survey, with 4x4 m nested plots, for shrub and sapling layer survey, were chosen due to their broad acceptance for surveying plant community composition in forests.

The Jacob's Electivity Index was sound in theory, but not in practice during this study. The woody plant community compositions at nearly all sites were not conducive to study with an electivity index. Four out of five sites faced intermittent to frequent flooding events, which may in the long term have led to naturally low woody species diversity, (i.e. Silver maple dominated floodplains with other species in low abundance if present). Additionally, not all had available browse within the range of white-tailed deer as they had crown branches only with little to no foliage at ground level. That combination of factors led to skewed species electivity. Several species' electivity could not be assessed due to low abundance; e.g. *S. nigra*. Alternatively, species with high abundance and corresponding high levels of available browse sometimes had neutral electivity due to lack of available browse from other species; e.g. *A. saccharinum*, which was often both the most abundant and heavily browsed. Electivity indices are based on the ratio of consumed browse to available browse. If a species comprises fifty percent of the available browse and also receives fifty percent of the browsing then that species' electivity is neutral it has received the amount of expected browsing. Whereas if a species comprises fifty percent of the available browse and receives eighty percent of the consumed browse, then it has received more than the expected amount of browsing, and therefore its electivity is positive for the surveyed area. Also, there must be more than one species with available browse within a quadrat to get accurate electivity.

Despite the issues that occurred with the Jacob's Electivity Index at some of the sites, there were species in the canopy as well as shrub and sapling layer that were found to be consistently avoided. The following species were avoided in all quadrats present: *C. cordiformis, C. ovata, C. occidentali, C. alternifolia, F. americana, F. nigra, F. pennsylvania, L. benzoin, P. serotina, Q. biocolor, Q. palustris, Q. rubra, R. multiflora, T. americana, U. americana,* and, Vitis *spp*. In contrast, *C. carolinina* and *S. nigra* were consistently selected at all quadrats present at the canopy level. However, due to low abundance of each species, i.e. fewer than five individuals of a species, these results might not be deemed conclusive and require further study.

Although the electivity for *A. saccharum* and *A. saccharinum* varied among quadrats, the trends indicate that white-tailed deer prefer epicormic sprouts of both species over the available browse of other species. Epicormic buds are dormant meristematic tissues that sprout as a result of stress (Meier 2012). Sprouting is common in both species from stumps with a diameter of 30 cm or less (Gabriel 1990, Godman et al. 1990). *A. saccharum* epicormic sprouts at the Grand River site seem to form as a result of stress from beaver damage, whereas *A. saccharinum* epicormic sprouts seem to form primarily as a result of stress from flood damage, (although also with some beaver damage at the Shenango sites).

Worth noting is that while the two different *Acer* species represent two different ecotypes (*A. saccharinum* predominantly hydric floodplain; *A. saccharum* mesic upland forests) and produce epicormic sprouts due to two different stressors, the epicormic sprouts of both species seem to be a preferred browse for white-tailed deer. One possibility to explain the attractiveness of epicormic sprouts is chemical defense, and thus palatability. According to Bryant and Raffa (1995) chemical defenses vary at the species and individual level, including their growth stage. Seedlings have a lower level of chemical defense than saplings due to a higher demand in seedlings for carbon for growth that reduces its availability for defense compounds (Bryant et al. 1991). However, seedlings and saplings have higher levels of chemical defenses than adults of the same species due to threat of damage by herbivory (Bryant et al. 1983). It is possible that *A. saccharum* and *A. saccharinum* epicormic sprouts are not as heavily chemically defended as seedlings and saplings from the same species within the browse range of white-tailed deer, because the sprouts are from adult trees. Epicormic sprouts may have a relatively low fitness value, except in cases of tree regeneration after the loss of the main stem. Therefore it is unlikely that resources would be spent on their chemical defense, and thus they may be generally more palatable to white-tailed deer. However, during this study the browsing severity on epicormic sprouts did appear to vary between species. *S. nigra* sprouts were severely browsed, *Acer* spp. and *Crategus* spp. sprouts were variably browsed among quadrats, and *U. americana* sprouts were not browsed at all. This suggests that further research is required comparing the chemical defense, nutritional value, and palatability of epicormic sprouts among different species, and between growth stages within species.

The important question to answer might not necessarily be white-tailed deer browsing preferences on a plant-by-plant basis, but how deer select patches within which to browse. The Marginal Value Theorem (MVT) states that an overall rate of energy intake is maximized if a herbivore leaves a patch once the rate of intake of browse is less than the average rate of intake across an entire habitat (Charnov 1976). Studies have shown that browsing behavior of a number of large ungulate species conforms to the MVT: e.g. elk (*Cerveus epalphus*) in Jaing and Hudson (1993), moose (Danell et al. 1991) and, moose and white-tailed deer in (Shipley and Spalinger 1995). Bailey et al. (1996) state that the application of the MVT depends heavily on the scale of the patch. Danell et al. (1991) stated that it was important to determine the scale of the patches, i.e. tree vs. stand, concluding that moose determine the quality of stands at the tree level. However, they suggest that individual plant selection occurs at multiple scales at the same time. Shipley and Spalinger (1995) confirmed that moose and white-tailed deer evaluate the quality of a patch and modify browsing behavior at small spatial scales (i.e. tree level).

Trends in the present study suggest that white-tailed deer may select patches in riparian zones based in part off the amount of *A. saccharum* and *A. saccharinum* epicormic sprouts available as browse. For example, Figure 6 suggests that quadrats with canopy compositions that are strongly influenced by the abundance of *A. saccharum* or *A. saccharinum*, both of which provided abundant sprouts, had an overall higher total browsing units consumed. Therefore, white-tailed deer may be selecting and browsing longer in patches that have an abundance of *Acer* spp. epicormic sprouts.

The results of the present study also suggest that *A. saccharum* and *A. saccharinum* epicormic sprouts may be preferred browse of white-tailed deer and are thus used in patch selection. Further research is needed to assess at what scale white-tailed deer choose patches, and the factors that affect patch selection. Additional research is also needed to study the impact on the regeneration of beaver damaged as well as flood damaged members of *A. saccharum* and *A. saccharinum* in Northeastern riparian zone communities due to the integral part that epicormic sprouts play in the regeneration of those species.

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