

# **VEGETATIONAL PATTERN WITHIN AN ABANDONED HAY-FIELD ADJACENT TO OLD-GROWTH AT GRIFFITH WOODS, HARRISON COUNTY, KENTUCKY**

[In the following two parts; Part II is in a separate file]

## **I. SPATIAL PATTERN IN RELATION TO APPARENT EFFECTS OF HERBIVORY**

## **II: COMPOSITIONAL GRADIENTS IN RELATION TO DISTANCE FROM ROAD (WITH PROBABLE POLLUTION) AND APPARENT EFFECTS OF HERBIVORY**

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**Preface for current drafts (Jan 2016).** I have updated Part I (from 2014-15) and now completed Part II in a separate file. My goal for these materials is to publish a succinct summary in a standard scientific journal, and to develop further plans for research at this site. Their current format resembles a thesis or dissertation, with too much detail for regular publication in a standard journal. It is first important for interested people to communicate more and develop cooperative goals, ideally across the central Bluegrass region.

**EXECUTIVE SUMMARY [for Parts I and II].** Before Virginian settlement, the central Bluegrass region of Kentucky was largely covered by unusual mixed woodland (maples, hickories, elms, walnuts, ashes, oaks, etc.) with much apparent influence from herbivores, which concentrated here at least seasonally due to high nutrient content in the soil and “dense herbage” (cane, peavine, wild ryes, buffalo clovers, etc.). Griffith Woods, in Harrison County, offers our best opportunity for restoration of something like the original woodland. However, a serious long-term effort here and across the region will require more fundamental cooperation among interested people. Within the 20 acre “Collection Field” at Griffith Woods, adjacent to the northern block of ancient trees, I established an initial set of plantings for selected native plants during 2003-2007, and conducted an initial survey of the vegetation. Reports below provide some details of this research. There has been virtually no previous published research in eastern North America that explores spatial effects of herbivory at such small scales. Moreover, there has been virtually no extended work on old field vegetation in Kentucky, despite much general ecological theory having been developed from old fields in other states (KS, MN, WI, NJ, NC). A pronounced feature of the Collection Field is that herbivory does appear to be a major factor controlling the spatial pattern of succession to woody plants, perhaps more so than in typical old fields studied elsewhere. But a surprising added feature is the apparent effect of pollution from the adjacent road (US 62). It is important to continue research on variation in soil chemistry, especially potential relationships with nitrogen, and to explore general application of Vera’s Hypothesis (2000) here in North America. This research also reveals interesting patterns in toxic plants versus spiny plants, and it should be extended into other fields at Griffith Woods, including areas with abundant poison hemlock—an invasive nitrophilous alien that may be reduced by planting competitive native plants like cane (*Arundinaria*). Interdisciplinary work of this type is critical to understanding how restoration should proceed from old fields to woodlands on eutrophic sites in this region and elsewhere.

## PART I: ABSTRACT

Herbivory's potential role in shaping spatial patterns of woodlands across eastern North America remains an elusive topic in ecological research. Yet there has been virtually no attempt to map out the local patterns in herbaceous vegetation or woody populations at sites with intensive effects by deer or other herbivores. This study explores such pattern in northern Kentucky, at a rectangular 20 acre [8 ha] hay-field last cropped during 2003, between a busy two-lane highway and a woodland remnant with trees up to 200–350 years old. A grid-based survey of 199 vegetation plots was conducted here during September of 2007. Also, a few hundred seedlings or saplings of three native woody species were planted in transects across the field during 2004–2005, so that their fate could be observed. Spatial patterns within existing vegetation were interpreted using trends in 'browsing-associated' groups of species (assigned with a review of the literature), and trends in direct evidence of herbivory, especially on the planted blue ash. Variation in the vegetation was not clearly related to topography, but primarily to a general diagonal pathway travelled by deer across the field. There was a concentrated zone of highway-crossing near one corner of the field, and concentrated zones of browsing towards the back where animals were more sheltered from the road and closer to the ancient woodland. Herbivory from deer and perhaps smaller mammals (with review of literature) is probably a major factor controlling succession within this field. The suggested distinction here of more sensitive tree species (including *Acer*, *Celtis*, *Fraxinus*, *Morus*, *Ulmus*) versus more tolerant species (including *Carya*, *Juniperus*, *Gleditsia*, *Gymnocladus*, *Juglans*, *Prunus*, *Quercus*, *Robinia*) does accord with a broad review of the literature on eastern woodlands. These results help to build a general hypothesis for how herbivores controlled much of the dynamics in woodlands on more eutrophic soils before human settlement, and how such processes might be partially restored.

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## INTRODUCTION

The potential role of herbivory in shaping fine spatial patterns of woodlands (broadly defined) across eastern North America remains an elusive topic, with little published research. There has been considerable research into patterns of herbivory at larger scales (e.g., Finder et al. 1999, Shi et al. 2006), and similar studies have been conducted in other temperate regions (e.g., Wallace et al. 1995, Etzenhouser et al. 1998, Morellet & Guibert 1999). However, there appears to have been almost no attempt in temperate woodland anywhere to map out patterns in herbaceous vegetation and woody stems at scales of less than 1 ha within sites where intensive local effects by deer or other herbivores are likely to occur. Given that large herbivores can create distinct pathways, it is surprising that there have been so few published studies that thoroughly describe the zonation of vegetation along such pathways.

There are a few studies in eastern North America that have approached this subject, as in analysis of how herbivory by large or small mammals on woody plants in old fields is related to distance from forest edges (e.g., Myster & McCarthy 1989, Myster & Pickett 1992, Ostfeld et al. 1997, Cadenasso & Pickett 2000, Manson et al. 2001, Meiners & Martinkovic 2002, Flory & Clay 2006, Ruzicka et al. 2010). Similar patterns are expected in clearcuts or other canopy gaps in forests, but there is virtually no documentation (e.g., Heinen & Curry 2000). Other relevant work has shown that herbivory by deer is clearly reduced on inaccessible rocky sites (Comisky et al. 2005), and that it is reduced among dead woody material in some situations but not others (Chantal & Granström 2007, Cipollini et al. 2009, Kruger & Peterson 2009). But there has been little published research on the potential effects of steep slopes in general, with or without rocks, and on the potential role of dense thickets, especially with thorns (e.g.,

Forrester et al. 2006). Such effects have often been noted in Europe (e.g., Vera 2000, Grove & Rackham 2001, Fletcher 2007).

Elsewhere in temperate regions, Vera (2000) has presented a profound new view of the prehistoric dynamics within woodlands of the central European plains. He invoked the continually shifting trail system of larger herbivores as a major factor. Much associated research has been published in Europe, and although a few of these studies have pointed to some exaggerated interpretations by Vera (e.g., Mitchell 2005), there is general agreement that larger herbivores probably had great local impacts on fertile soils with productive accessible vegetation (e.g., Bakker et al. 2004, Johnson 2009, Sommer et al. 2011). But even within Europe, there has been little detailed study of the local spatial patterns in vegetation along animal trails within woodland, shrubland or grassland.

I have adapted Vera's (2000) concept into a hypothesis for how large herbivores contributed to the diversity of original woodland on deep eutrophic soils of the Bluegrass region within the central Ohio Valley (Campbell 2012). This type of woodland, broadly defined, used to occur on much of what became 'prime agricultural land' in the east-central U.S.A. (Campbell 1989, 2013). Several imperiled species in such woodland appear to have been largely dependent on the disturbances of larger herbivores, including the federally endangered *Trifolium stoloniferum* (Campbell et al. 1988) and the newly described *T. kentuckiense* (Chapel & Vincent 2013). The 'herbivore hypothesis' can be elaborated into a dynamic model with two basic processes overlaid on the somewhat independent gradient from deep shade to full sun: (1) large herbivores concentrate their effects in productive palatable vegetation, especially vigorous regrowth after disturbances of the canopy; (2) with time, more 'tolerant' (effectively resprouting) or 'resistant' (thorny, toxic or repellent) plants accumulate

within such regrowth, leading to a shift in canopy composition as the woodland recovers to a more mature shady condition. A somewhat cyclical pattern is envisaged, although undoubtedly subject to many unpredictable variations. The resulting dynamic braiding of paths and zones with varied degrees of herbivory may be essential to the natural ecology of woodland with unusually productive “herbage”—as suggested by historical information from the central Bluegrass. This paper is an initial exploration of such processes within the region.

Griffith Woods lies on a 745 acre [300 hectare] tract in Harrison County, Kentucky, formerly known as Silver Lake Farm. This tract provides the best opportunity for restoration of something like the original woodland within the central Bluegrass. The whole farm was initially purchased by The Nature Conservancy in 2003, and the University of Kentucky became a partner in ownership, management and research after 2004. However, the site has now been transferred to ownership by Kentucky Department of Fish and Wildlife Resources. The most complete account of the site that is now widely available is the master’s thesis of Berry (2007); see also provisional materials at various websites.

The study reported below is based on detailed mapping of a 20 acre [8 ha] hay-field at the northern side of the farm, last cropped in 2003. In addition, a few hundred seedlings or saplings of three native woody species were planted in transects across the field during 2004–2005, so that their fate could be observed. The initial design for this ‘Collection Field’ focussed on plantings of selected species that will be needed in general restoration of diverse native vegetation across the region, from deep shade to full sun. The field is approximately rectangular, between a busy two-lane highway and a woodland remnant with ancient trees up to 200–350 years old. Deer were frequently observed in the field, and they often crossed the highway near the southwest corner, where several animals were hit and killed during 2005–

2007 (as mapped by J. Cox, pers. comm.). A grid-based survey of 199  $20 \times 5$  m vegetation plots was conducted here during September of 2007. By that time many self-sown woody plants had grown up to 2–3 m tall, but there was much variation in stem density across the field. Existing non-woody vegetation within the field appeared at first to be relatively homogeneous, but the 2007 survey revealed interesting patterns that are reported here. Interpretation below relies partly on an ‘indicator species’ approach as well as on direct observations of herbivory. With the overall ‘herbivore hypothesis’ (Campbell 2012) as general background, results here are used to develop a more specific application of the hypothesis for this field. Potential subsequent tests are outlined in the Discussion.

## METHODS

In 2003, ten rows across the field were established for plantings, parallel to the road: numbered 1 to 10 from the road towards the woods (Figure 1). Each row was about 7.5 m wide and each was divided into a northeast (“N” in figures below) and a southwest (“S”) section by a central mowed path for access into the field. Center-lines of rows are about 17.5 m apart on average, but diverge to about 20 m in the southern corner of the field. Paths about 10 m wide were mowed between rows about twice per year from 2004 to 2007. The 20 row sections (10 N plus 10 S) were divided into four blocks of five sections each. Within each block, the five row sections were randomly assigned five long-term treatments: (1) continued grassland without woody plantings; (2) shrub plantings; (3) plantings of browsing-sensitive trees; (4) plantings of browsing-tolerant trees; (5) plantings of trees that typically occur in the deepest woods.

This paper reports only results from the most abundant initial plantings, as follows.

(a) 102 seedlings of roughleaf dogwood (*Cornus drummondii*) were planted during the winter of 2004-2005 at irregular intervals of 5–10 m along the four row sections with shrub-plantings (treatment 2). Seedlings were 2 years old and mostly 0.5–1 m tall. The row sections received the same overall density of seedlings, but an effort was made to place plants at quasi-random positions along the center-line of each row.

(b) 262 seedlings of sugar maples (mixed *Acer saccharum* and *A. nigrum*) were planted during the winter of 2004–2005 in the four row sections for trees of deeper woods (treatment 5). Seedlings were 2–4 years old and mostly 0.1–0.3 m tall. The row sections received the same overall density of seedlings, but with a roughly zig-zag pattern of placements within 3 m from the center line.

(c) 167 saplings of blue ash (*Fraxinus quadrangulata*) were planted during Feb–Mar of 2004 along the 12 row sections designed for trees (treatments 3, 4 and 5). Saplings were mostly 3–5 years old and 1–1.5 m tall, and came from four local provenances with different nursery history, which were uniformly mixed along the rows. Plantings were placed at irregular intervals of 10–15 m along the center lines of each row, but maintaining the same overall density along all rows. In a few cases (especially treatment 3), trees that died after 1–2 years were replaced; replacements are excluded from survival percentages reported below, but they are included in statistics on extension growth. [Because a large number of blue ash saplings were available from the nursery, these were planted more widely than the final focus for blue ash on treatment 3.]

In all cases (a, b and c), planted trees were each provided with a ca. 1 m<sup>2</sup> weed-control mat cut out of old carpet, which was then removed in 2007–2008. These mats helped locate planting

positions during the survey. Additional weed control, using black plastic sheets and herbicide, was employed during early management of 2003–2004 within the two lower left row sections (S9 and S10).

The vegetation was surveyed during September of 2007 within 199 unmowed plots, each  $20 \times 5$  m [ $100 \text{ m}^2$ ] and contiguous along the 20 row sections. Within these plots, all vascular plant species were recorded. Nomenclature generally follows Weakley (2014). Each herbaceous species was assigned cover-class, using a quasi-logarithmic eight-point scale (Table 1). For each woody species, numbers of stems were estimated, using classes for denser thickets: 10–20; 20–30; 30–40, etc. Height of each stem was estimated, largely using 0.5 m classes: <1 m; 1–1.5 m; 1.5–2 m; 2–2.5 m, etc. Along fencerows and woodland edges around the field, trees at least 10 cm dbh were recorded in units adjacent to each of the peripheral  $20 \times 5$  m plots within the field. The recorded trees were in zones up to 10 m wide: generally ca. 5 m wide along the road on NW side, 5–10 m along the NE side, and 10 m wide along the SW side and along the back edge transitional to the old growth on SE side. Percent species-composition of these trees, in terms of basal area, was visually estimated at each location around the field.

For planted species, the fate of each individual was examined in 2007, but many maples and dogwoods had died and disappeared. In the blue ash saplings, annual extension growth of leading shoots was measured from bud scars for 2007 and 2006. But in many blue ash saplings, leaders had been browsed, otherwise damaged or died. In these cases, extension growth of the most vigorous remaining shoots was measured. Blue ash saplings were classified as follows:

- (a) original leader intact, healthy with little or no unusual sprouting of lateral or lower shoots;
- (b) original leader intact but some unusually strong growth by lateral branches or lower shoots;
- (c) original leader dead and in most cases largely replaced by a lateral branch or lower shoot.

After inspection of distributional trends for each of the more common plant species, it was possible to distinguish several species with concentration in southern parts of the field, especially along or near the approximately diagonal pathways used by deer (Figure 2c). General knowledge and review of literature supported the concept that these species tend to be more ‘browsing-associated’ (or even “tolerant”) compared to the remaining species; selected references are cited in the footnotes to Tables 3 and 4. Most of the other species exhibited no clear concentration of this type, and only one common species had a distinct opposite concentration in the northern part of the field: *Verbesina alternifolia* (Figure 2c).

Two groups of species were established based on local distribution patterns within this field (e.g., Figure 2c) plus general review of preference-versus-avoidance by deer and other ecological traits: (1) generally ‘browsing-associated’ species (Tables 3a, 4a); and (2) the largely ‘neutral’ or ‘browsing-sensitive’ remainder (Tables 3b, 4b). Among forbs, grasses, subshrubs and ground-covering vines, 25 species were classified as ‘browsing-associated’; the remaining 26 were not clearly associated with browsing, although they may well have small to moderate positive or negative reactions in some situations. Species with cover of at least 0.1% in less than 5 plots were excluded. With this division, a provisional index for browsing influence in the herbaceous vegetation was the total estimated cover for these browsing-associated species, using the same quasi-logarithmic scale for individual species (Table 1). Means of this index in plots can thus provide estimated geometric means for percent cover. Among trees and shrubs there were 16 with browsing-associated and 9 without such association. Indices of browsing influence on these woody species in each plot was the proportion of browsing-associated species among ‘seedlings’ (<1 m tall) and among ‘saplings’ ( $\geq 1$  m tall).

In the analysis, ‘subshrubs’ were included with the forbs: these are mostly common blackberry (*Rubus pensylvanicus*) and coralberry (*Symphoricaros orbiculatus*), with spreading patches of clonal stems up to about 1–2 m tall. Some woody vines were also included with the forbs, since these species behaved in this field largely as ground-covering subshrubs (*Campsis radicans* and *Toxicodendron radicans*). These vines generally formed a minor proportion of the total woody density (< 1%); their irregular growth forms hindered meaningful stem counts; and they would have added unnecessary ‘noise’ to tree and shrub data. However, the grapevine *Vitis vulpina* was included with trees and shrubs, since it usually appeared as more distinct seedlings and did not cover distinct patches of ground.

The vegetation survey noted any clear signs of herbivory or associated damage by mammals during the growing season of 2007. However, there was no thorough effort to search for signs below 1 m in height above ground. Although most of these signs were on woody plants, in a few cases they were on forbs, especially taller herbs. The most obvious signs were concentrated on the planted blue ash saplings, many of which had browsed or broken leaders, rubbed stems or chewed basal bark. The damage to basal bark may be attributed to smaller mammals, especially voles (e.g., Inouye et al. 1994, Manson et al. 2001). In the case of multiflora rose, causes of herbivory were more obscure, since invertebrates (including Japanese beetles) or pathogens (Epstein & Hill 1999) also appeared to be involved. For each rose bush, an approximate tally of dead or “sick” stems was made, as well as healthy ones.

**Table 1. Abundance scores for visual estimates of leafy cover within unmowed vegetation plots.** This quasi-logarithmic scale reflects the interest in finer differences between less common species, since most species usually have <1% cover. Means based on these numbers for each plot can thus provide estimates of geometric mean abundances for groups of plots.

\* There was an effort to record additional species observed only within adjacent mowed lanes between rows, up to 5 m from each plot. These records are excluded from quantitative analysis, but they are used in the maps for each species, as illustrated in Figure 2c.

Score	Percent Cover
0	absent/adjacent*
1	present: 0–0.1%
2	0.1–0.3%
3	0.3–1%
4	1–3%
5	3–10%
6	10–30%
7	30–100%

**Table 2. Description of each vegetation type. Species not listed usually had <10% cover.**

<b>Label for Map</b>	<b>Name of Type</b>	<b>Description</b>
grass-dominated	strongly grass-dominated	bluegrass and fescue both usually >30%; other species each <10%
goldenrod codominant	grass, goldenrod (major)	bluegrass usually >30%; fescue >10%; goldenrod >30%
goldenrod common	grass, goldenrod (minor)	bluegrass usually >30%; fescue >10%; goldenrod 10-30%
aster abundant	grass, goldenrod, aster	bluegrass > 30%; fescue >10%; goldenrod >10%; aster 10-30%
hemlock abundant	grass, goldenrod, hemlock	bluegrass or fescue >10%; goldenrod >30%; hemlock >10%;
crown-vetch abundant	grass, goldenrod, crown-vetch	bluegrass, fescue, goldenrod and crown-vetch all >10%
trumper-creeper abundant	grass, goldenrod, trumpet-creeper	bluegrass or fescue >10%, goldenrod >10%, trumpet-c.10%,
blackberry abundant	blackberry, grass, goldenrod.	blackberry >30%, goldenrod >10%; bluegrass or fescue >10%,

**Table 3 [next pages]. (a) More ‘browsing-associated’ forbs and subshrubs defined for the analysis; (b) other forbs, graminoids and subshrubs, not clearly associated with browsing.**

Species were assigned to these two groups based on distributional patterns and traits (see text). Only species that occurred in at least 7 plots (of the 199) are included in these lists.

Asterisks (\*) indicate clearly alien species. Selected traits of interest are coded as follows:

A = annual species (summer or winter); B = biennial or short-lived monocarpic species.

References: Fernald (1950), Gleason & Cronquist (1991), Yatskievytch (1999-2013), etc.

F = seed appears adapted to dispersal in mammalian fur (references as in A, B and some F).

G = seed may be often dispersed through gut of deer or other mammals; g = minor extent.

References: Janzen (1984), Myers et al. (2004), Rosas et al. (2008), Williams et al. (2008), Iravani et al. (2011), Panter & Dolman (2012), Blyth et al. (2013), Frost et al., (2013) and their citations. This is a provisional indication based on few studies.

R = species with running roots, rhizomes or stolons; r = less vigorous runners (ca. 1-10 cm).

S = spines (or thorns) present on leaves or stems (references for R and S as in A and B).

X = generally toxic to mammalian herbivores; x = slightly toxic or highly unpalatable.

References: Muenscher (1961), Burrough & Tyrl (2001), Bryson & Felice (2009), and their citations. See also further details in references below.

Under “Reported deer-browsing degree” the four following general ranks are suggested.

- 1. None or negligible:** typically among the lowest ranked 20% of species; or if reported without comparison to many other species, such species are clearly avoided (<1% of stems browsed) even by dense animal populations during the most attractive season.
- 2. Low:** not among the 20% least used but typically among the other 30% below median.
- 3. Moderate:** not among the 20% highly used but typically among other 30% above median.

**4. High:** typically among the highest ranked 20% of species; or if reported without comparison to many other species, such species are subjected to high levels of consumption (at least 25% of available stems browsed) by dense animal populations during the most attractive season.

These ranks are supported by diverse literature, but for many species data are sparse and only tentative suggestions are made, indicated here by question marks. Ranks are often based partly on information about other species in the genus, since palatability and secondary chemistry are usually somewhat consistent within genera. Alphanumeric codes for sources are as follows:

A1 Allen (1968); A2 Anderson et al. (2007 and his other papers); A3 Atwood (1941); B1 Blair (1960); B2 Bryant et al. (1981); B3 Bullock et al. (1994); B4 Burnett et al. (1977); C1 Cain et al. (2010); C2 Campbell & Johnson (1983); C3 Castleberry et al. (1999); C4 Cheplick et al. (1988); C5 Christopher et al. (2014); C6 Cooke & Farrell (2001); C6 Corrigan (2003); D1 Dahlbery & Guettinger (1956); D2 Dale (1974); D3 DeJaco (2006); D4 Deliberto (1987); D5 Desrochers et al. (1988); D6 DiTommaso et al. (2014); D7 Dostaler et al. (2011); E1 Edwards et al. (2000); E2 English & Bowers (1994); E3 Englund & Meyer (1986); F1 Frost et al. (2013); G1 Gubanyi et al. (2008); H1 Halls & Dell (1966; Halls 1975); H2 Heinrich & Predl (1993); H3 Hickman & Hartnett (2002); H4 Hilty (2012); H5 Hochwender et al. (2000), H6 Hutchings & Price (1999); J1 Jull (2001); K1 Kindscher et al. (2012); K2 Kirby (2001); K3 Kohn & Mooty (1971); K4 Korsgen (1962); L1 Leif (2013); O1 Ortega et al. (1997); M1 MacDonald & Cavers (1991); P1 Parks et al. (2008); P2 Pitcher (1989); R1 Richens (1947); R2 Riem et al. (1995); R3 Rose et al. (1985); S1 Sanderson et al. (2003); S2 Sauer et al. (1969); S3 Schneider et al. (2006); S4 Sotala & Kirkpatrick (1973); S5 Stewart-Wade et al. (2002); T1 Taylor (1956); T2 Torgenson & Pfander (1971); T3 Tu et al. (2003); V1 Viehoveer et al. (1916); V2 Vila et al. (2005); W1 Warren & Krysl (1983); W2 Warwick & Black (1982); W3 Webster et al. (2005).

**Table 3a. More ‘browsing-associated’ species; see explanation on preceding pages.**

Latin Binomial	Traits	Reported deer browsing degree
<i>Achillea millefolium</i> L. [yarrow; possibly native]	R	LOW: A3, W2, horticultural info
* <i>Allium vineale</i> L. [field-garlic]	x	NONE: R1, E2, E3
* <i>Barbarea vulgaris</i> L. [bittercress]	B g? x?	?NONE-LOW: A3, D6, M1
* <i>Carduus acanthoides</i> L. [plumeless thistle] * <i>Carduus nutans</i> L. [musk or nodding thistle]	B S B S	NONE: D5
* <i>Cirsium arvense</i> (L.) Scop. [creeping thistle] <i>Cirsium discolor</i> (Muhl. ex Willd.) Spreng. [field thistle] * <i>Cirsium vulgare</i> L. [bull thistle]	R S B S B S	LOW: A3, B3 and citations ( <i>vulgare</i> ); E1 ( <i>arvense</i> ) ?HIGH: D3 ( <i>arvense</i> )
* <i>Conium maculatum</i> L. [poison-hemlock]	B X	NONE: P2
* <i>Daucus carota</i> L. [wild carrot or Queen Anne’s lace]	B F	LOW: A3, D2
<i>Desmodium perplexum</i> B.G. Schub. [(common old field tick-trefoil)]	F R	?MOD: A3, D4, L1
<i>Erigeron annuus</i> (L.) Pers. [eastern daisy fleabane]	A	?MOD: A2, A3, C2, D6, W1
* <i>Glechoma hederacea</i> L. [gill-over-the-ground or ground-ivy]	R x	LOW: C6, H6, K2
* <i>Hypericum perforatum</i> L. [common Saint John’s wort]	R x	NONE: V2
* <i>Pastinaca sativa</i> L. [wild parsnip]	B x	NONE: C1
<i>Physalis longifolia</i> Nutt. [smooth ground-cherry; var. <i>lanceolata</i> ] <i>Physalis heterophylla</i> Nees [hairy ground cherry; var. <i>ambigua</i> ]	R x? R x?	?LOW-MOD: D3, K1, W1
* <i>Potentilla recta</i> L. [sulphur cinquefoil]	g	?LOW-MOD: A3, F1, P1

<i>Solanum carolinense</i> L. [horse-nettle]	G R S X	NONE-LOW: A3, E2, H2
* <i>Trifolium pratense</i> L. [red clover] and other clovers <sup>1</sup>	b g	HIGH: A3, D7
* <i>Verbascum blattaria</i> L. [moth mullein] <sup>2</sup>	B	NONE: C2, W1
<i>Vernonia gigantea</i> L. [common old-field ironweed]	f? x?	NONE: B4, T2
<b>Subshrubs: laterally suckering woody plants usually &lt;2 m tall</b>	<b>Traits</b>	<b>Reported deer browsing degree</b>
<i>Rubus flagellaris</i> Willd. [common dewberry]	G R S	?LOW: A3
<i>Rubus pensilvanicus</i> Poir. [common old-field blackberry] <sup>3</sup>	G R S	?MOD: A3, D1, H1, T1
<i>Symphoricarpos orbiculatus</i> Moench [coralberry or buckbush]	g R	LOW-MOD: A3, C2, D1, D4, G1, H2, J1

Footnotes to Table 3a. <sup>1</sup> Assignment of *Trifolium pratense* (red clover) to this group (versus those in Table 3b) is somewhat arbitrary but it has negligible influence on the analysis. There were only 9 records of all clover species in the plots or in adjacent mowed zones: mostly *T. pratense* plus minor amounts of *T. campestre* and perhaps *T. repens* (flowering season missed), with cover no more than 0.1–0.3% in any one plot. Although these species are highly palatable, records here were all restricted to the back three rows of the field where deer appeared to have relatively strong influence: 8, 9 and 10.

<sup>2</sup> *Verbascus thapsus*, another browsing-resistant species, was also present in small numbers.

<sup>3</sup> *Rubus allegheniensis*, the relatively shade tolerant blackberry, can be more intensively browsed and much reduced by deer (e.g., Horsely et al. 2003); comparative studies are needed.

**Table 3b. Other forbs, graminoids and subshrubs not clearly associated with browsing.**  
Some of these may increase locally due to deer, but there is probably no general strong effect.

Forbs: latin binomial [and common name]	Traits	Reported deer browsing degree
<i>Ambrosia artemisiifolia</i> L. [common / lesser ragweed]	A fg?	?LOW-MOD: A3, D3, D4, T2, W1
<i>Ampelamus albidus</i> (Nutt.) Britt. [honeysuckle milkweed]	R	?MOD: D6
<i>Apocynum cannabinum</i> L. [dogbane] <sup>1</sup>	R x	?LOW-MOD: A1, A3, K3
<i>Asclepias syriaca</i> L. [common / field milkweed] <sup>1</sup>	R x	?LOW: A3, H5
<i>Calystegia fraterniflora</i> (Mack.) Brummitt [eastern bindweed]	R	?LOW-MOD: A1, A3, D3, C7
* <i>Cichorium intybus</i> L. [chicory]	B	?HIGH: S1 and citations
* <i>Plantago lanceolata</i> L. [English plantain]	g	?HIGH: A3, D3, S1, S4, W1
<i>Ruellia strepens</i> L. [common wild petunia]	R	?HIGH: O1, H3
* <i>Securigera varia</i> (L.) Lassen = <i>Coronilla varia</i> [crown-vetch]	g R x?	?MOD: S3, T3 [toxic to rodents]
<i>Solidago altissima</i> L. [common old field goldenrod] <sup>2</sup>	fg R	LOW-MOD: A3, D3, E3, H4, R3, S2
<i>Symphyotrichum ontarionis</i> (Wieg.) Nesom [downy aster]	fg R	?MOD: A3, E3, K4
<i>Symphyotrichum pilosum</i> (Willd.) Nesom [common old field aster]	fg?	MOD: A3, D3, E3, H3, K3, T2
* <i>Taraxacum officinale</i> L. [dandelion] <sup>3</sup>	g	MOD-HIGH: A3, D3, S5
<i>Verbesina alternifolia</i> (L.) Britt. ex Kearney [lowland wingstem]	f?	?MOD-HIGH: A3, D4
<i>Viola papilionacea</i> Pursh p.p. [common yard violet]	g? r	MOD-HIGH: A3, C5, D3, R2,

		W3
<b>Graminoids: grasses and sedges</b>	<b>Traits</b>	<b>Reported deer browsing degree</b>
<i>Andropogon virginicus</i> L. [common broom-sedge]		?LOW: A3, B2
* <i>Bromus inermis</i> Leyss. [smooth bromegrass]	g R	?LOW-MOD: A1, A3, D4
<i>Carex</i> spp. especially <i>C. blanda</i> Dewey [a common weedy sedge] <sup>4</sup>	g	?LOW: A3, B2, C2, R3, W1
* <i>Dactylis glomerata</i> L. [orchard grass]	g r	?LOW-MOD: A3, R3
<i>Dichanthelium clandestinum</i> (L.) Gould [deer-tongue grass]	r	?LOW-MOD: D4
* <i>Festuca arundinacea</i> Schreb. [tall fescue]	r x?	LOW: A3, D4
(*) <i>Poa pratensis</i> L. common bluegrass [ssp. <i>angustifolia</i> (L.) Lej.] <sup>5</sup>	g R	MOD-HIGH: A3, C2
* <i>Sorghum halepense</i> (L.) Pers. [Johnson grass] <sup>6</sup>	g R x?	LOW-MOD: A3, B2
<i>Tridens flavus</i> (L.) Hitchc. [grease grass or purple top]		?LOW: C4, V1
<b>Woody vines that behave here as subshrubs</b>	<b>Traits</b>	<b>Reported deer browsing degree</b>
V: <i>Campsis radicans</i> (L.) Seem [trumpet-creeper] <sup>7</sup>	R	MOD: A3, B1, C3, H1, J1
V: <i>Toxicodendron radicans</i> (L.) Kuntze [poison-ivy] <sup>8</sup>	R x?	MOD-HIGH: A3, H1, S4, T2

Footnotes to Table 3b. <sup>1</sup> *Apocynum cannabinum* and *Asclepias syriaca* are generally considered poisonous to livestock, but there are some reports of deer browsing on these species; here they are more frequent in zones with less browsing.

<sup>2</sup> There is remarkably little published comparative data on mammalian browsing of *Solidago altissima*, *S. canadensis* (sensu lato) or related species; Anderson et al. (2001) found that *canadensis* increased with deer, but DiTomaso et al. (2014) noted much browsing on

*altissima*. Hilty (2012) noted more mammalian herbivory on *S. gigantea* (which has less hairiness and less strongly bitter terpenoid taste).

<sup>3</sup> *Taraxacum* (like *Trifolium* spp.) may be generally palatable but able to withstand much browsing and trampling; see D3 for example of varied responses.

<sup>4</sup> Other locally frequent species of *Carex* within the field include *C. aggregata* and *C. grisea*; species present in more wooded transitions around the edges include *C. conjuncta*, *C. jamesii*, *C. normalis* and *C. rosea*.

<sup>5</sup> The native-versus-alien status of *Poa pratensis* remains uncertain. Although much seed of this species was introduced from Europe by Virginian settlers, it is possible that a native race did occur in North America, including plants that may be referable to ssp. *angustifolia* (Gleason & Cronquist 1991; plus associated taxonomic literature).

<sup>6</sup> *Sorghum halepense* is known to produce cyanogenic glycosides under some conditions, but this nutritious warm-season grass is also highly preferred by cattle before flowering; there is little published information on use by deer.

<sup>7</sup> Assignment of *Campsis radicans* remains uncertain, but it was excluded here as an indicator. It is locally abundant and occurs mostly in the southern sections of the field, but it is concentrated in somewhat linear strips that might be interpreted as former fencerows or previous woodland boundaries.

<sup>8</sup> Despite the well-known dermatitis caused by urushiols in *Toxicodendron radicans*, this plant is often reduced due to consumption and trampling by ruminants.

**Table 4 [next pages]. (a) ‘Browsing-associated’ trees and shrubs used in the analysis. (b) ‘Browsing-neutral’ or ‘-sensitive’ trees and shrubs.** Species were assigned to these two groups based on local distribution, literature review and traits (see text). Asterisks (\*) indicate alien species.

Under “Zon” distributional trends across the zonation of Figure 3 are summarized for plants <1 m tall (1st letter) and plants at least 1 m tall (2nd): O = most dense in OUTS, M in MARG, P in PATH; lower case indicates non-significant trend; parentheses indicate that infrequent species were combined for analysis.

Under “Sap” percentages of surveyed stems at least 1 m tall are presented for each species; sprouts <1 m tall were not counted if they were clearly attached to a larger individual.

Under “Mow” numbers of stems noted in mowed strips between the surveyed rows are presented as percentages of total stems in the surveyed rows (<1 m and >1 m); these mowed-over stems were almost all <1 m tall. Parentheses ( ) indicate total plants <5.

Under “Traits” selected traits of interest are coded as follows.

I = Intolerant of shade; these are generally unable to survive for long in deeper shade.

References: Fowells (1965), Valladares & Niinemets (2008), and their citations.

B = fruits generally dispersed by birds; M = fruit often dispersed in guts larger mammals;

N = nuts, dispersed especially by rodents; W = wind-dispersed seed.

Lower case letters indicate less consistent traits, probably with mixed dispersal methods.

References: for general morphology, see Fernald (1950), Gleason & Cronquist (1991), Yatskievytch (1999-2013); for detailed studies of dispersal, see McCullough (1985)<sup>1</sup>, Willson (1993), Buttenschøn & Buttenschøn (1998)<sup>1</sup>, Myers et al. (2004), Williams & Ward (2006), Fedriani & Delibes (2009)<sup>1</sup>, Castellano & Gorchov (2013), and their

citations. <sup>1</sup>These confirm that in *Crataegus*, *Malus* and *Pyrus*, fruit-consumption, seed-dispersal and germination is often associated with medium-sized or larger mammals.

R = species with running roots, rhizomes or stolons; r = less vigorous runners (< 1 m).

T = thorns present on stems; t = less pronounced thorns on stems or spiny leaves

References for R and T as in B etc.

X = generally toxic to mammalian herbivores; x = slightly toxic or strongly repellent.

References as noted under Table 3; see also further details in some references below under ‘deer-browsing degree.’ Note that tentative (“?”) indication of slight toxicity or highly repellent (bitter) chemistry in *Carya cordiformis* and *Lonicera maackii* is based only on personal experience of these species, and on studies with fruits of other species in these genera (e.g., Ehrlén & Eriksson 1993, Porto et al. 2013). The demonstrated mammalian effects of *Lonicera* may be generally medicinal rather than pathological (e.g., Shang et al. 2011); although toxic effects of *L. maackii* extracts on invertebrates and amphibians (e.g., Watling et al. 2011) are known, no toxic effects of *L. japonica* extracts could be shown on rats (e.g., Thanabhorn et al. 2006).

Under “Reported deer-browsing degree” see Table 3 for explanation. Uncertain ranks are noted with question marks (?), and are based at least partly on information from other species in the genus. Alphanumeric codes for sources are as follows, with underlined indicating studies based at least partly on exclosures: A1 Ashton & Lerdau (2008; Howery et al. 1999, Johnson et al. 1995, etc.); A2 Atwood (1941); B1 Benavides (2002); B2 Bressette et al. (2012); C1 Campbell & Johnson (1983); C2 Castleberry et al. (1999); C3 Cogger et al. (2014, etc.); C4 Conover & Kania (1988); C5 Curtis & Rushmore (1958); D1 Dahlbery & Guettinger (1956); D2 Deliberto (1987); F1 Fargione et al. (1991); F2 Fowells (1965); G1 George & Powell (1977); G2 Gubanyi et al. (2008); H1 Halls (1975); H2 Heinrich & Predl (1993); H3 Horsley et al. (2003);

K1 Knapp et al. (2008); L1 Long et al. (2007); J1 Jull (2001); M1 Masters et al. (1991); P1 Parks Canada Agency (2011); P2 Petrides (1941); P3 Pogge (1967); R1 Rawinski (2008); R2 Rossell et al. (2007); R3 Ruzicka et al. (2010); T1 Taylor (1956); T2 Tilghman (1989); T3 Torgenson & Pfander (1971), T4 Tripler et al. (2002); W1 Wakeland & Swihart (2009); Z = personal impressions of the author (JC) in Kentucky.

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**Table 4a. List of ‘browsing-associated’ trees and shrubs used in the analysis.**

Large trees: latin name [and common]	Zon	Sap	Mow	Traits	Reported deer browsing degree
<i>Carya cordiformis</i> (Wangenh.) K. Koch. [bitternut hick.]	(mo)	(0)	(0)	N x?	LOW (A2 T1 Z) MOD (B2 C3)
<i>Gleditsia triacanthos</i> L. [honey locust]	(mo)	17	50	I M r T	LOW (A2 F1 H2 J1 M1 T1 Z)
<i>Gymnocladus dioicus</i> (L.) K. Koch [coffee tree]	(mo)	(0)	(33)	I M R X	NONE (A2 H2 J1 Z)
<i>Juglans nigra</i> L. [black walnut]	(mo)	40	60	I N x	LOW (A2 H2 T1 W1 Z) ?MOD (C3)
<i>Juniperus virginiana</i> L. [eastern red-cedar]	Mo	75	3	I B t x	LOW (M1 T1 Z) MOD (A2 C2 C4 F1)
<i>Quercus macrocarpa</i> Michx. [bur oak]	----	(--)	(100)	I N	LOW (A2 C3 D1 Z) MOD (P3 T1 W1)
<i>Prunus serotina</i> Ehrh. [black cherry]	Mm	27	4	B X	LOW (B2 C4 H3 R2 T2 W1 Z) MOD (A2 D1 F2 L1 P2 P3 T1 T4)

<i>Platanus occidentalis</i> L. [sycamore]	----	(--)	(100)	I W	NONE (R3 W1 Z) LOW (A2 C1 J1)
<i>Robinia pseudoacacia</i> L. [black locust]	----	87	27	I b m R T x	LOW (B2 C3 J1 T1 Z) MOD (A2)
<b>Small trees and shrubs</b>				<b>Traits</b>	<b>Reported deer browsing degree</b>
<i>Crataegus mollis</i> Scheele [downy hawthorn]	Pm	18	0	I b M T	LOW (A2 B2 F1 H2 J1 M1 P2 T1 W1 Z); applies broadly to genus
* <i>Crataegus phaenopyrum</i> (L.f.) Medik. [Wash. thorn]	(--m)	(100)	(0)	I b M T	as above
* <i>Elaeagnus umbellata</i> Thunb. [autumn olive]	----	(100)	(0)	I BM? R T	LOW (A2 C4 H2 J1 K1 M1 Z)
* <i>Malus baccata</i> (L.) Borkh. [Siberian crabapple]	mM	93	9	I b M r t	?MOD (B2 C2 J1 M1 P2 T1 Z); but more on cultivated apples
* <i>Pyrus calleryana</i> Decne. [Callery / Bradford pear]	(mo)	86	14	I b M r T	?LOW (C2 C4 Z) ?MOD (F1 J1)
* <i>Rosa multiflora</i> Thunb. ex Murr. [multiflora rose]	MO	95	2	I b M R T	?LOW (A2 J1 R1 T1 Z) ?MOD (C1 D3 F1)
<i>Sambucus canadensis</i> L. [eastern elderberry]	(--o)	(100)	(0)	B R x	LOW (D1 T1 Z) MOD (A2 W1)

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**Table 4b. List of other trees and shrubs not increasing with browsing signs.**

Large Trees: latin name [and common]	Zon	Sap	Mow	Traits	Reported deer browsing degree
<i>Acer negundo</i> L. [boxelder]	OP	14	3	W	LOW (A2 C3 D1 H2) MOD (B2 R3 Z) HIGH (D2 R1); much variation
<i>Acer saccharinum</i> L. <sup>1</sup> [silver maple]	Oo	23	2	W	MOD (A2 M1 R3 W1 Z) HIGH (C3)
<i>Celtis occidentalis</i> L. [hackberry]	oo	8	1	Bm r	LOW (A2 C3 R2) MOD (G2 T1 Z) HIGH (R2); much variation
<i>Fraxinus americana</i> L. [white ash]	OO	21	<1	W	LOW (B2 D1 J1 R2) MOD (C3 C5 P2 P3 T1 T4) HIGH (A2 F2 G2 L1 Z); much variation
* <i>Morus alba</i> L. [white mulberry]	(--m)	(100)	(<1)	I Bm	HIGH (B1 Z)
<i>Morus rubra</i> L. [red mulberry]	(--m)	(100)	(<1)	Bm	LOW (A2 T1) MOD (P1) HIGH (H1 Z); much variation
<i>Ulmus americana</i> L. [American elm]	Mm	15	5	W	LOW (D1 P2) MOD (C3 F2 T1 Z) HIGH (A2 G1 G2 P3 R3); much var.
Shrubs and Vines					
* <i>Lonicera maackii</i> (Rupr.) Herder [Amur honeysuckle]	mo	34	3	Bm x?	?LOW (T1) ?MOD (D1 Z)
<i>Vitis vulpina</i> L. [fox grape]	Mm	10	2	Bm	?MOD (A1 A2 T3 Z)

<sup>1</sup> *Acer saccharinum* is here due to seed blown in from planted trees in nearby yards; the species is not strictly native to this site but it is a native plant along riverbanks a few miles away.



**Figure 1a. The Collection Field at Griffith Woods, 12 Nov 2004, from Google Earth, centered on  $38.34^{\circ}\text{N}$ ,  $84.35^{\circ}\text{W}$ .** Road along upper edge is US 62, running to right at  $43.5^{\circ}$  NE. Rows are about parallel to road, but slightly divergent to the lower left. Pale patches along some rows are weed control for small plantings of selected herbaceous species. The only buildings within 500 m of the field are those seen here at upper right; a house has been here since 1870 or earlier. A small electric utility line runs across the northern corner of the field.

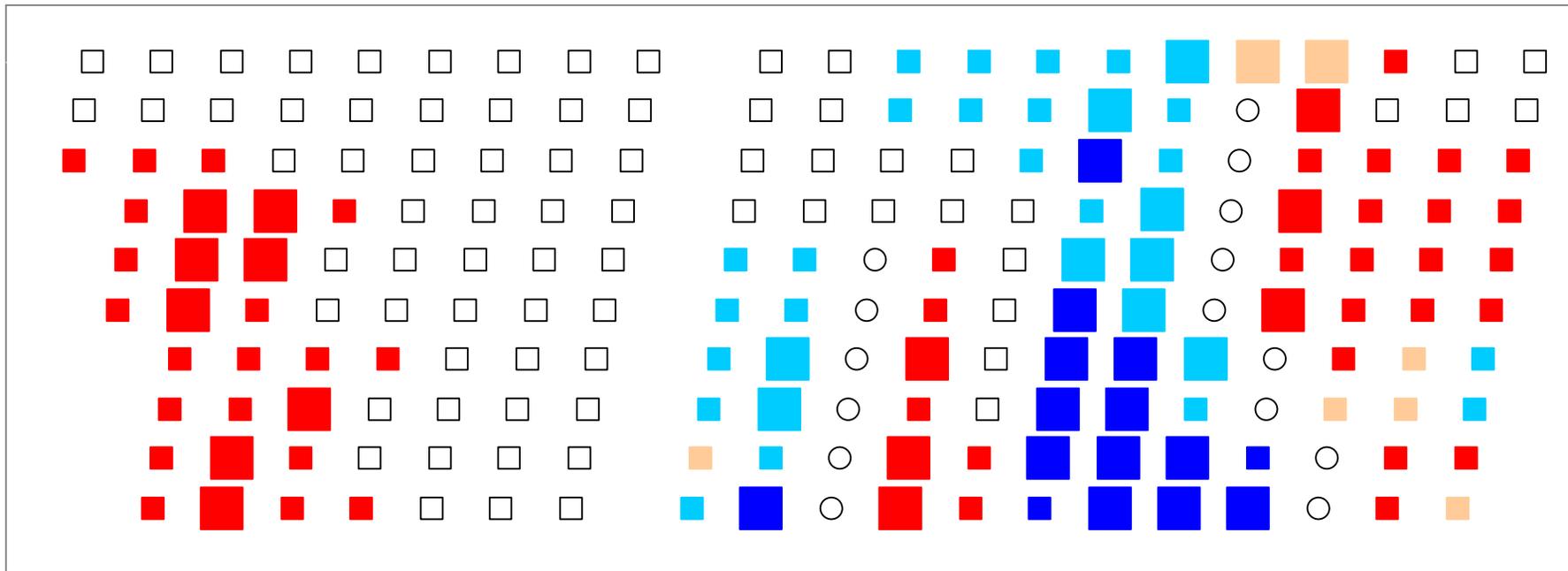
Elevation: feet a.s.l

■ 855-59 ■ 860-864 ■ 865-869 ■ 870-874 ■ 875-879 ■ 880-884 ■ 885-889 ■ 890-894



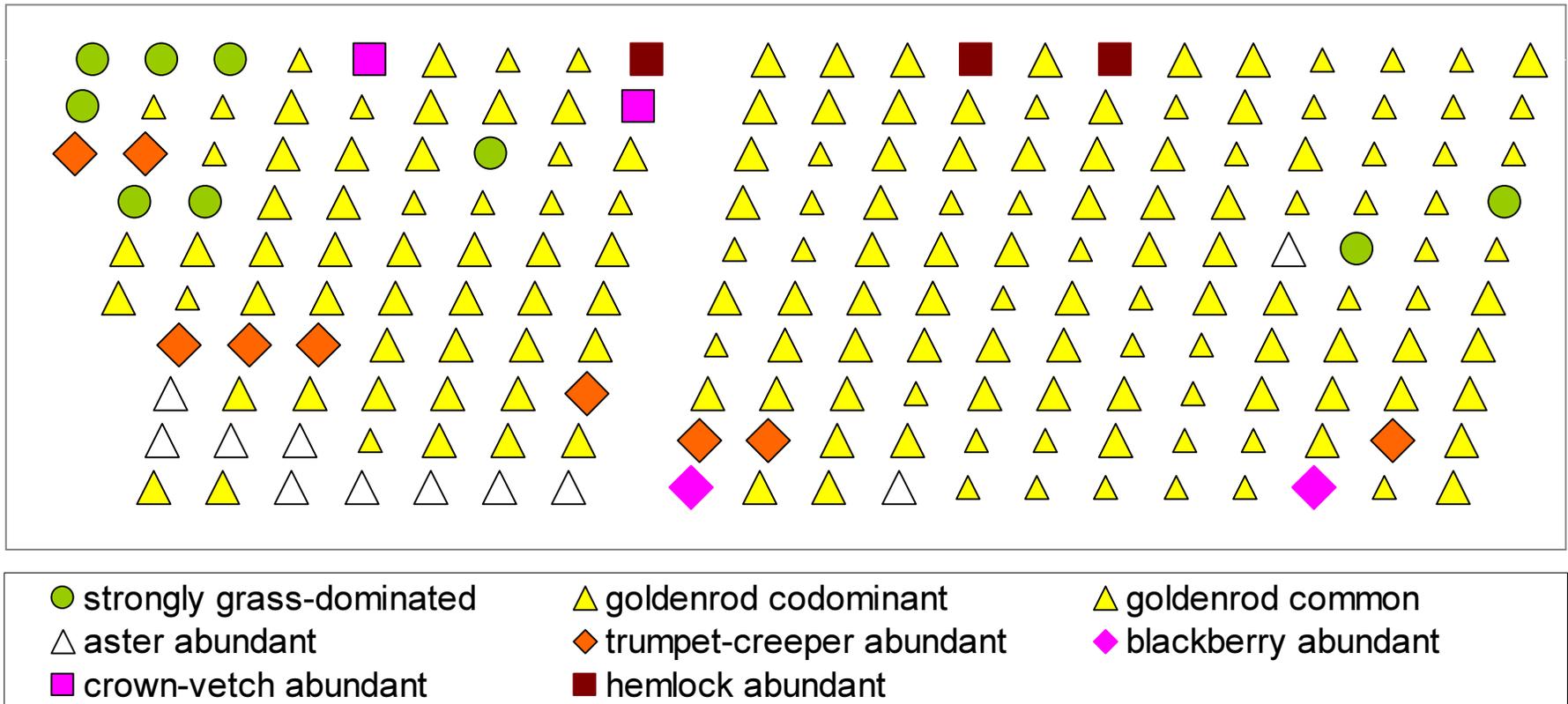
Figure 1b. Elevation at  $20 \times 5$  m plot centers (data from Google Earth).

Slope and aspect: larger squares are steeper



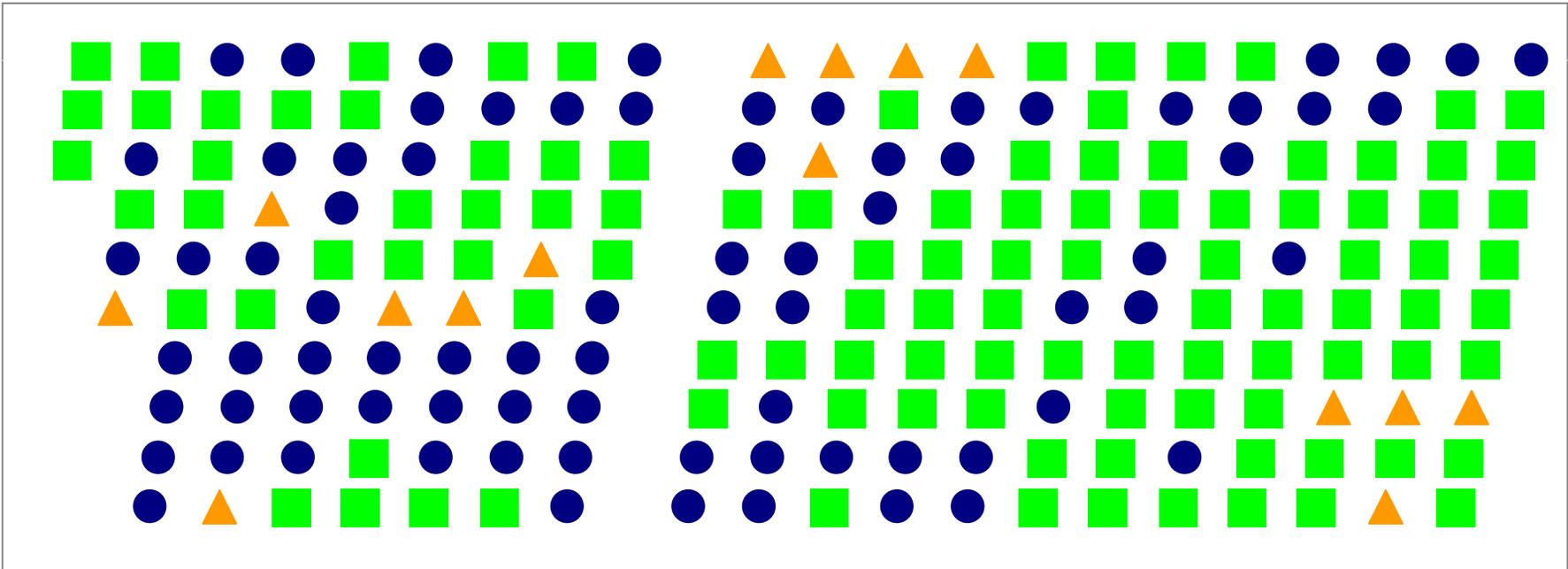
**Figure 1c. Aspect of slope at  $20 \times 5$  m plot centers: larger squares indicate steeper slopes.** “Level” ground had slopes generally less than 4%. “Bottoms” had variable slopes and aspects along small gullies.

Vegetation types: see Table 2 for description of each type  
and see Table 3 for latin names of each species

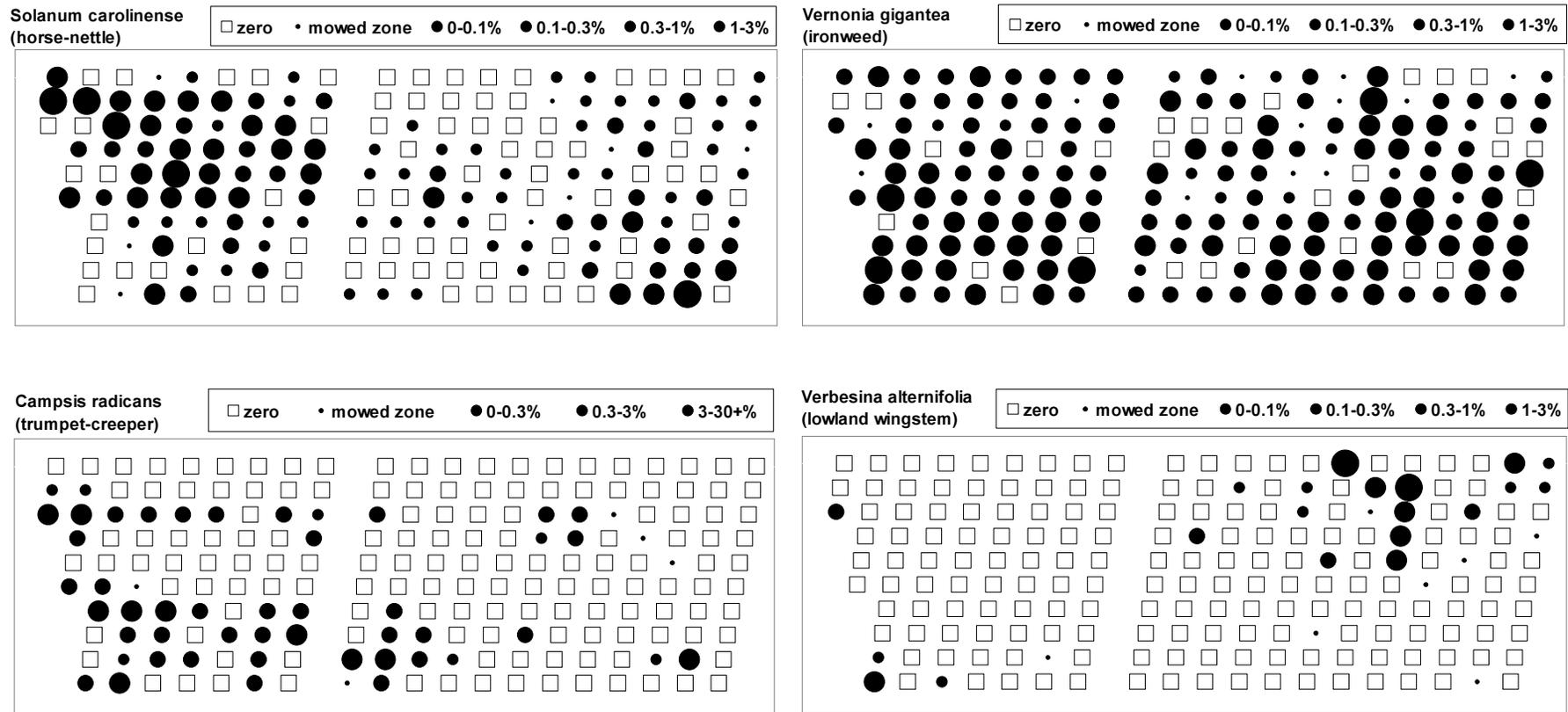


**Figure 2a. Provisional classification of vegetation based on most abundant species in each plot.**

## Bluegrass versus fescue



**Figure 2b. Balance of bluegrass (*Poa pratensis*) versus fescue (*Festuca arundinacea*) in the plots, based on cover classes (Table 1). “Dominant” indicates that the species had a distinctly greater cover class than the other species, but in some cases cover was only 10-30%.**



**Figure 2c. Distribution of selected species to illustrate varied patterns.**

Examples of browsing-associated species (see text).

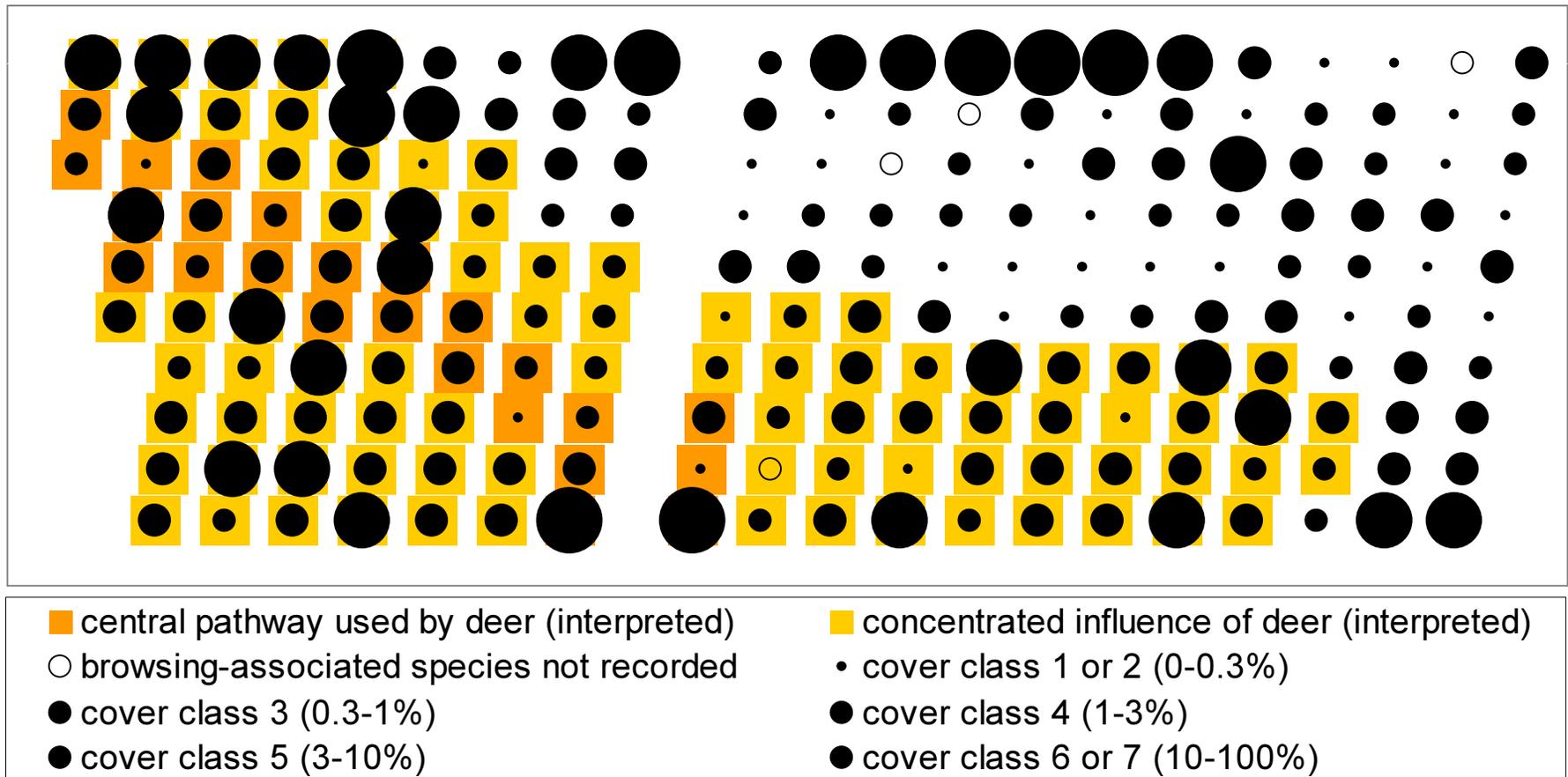
Upper left: *Solanum carolinense*, with diagonal (strong) concentration from W to E corner.

Upper right: *Vernonia gigantea*, with general (weak) concentration toward back of field.

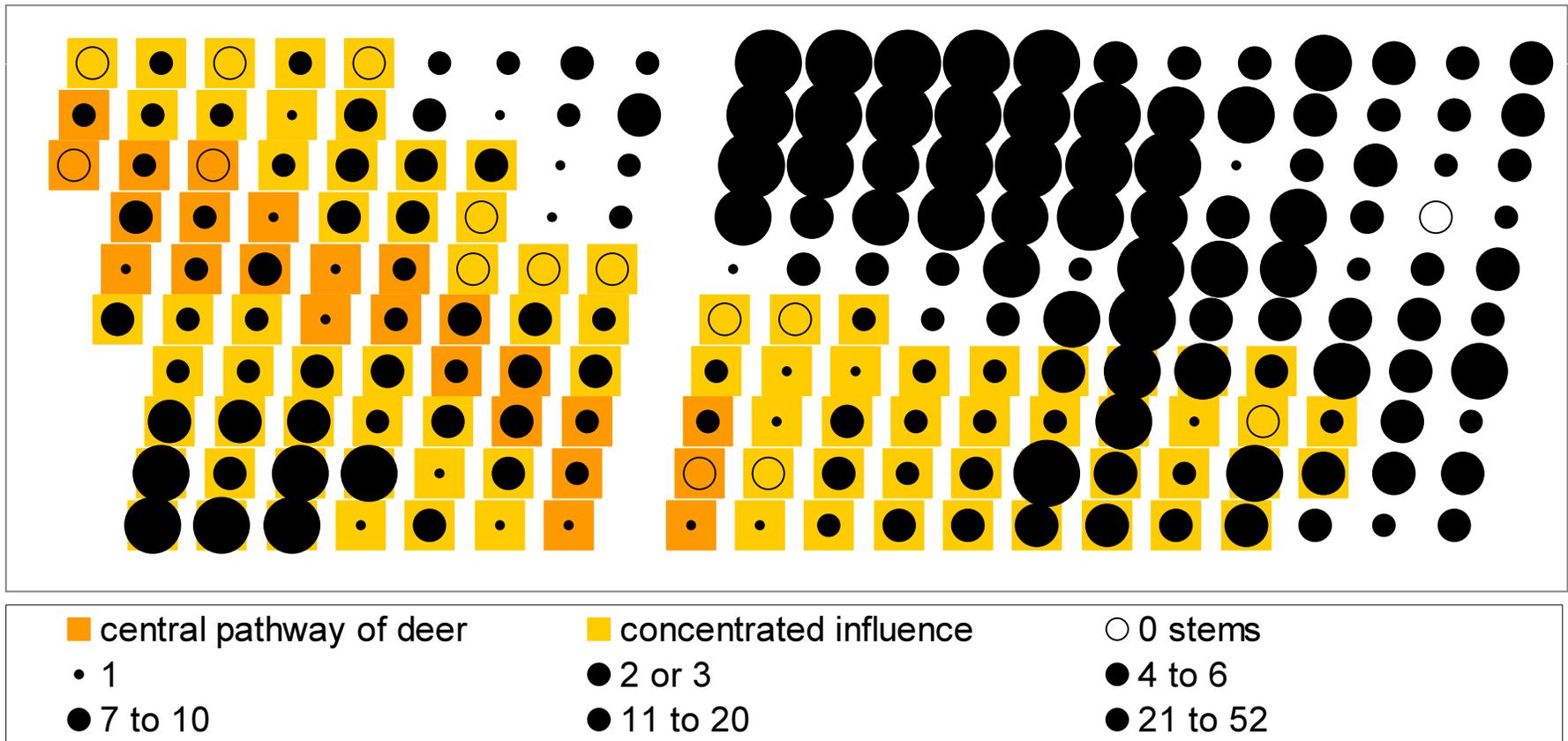
Browsing-neutral or -sensitive species mostly had no clear trend across the field; such species are not shown here, but the following two species did exhibit patterns of interest.

Lower left: *Campsis radicans*, with somewhat bimodal distribution to sides of the diagonal.

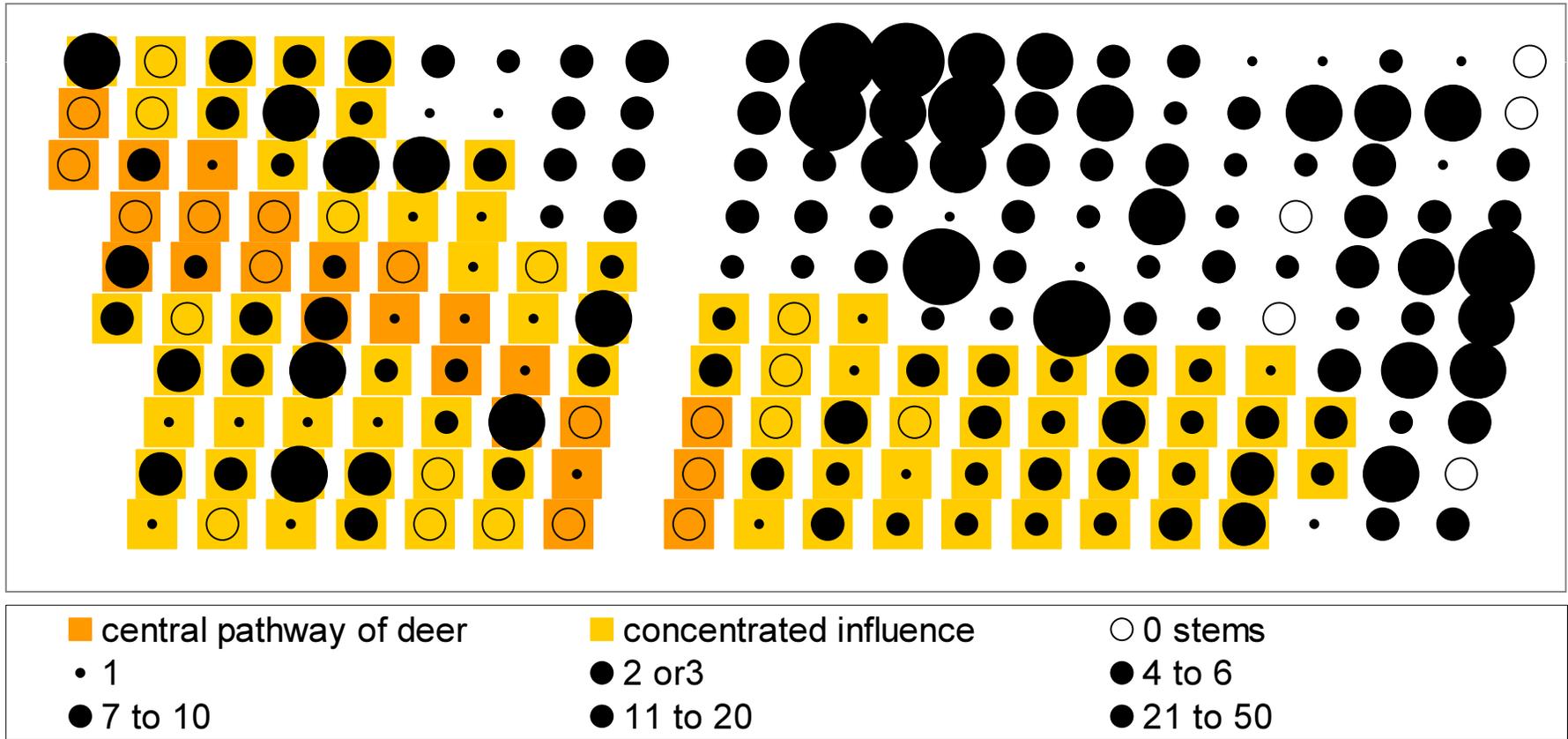
Lower right: *Verbesina alternifolia*, the only species concentrated in the northern sector.



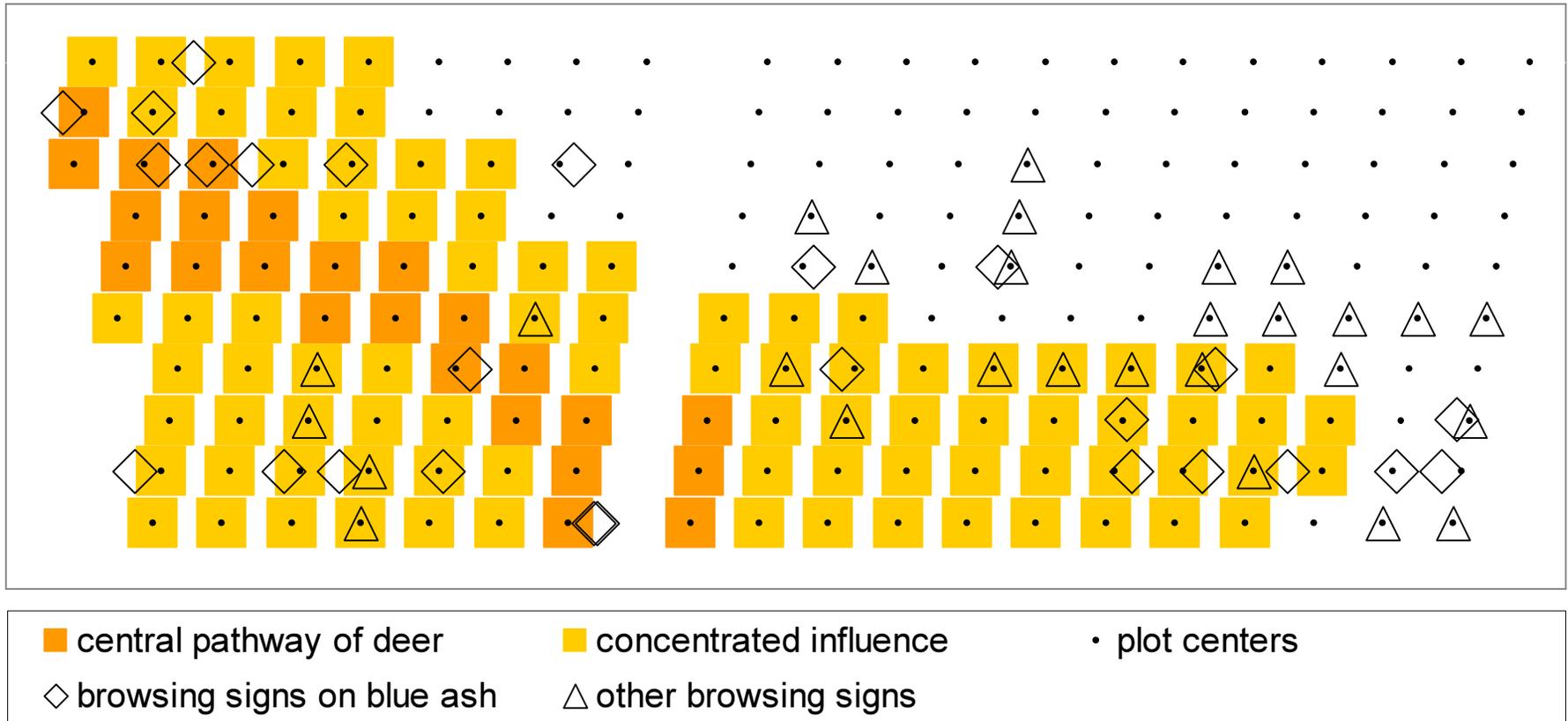
**Figure 2d.** Total abundance of ‘browsing-associated’ forbs (Table 3a) in the plots, using percent cover classes of Table 1. The shaded zones here and in subsequent figures (d,e,f) indicate where deer appear to have concentrated travel across the field, with accumulated influence from foraging. These zones are interpretations based on the vegetation patterns in these figures (especially e and h) plus general observations of deer in the field.



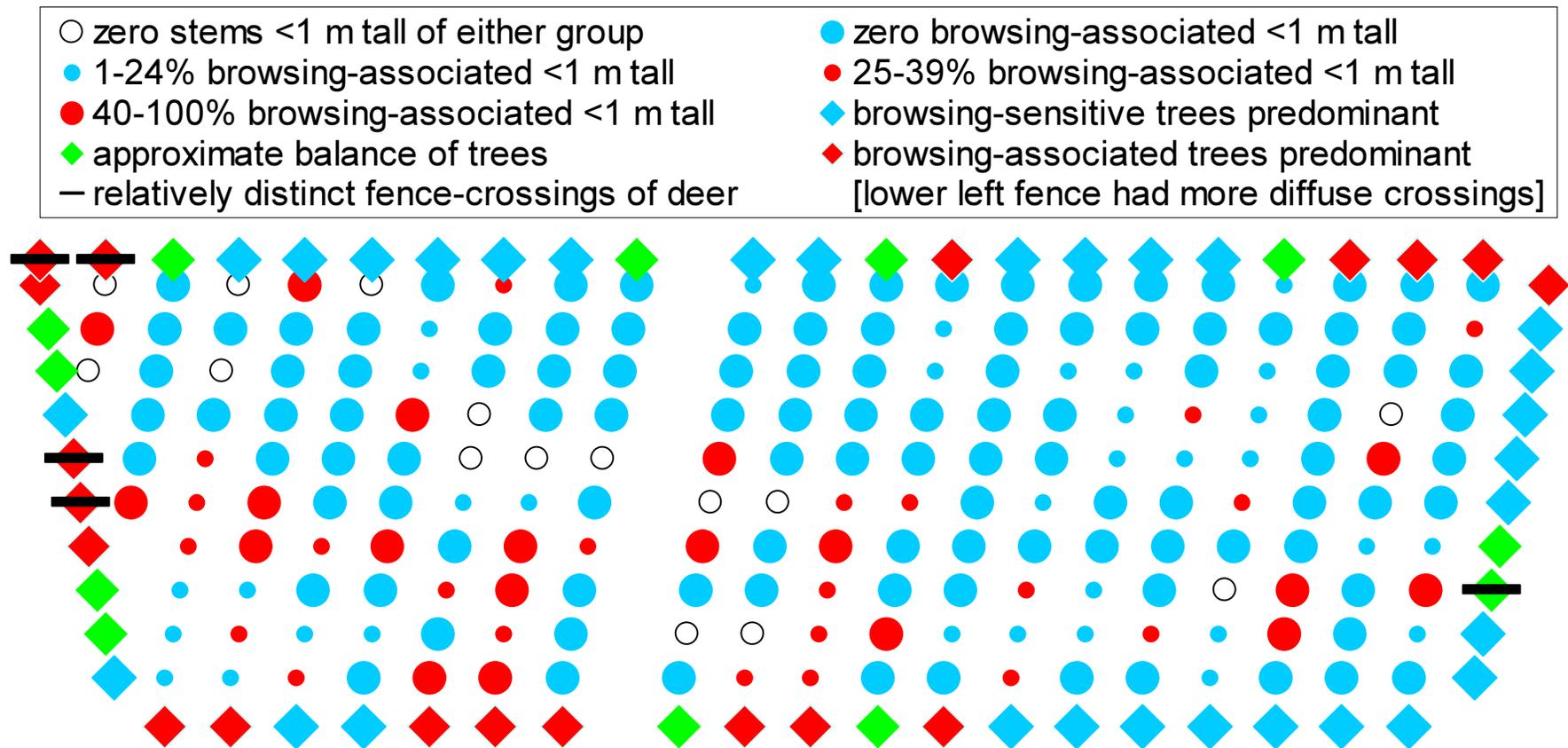
**Figure 2e.** Stems per plot [100 m<sup>2</sup>] of woody plants that are <1 m tall, excluding ‘subshrubs’ (*Rubus*, *Symphoricarpos*) and ground-covering vines (*Campsis*, *Toxicodendron*).



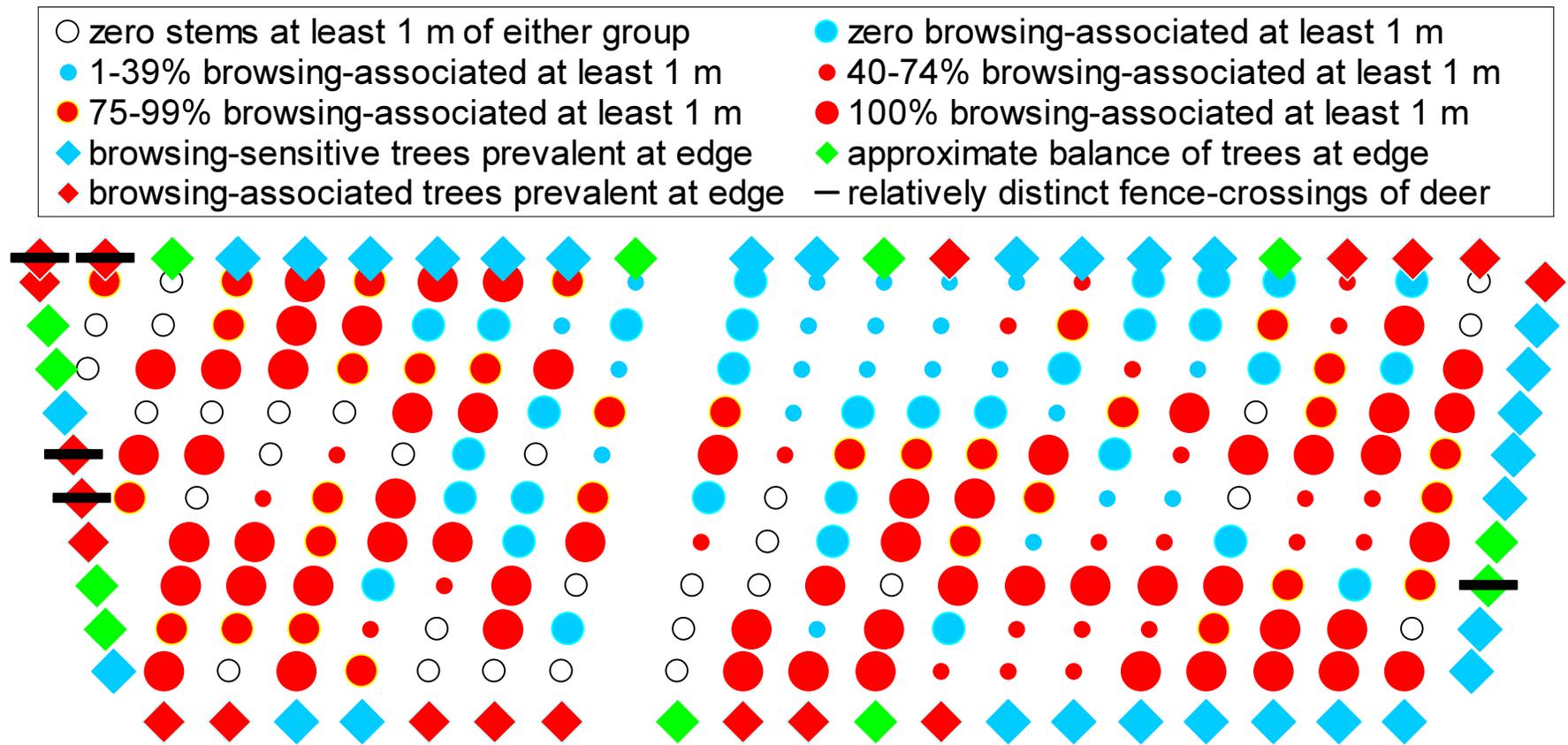
**Figure 2f. Stems per plot of woody plants that are at least 1 m tall, excluding ‘subshrubs’ (*Rubus*, *Symphoricarpos*) and ground covering vines (*Campsis*, *Toxicodendron*).**



**Figure 2g. Direct signs of recent browsing on blue ash and other plants in surveyed plots during September 2007.** In most cases, only one obvious sign was noted within each plot, but in a few cases there were two or three. Note that signs within the “central pathway” were limited to blue ash. Also, signs to the lower right may indicate a continued expansion of influence by deer in this direction.



**Figure 2h. Concentrations of browsing-associated trees and shrubs <1 m tall within the field (circles), plus concentrations of browsing-associated trees at least 10 cm dbh along adjacent fencerows and woodland edges (squares). Red-versus-blue indicates concentration of browsing-associated species versus browsing-sensitive (or neutral) species. [These data include the most abundant species, white ash and multiflora rose, which are excluded from Figure 5e in order to reveal trends there among less abundant species.]**



**Figure 2i. Concentrations of browsing-associated trees and shrubs  $\geq 1$  m tall within the field (circles), plus concentrations of browsing-associated trees at least 10 cm dbh along adjacent fencerows and woodland edges (squares).** Red-versus-blue indicates concentration of browsing-associated species versus browsing-sensitive (or neutral) species. [These data include the most abundant species, white ash and multiflora rose, which are excluded from Figure 6f in order to reveals trends there among less abundant species.]

**Figure 3 [subsequent pages]. Densities of trees and shrubs in three zones of the field.** See Figure 2 for mapping of these three zones. See Table 4 for common names of species. Blue charts indicate the “browsing-sensitive group” (including any “browsing-neutral” for provisional simplicity); orange charts indicate the “browsing-associated” group.

The three zones are abbreviated as follows.

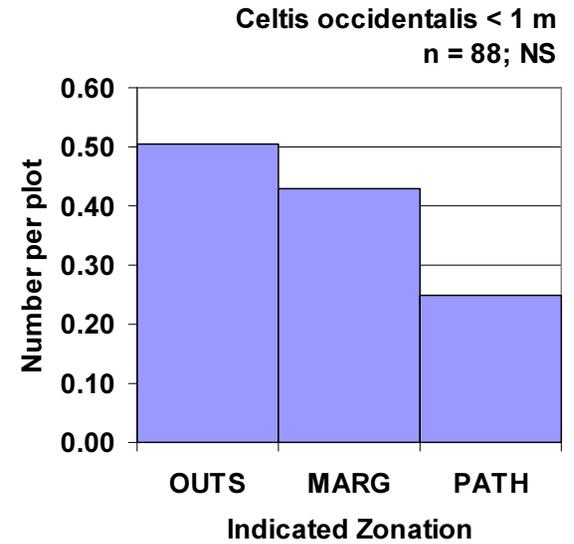
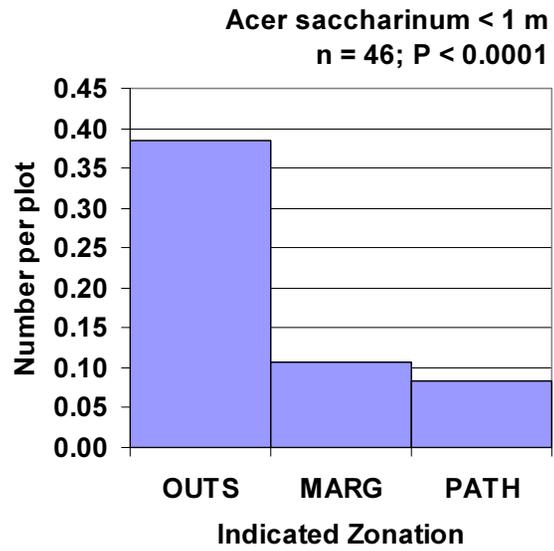
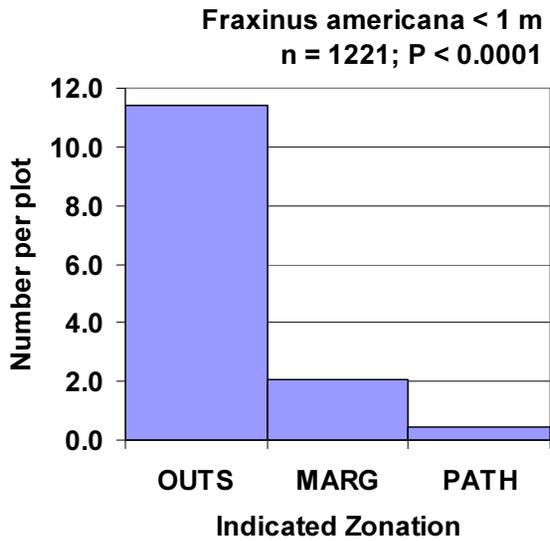
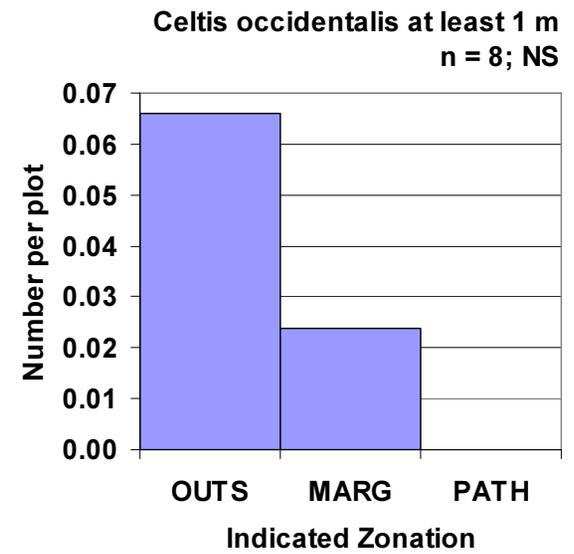
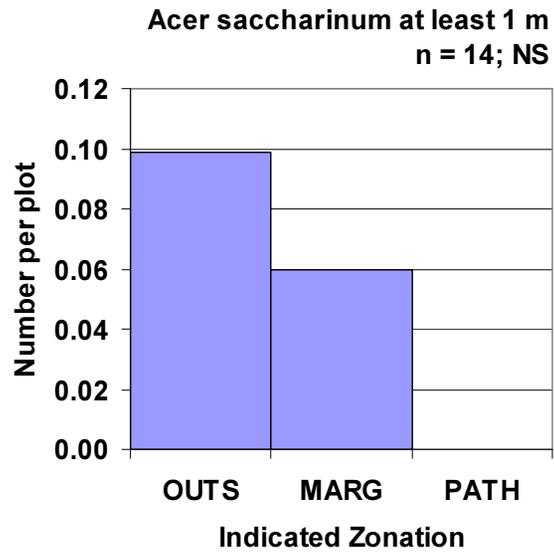
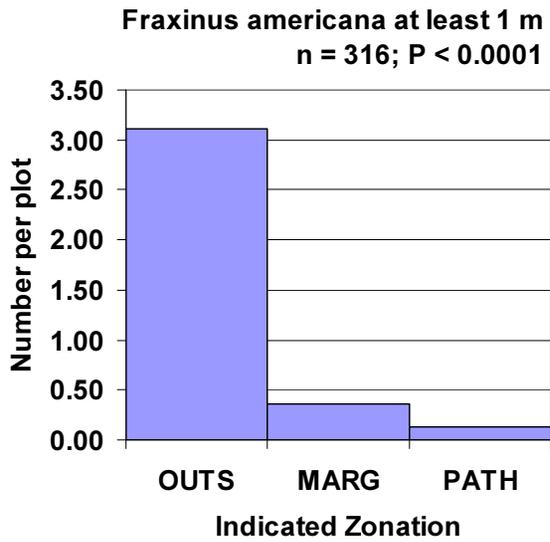
OUTS: outside concentrated influence and pathway of deer (mostly in northern section).

MARG: concentrated influence of deer marginal to central pathway.

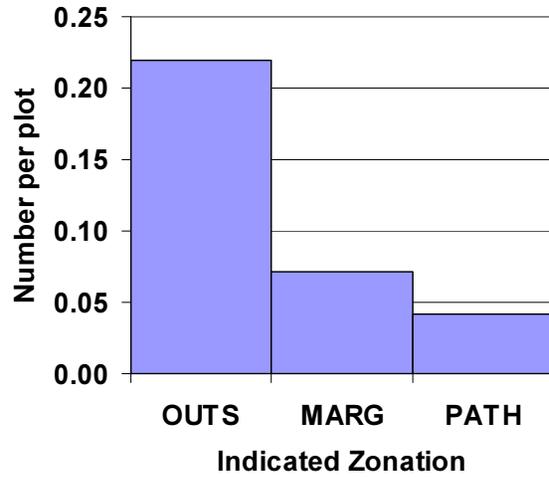
PATH: central pathway used by deer across the field (from west to east).

The combined “other species” are all classified here provisionally as “browsing-associated”:  
*Carya cordiformis*, *Elaeagnus umbellata*, *Gleditsia triacanthos*, *Gymnocladus dioicus*, *Juglans nigra*, *Pyrus calleryana*, *Robinia pseudoacacia* and *Sambucus canadensis*. The few stems of “browsing-sensitive” *Morus* spp., are excluded (all  $\geq 1$  m; OUTS = 2; MARG = 3; PATH = 0).

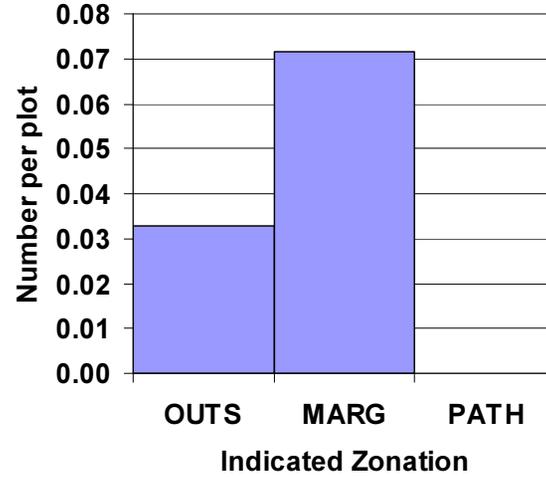
Chi-squared tests were used to compare observed distributions of stems with expected uniform distribution. In *Rosa multiflora*, stems spread clonally and are highly clumped, so the estimated numbers of multi-stemmed individuals were used for tests not the total numbers of stems.



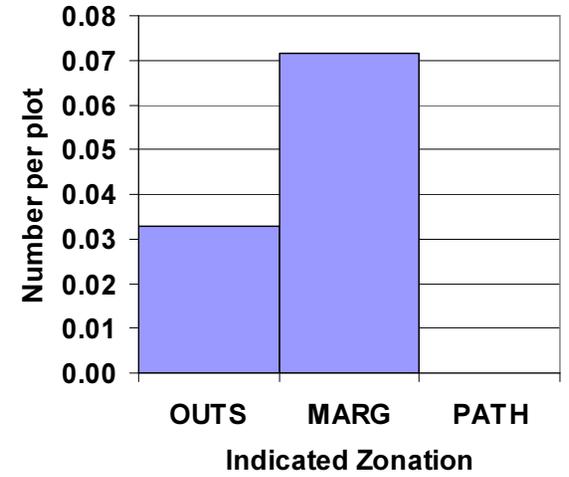
**Lonicera maackii at least 1 m**  
n = 8; NS



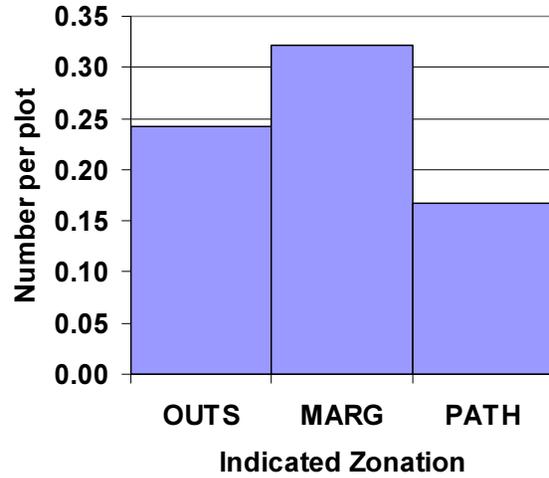
**Ulmus americana at least 1 m**  
n = 9; NS



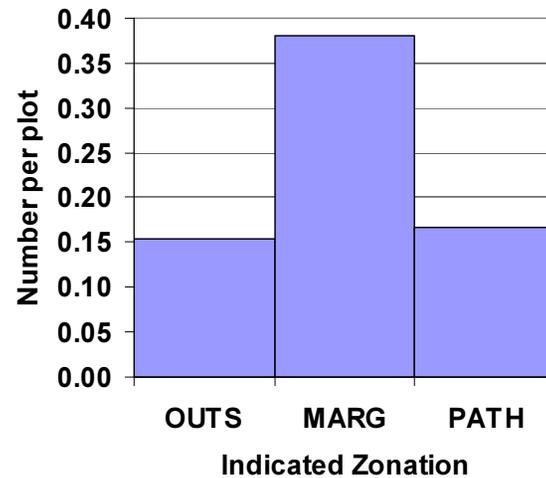
**Vitis vulpina at least 1 m tall**  
n = 9; NS



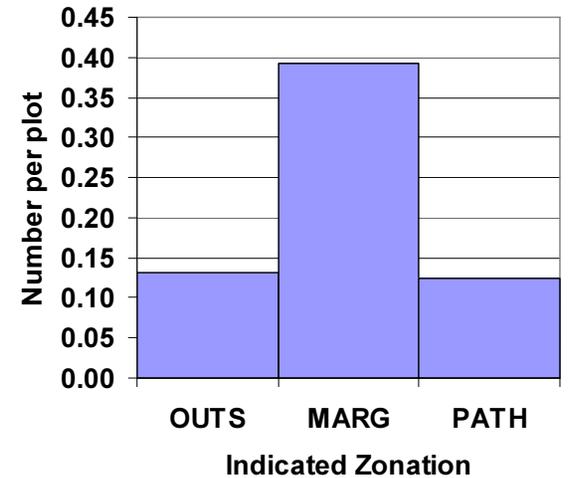
**Lonicera maackii < 1 m**  
n = 53; NS



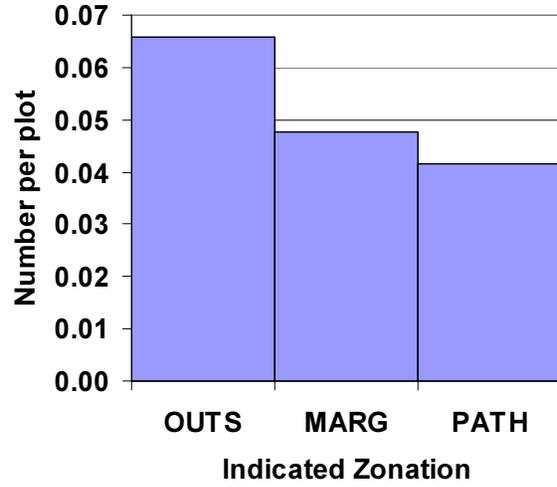
**Ulmus americana < 1 m**  
n = 50; P = 0.01



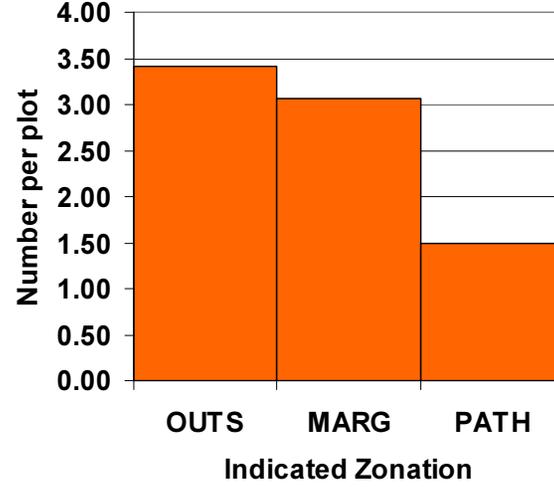
**Vitis vulpina < 1 m tall**  
n = 48; P = 0.001



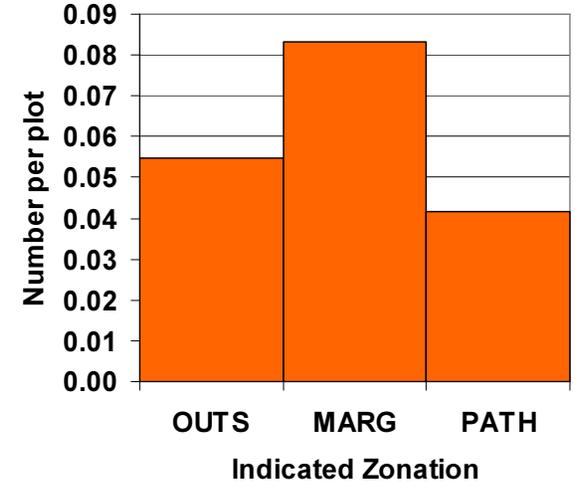
**Acer negundo at least 1 m**  
n = 11; NS



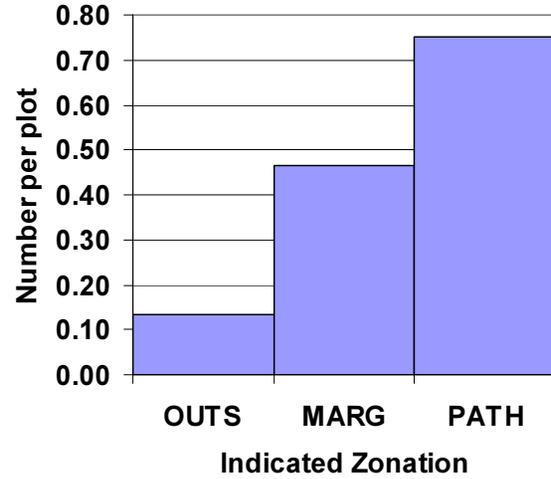
**Rosa multiflora at least 1 m**  
n = ca. 150; P = ca. 0.1



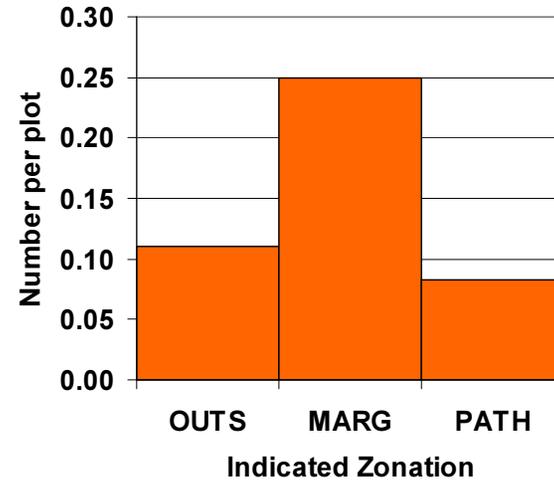
**Prunus serotina at least 1 m**  
n = 13; NS



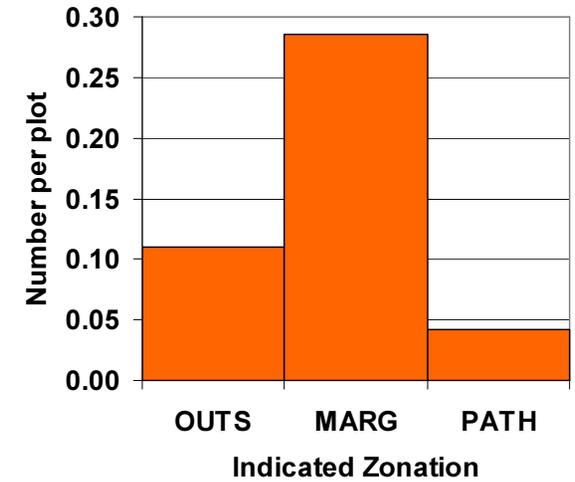
**Acer negundo < 1 m**  
n = 69; P < 0.0001

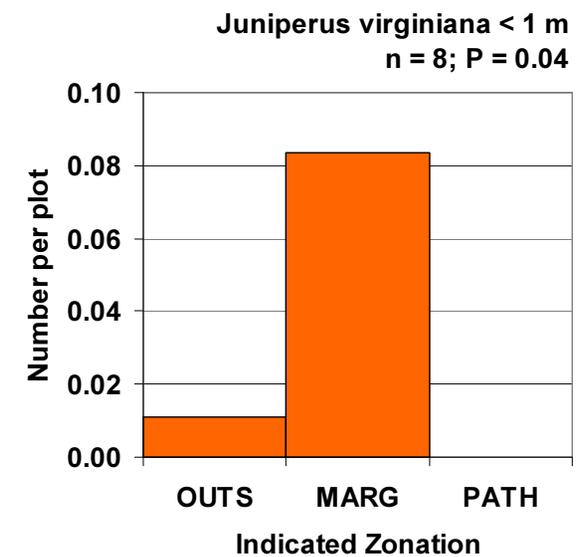
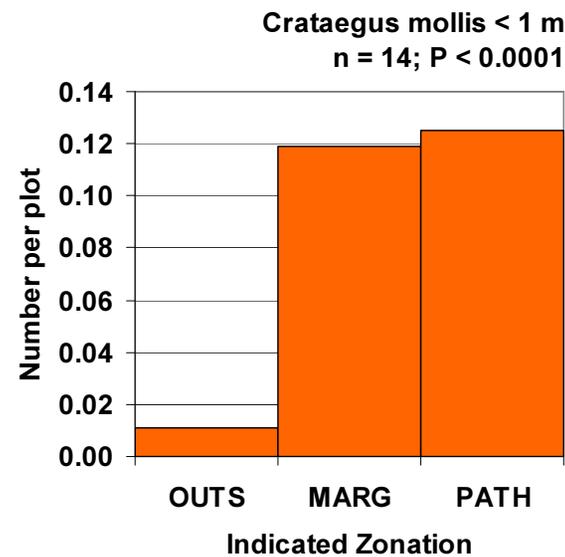
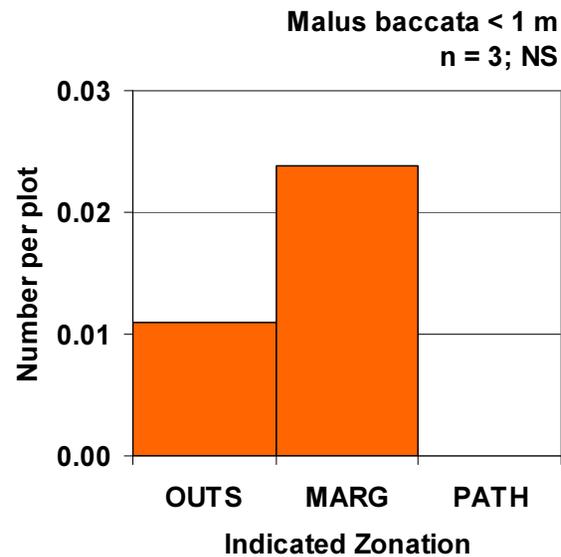
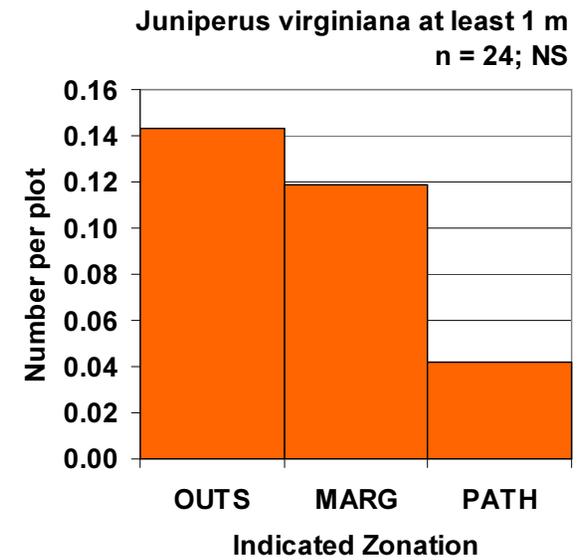
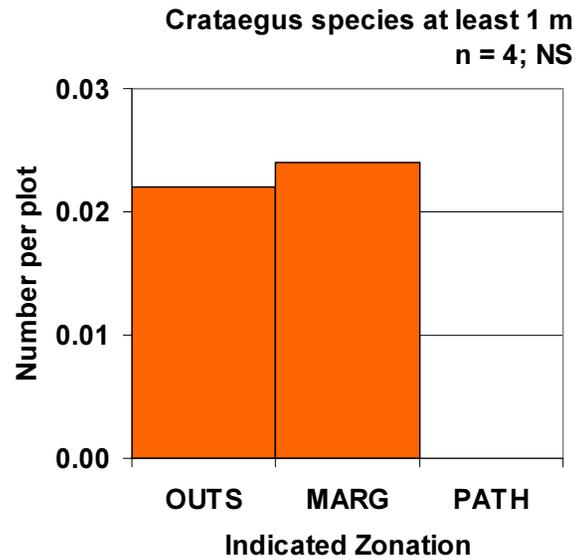
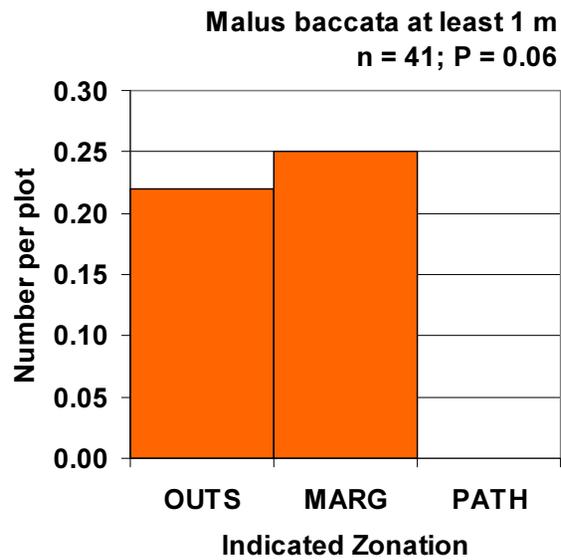


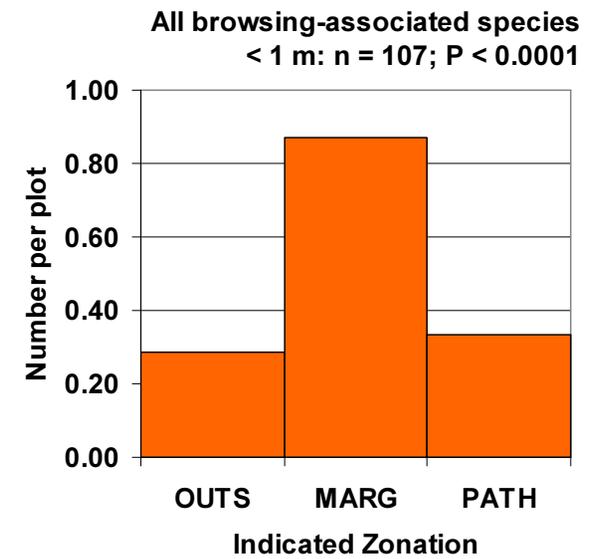
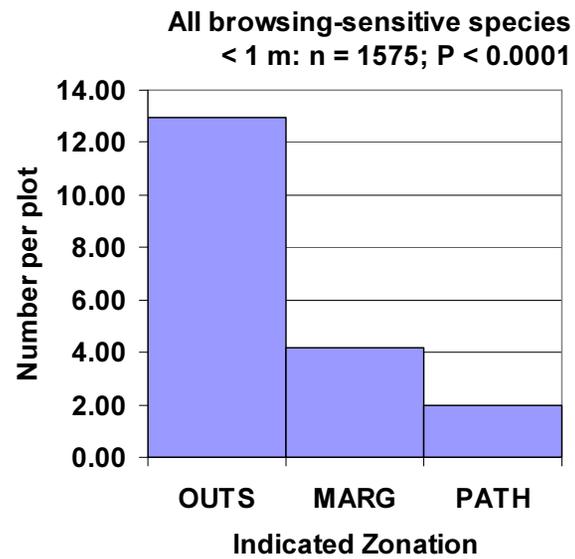
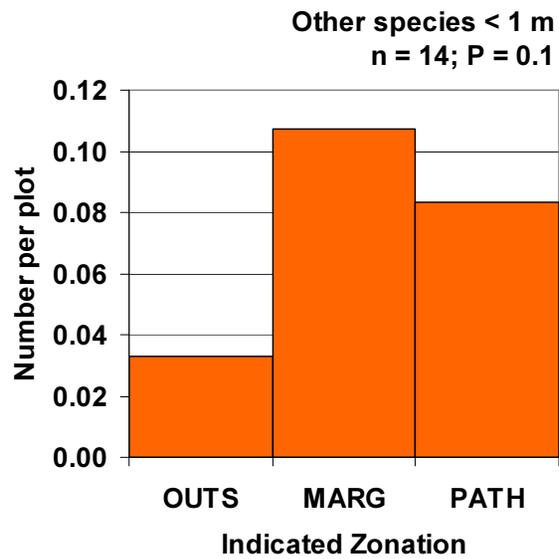
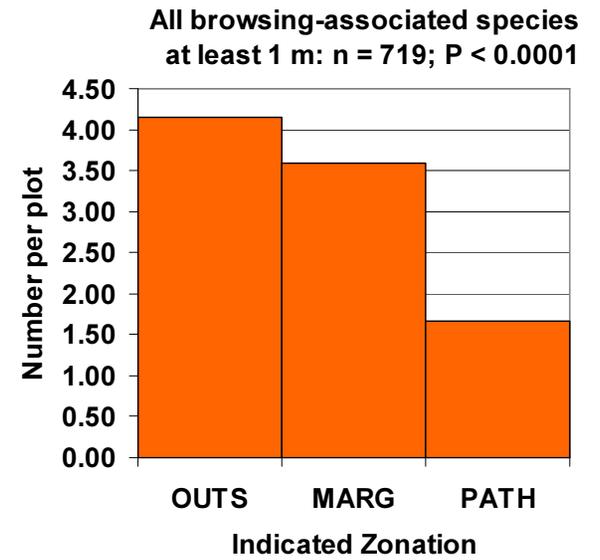
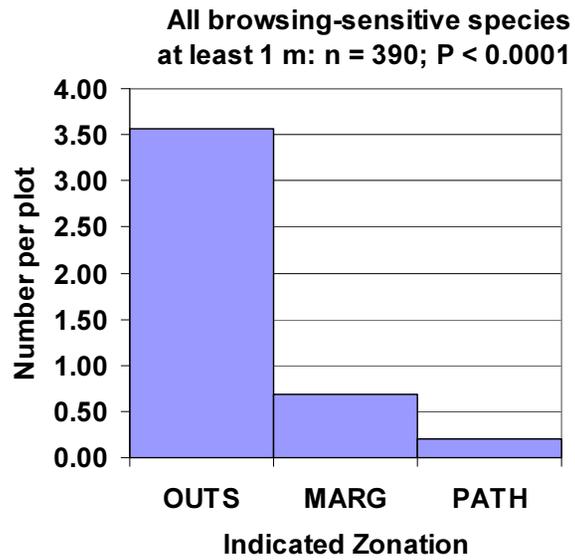
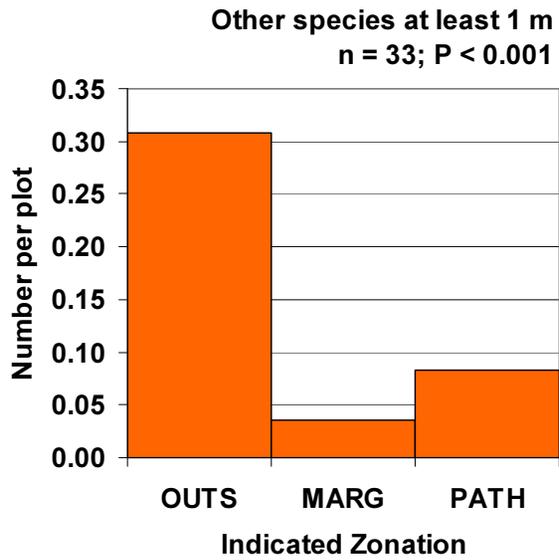
**Rosa multiflora < 1 m**  
n = ca. 15; P = ca. 0.1



**Prunus serotina < 1 m**  
n = 35; P = 0.005







**Table 5 [right]. Percent composition of trees in adjacent fencerows and woods.** See Table 4 for common names, and references to support division into the two groups. Asterisks indicate species not strictly native to this site.

**NOR:** composition of trees at least 10 cm dbh within 10 m around northern section of the field, where browsing-sensitive trees tend to predominate (south to include the fencerow adjacent to plots S1-7 and N10-6; Figure 2i).

**SOU:** composition of trees at least 10 cm dbh within 10 m around southern section of the field, where browsing-associated trees tend to predominant (north to include the fencerow adjacent to plots S1-08 and N10-5; Figure 2i).

**OLD:** composition of trees at least 50 cm dbh within the whole northern block of old-growth at Griffith Woods adjacent to Collection Field, covering about 25 acres [10 ha]; trees were surveyed here in 2004-2005 by A. Berry (2007).

Shading indicates where each species is most abundant; darker shading indicates that the amount is at least 4 percentage points more than in the other habitats.

Browsing-sensitive species	NOR	SOU	OLD
<i>Acer negundo</i>	0.0	2.2	0.0
* <i>Acer saccharinum</i>	0.0	0.0	0.0
<i>Acer saccharum</i> s.l.	0.9	1.5	0.3
<i>Celtis occidentalis</i>	30.1	26.2	3.7
<i>Fraxinus americana</i> s.l.	40.0	2.2	2.7
<i>Fraxinus quadrangulata</i>	0.9	2.9	63.8
<i>Morus rubra</i>	0.0	0.7	0.0
<i>Ulmus americana</i>	1.4	3.6	0.0
Browsing-associated species	NOR	SOU	OLD
<i>Aesculus glabra</i>	0.0	1.1	0.0
<i>Carya cordiformis</i>	0.7	3.6	0.0
<i>Carya laciniosa</i>	0.0	0.4	0.0
<i>Crataegus mollis</i>	0.7	1.5	0.0
<i>Gleditsia triacanthos</i>	0.0	0.0	0.0
<i>Gymnocladus dioicus</i>	0.5	5.0	0.7
<i>Juglans nigra</i>	2.8	8.7	1.4
<i>Juniperus virginiana</i>	0.0	0.0	0.0
* <i>Maclura pomifera</i>	0.0	2.2	0.0
<i>Prunus serotina</i>	9.4	18.9	0.9
<i>Quercus macrocarpa</i>	1.2	1.8	12.4
<i>Quercus muhlenbergii</i>	0.5	1.5	13.5
<i>Quercus shumardii</i>	0.0	0.0	0.2
<i>Robinia pseudoacacia</i>	10.8	16.0	0.3

## RESULTS

### Little Relationship between Dominant Plants and Topography

There was little overall trend across the field in composition of the most common grasses (*Festuca arundinacea*, *Poa pratensis*) and forbs (*Solidago altissima*, *Symphotrichum pilosum*). The pattern among these species (Figure 2a,b) showed no general relationship to elevation or aspect (Figure 1b,c). Only one of these species was associated with topography: *Symphotrichum pilosum* was most common on lower ground ( $P < 0.01$  with Spearman's rank correlation). Based on known indicator species (e.g., Hill et al. 1999), there was no clear evidence of a soil-related gradient within the vegetation, but a detailed soil survey in this field has yet to be made and some provisional analysis will be pursued in Part II. The only soil series mapped here in the Harrison County soil survey (Odor et al. 1968) is a typic argiudoll, "Loradale silt loam", with two phases: 2-6% slopes and 6-12% slopes. [This series is generally derived from ancient alluvium or residuum of limestone and calcareous shale; on the uplands at this site, it may intergrade with the typic hapludalf, "Lowell silt loam", especially where the original mollic A horizons have been reduced by farming; slightly steeper slopes just below the field have the typic hapludalf, "Faywood silt loam".]

There are a few spatial trends among the locally abundant species. These remain largely unexplained, but perhaps related to local variation in soils or to past management.

1. There was some diagonal tendency (south to north) for three zones of bluegrass-dominance, in addition to a general concentration in the southern part of the field (lower left of Figure 2b). The balance within bluegrass-fescue mixtures has been much studied, but it remains somewhat

unpredictable (e.g., Cutulle et al. 2013); fescue tends to indicate less mesic conditions in full sun, often on more compacted base-rich soils with more seasonal fluctuations in moisture level (Hill et al. 1999; and pers. obs.). It is possible that old farm roads led out to the northern corner within this field (towards local markets at Cynthiana), leaving some influence on soils.

2. The local abundance of old field aster (*Symphyotrichum pilosum*) in the two row sections at lower left might be largely attributed to an anomaly in recent management. Initial planting of trees in the field involved more aggressive weed control in these two rows (S-9 and S-10), with black plastic sheets and some herbicide during 2003-2004. This weedy aster is well known to benefit from temporary reduction in grass cover (e.g., Chmielewski & Semple 2001).

3. The bimodal distribution of trumpet-creeper (*Campsis radicans*) is curious (Figure 2c), perhaps indicating in part the locations of older fencerows or woodland margins. This species is well known to be concentrated along fencerows. It is moderately browsed by deer (e.g., Castleberry et al. 1999), but reportedly allergenic to some humans (e.g., Yatskievytch 2006).

### **Browsing-associated Forbs, Subshrubs and Vines.**

The most frequent species in the browsing-associated group included poison hemlock (*Conium maculatum*), wild carrot (*Daucus carota*), tick-trefoil (*Desmodium perplexum*), wild parsnip (*Pastinaca sativa*), horse-nettle (*Solanum carolinense*) and ironweed (*Vernonia gigantea*), plus patches of the subshrubs, old field blackberry (*Rubus pensilvanicus*) and coralberry (*Symphoricarpos orbiculatus*). Only two of these (*Conium*, *Rubus*) were locally abundant in the field, exceeding 10% cover in a few plots. In contrast, the browsing-neutral or sensitive group included 6 of the 8 locally abundant species within the field (Figure 2a). The total cover of browsing-associated species increased away from the road in much of the field,

but there was also a concentration in the southwestern half of the field (to left in Figure 2d). The first row, close to the highway, was somewhat anomalous due to local dominance of poison-hemlock (*Conium maculatum*) in the north and locally frequent wild parsnip (*Pastinaca sativa*) in the south. Graphical display of the total cover indicates a general minimum within central rows (Figure 4), and some details of Figure 2 suggest a bimodal pattern from northern to southern corners.

In comparing the biology of these two groups (Table 3: a versus b), the browsing-associated group includes all species that have spines on leaves or stems (8 of 25 versus 0 of 26). It also includes most species with reported mammalian toxicity or highly repellent chemistry (10 versus 6), although this classification remains tentative. Most (17/25) of these browsing-associated species have one or both (*Solanum carolinense*) of these traits. This group also includes most annuals and biennials (10 versus 2), and all three subshrubs but not the two woody vines. It includes the two species with clear adaptation to dispersal in mammalian fur, and the three species with showy fruits that are probably dispersed often in mammalian guts. Several additional species appear to have occasional or frequent dispersal on fur or in guts but without clear specialization; see literature cited for Table 3. Under 'reported deer-browsing degree' the browsing-associated group includes 10 species with none or none-low, 9 with generally low, 5 species with moderate or variable usage, and only 1 with moderate-high or high (*Trifolium pratense*). The browsing-neutral or sensitive group includes 0 species with none or none-low, 7 with generally low, 11 with moderate or variable, and 8 with moderate-high or high.

## Browsing-associated Trees and Shrubs

The total density of invading trees and shrubs declined generally away from the road in the northeastern part of the field (Figures 2d, 2e, 5a, 6a), and the proportion of browsing-associated species generally increased. However, these trends were largely due to decline away from the road in density of the wind-dispersed white ash (*Fraxinus americana*), which is often preferred by deer (Figure 5b, 6b; Table 4). Moreover, the concentration of white ash regeneration near the front can be partly attributed to the concentration of seed-producing parents in the fencerow along the highway (Figures 2h-i, Table 5). Trees bordering the southern part of the field, where peripheral plots have “concentrated influence” of deer indicated in Figure 3, were dominated by browsing-associated species more frequently than trees around the northern part of the field: 14-7-11 (red-green-blue in Figure 2h-i) versus 5-5-19;  $P = 0.03$  with Fisher’s exact test. White ash was the tree species most concentrated around the northern part of the field. [The zone of “concentrated influence” overlaps to the right of the shift in trees.]

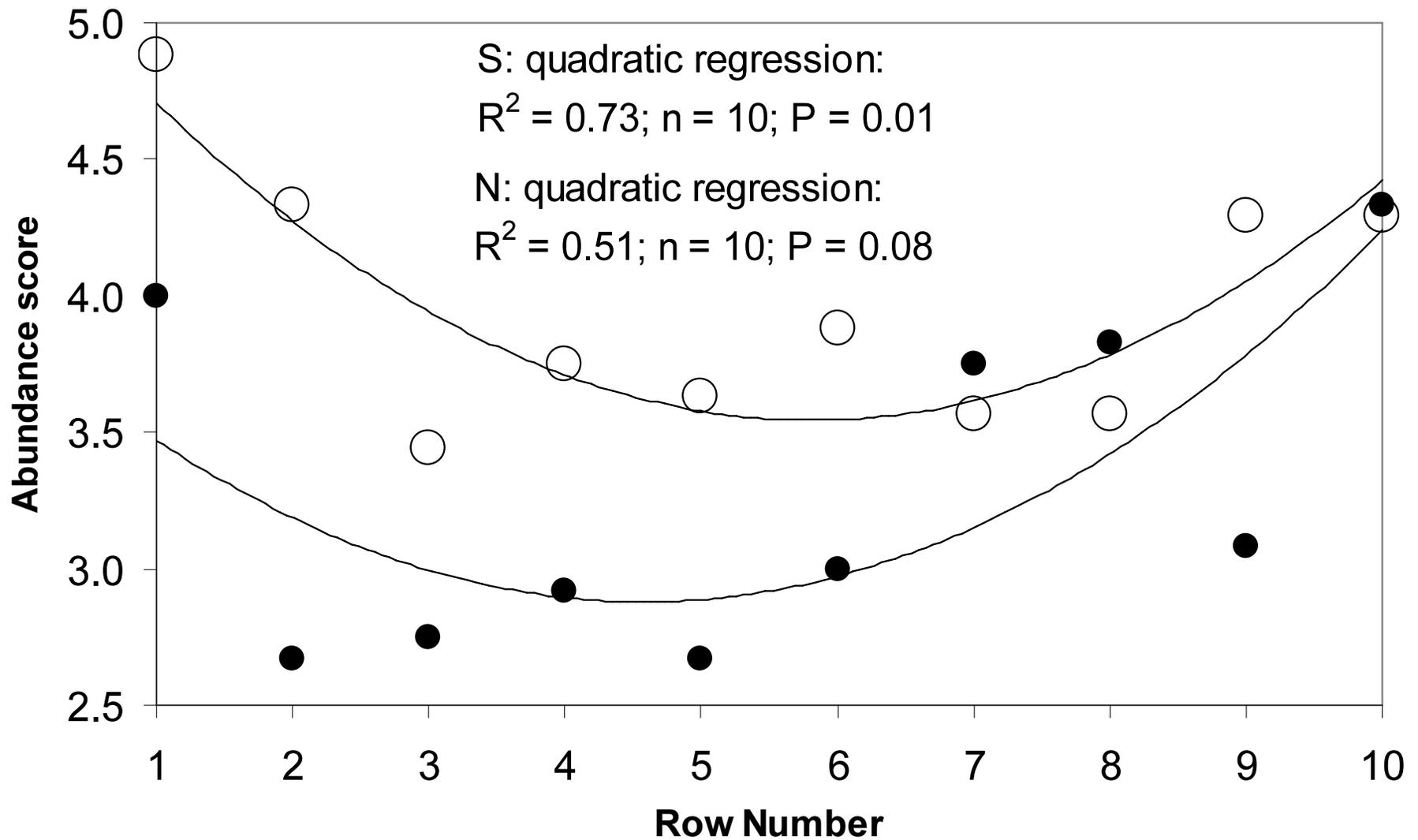
In contrast to white ash, with high preference by deer, the most common woody species with less preference is multiflora rose (*Rosa multiflora*), which tended to be concentrated in central rows (Figures 5c, 6c). However, stem numbers of multiflora rose displayed intense patchiness due to their clumping habit, and many older plants had dead or dying stems (Figure 6d). A less common thorny species, black locust, also displayed intense patchiness in its density, due to clonal spread from a few fencerow trees. If white ash, multiflora rose and black locust were excluded, there was little consistent trend across the field in total woody densities (Figure 5d, 6e). However, there was still a general increase away from the road in the proportion of browsing-associated species, especially within the northeastern part of the field

(Figure 5e, 6f). This pattern appeared to reflect the general route of travel by deer across the field (Figure 2d-g).

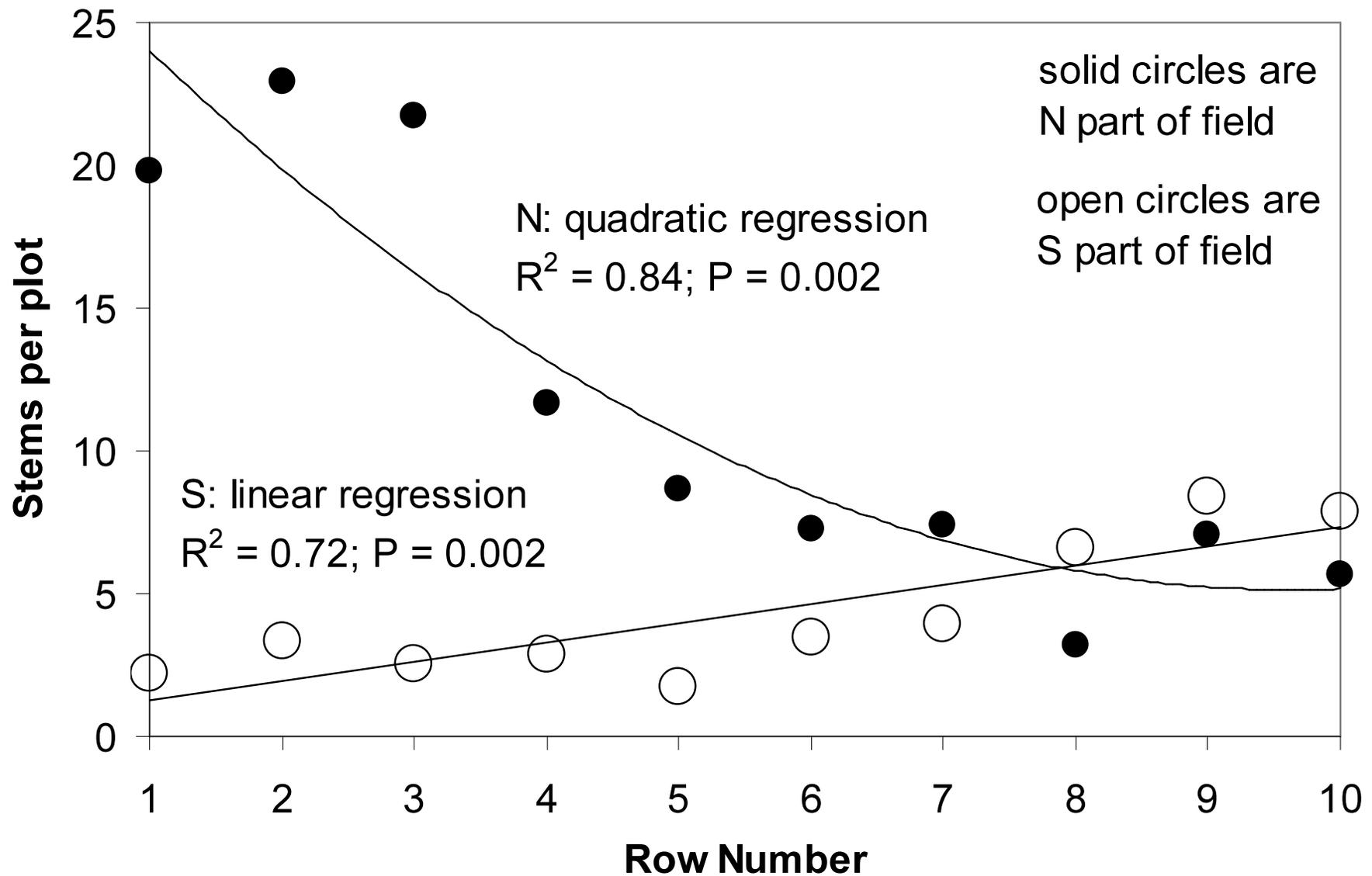
Division of the field into three zones based on the interpreted influence of deer allows the corresponding distributions of each woody species to be compared in more detail (Figure 3): the central pathway (PATH), the broad marginal zone with concentrated influence (MARG), and the zone outside concentrated influence (OUTS). Browsing-associated species (dominated by *Rosa multiflora*) were generally most dense in MARG or slightly more dense in OUTS. In *Crataegus mollis*, density of seedlings (<1 m tall) was highest within PATH. Browsing-sensitive or neutral species (dominated by *Fraxinus americana*) were generally most dense in OUTS and declined more strongly to MARG and then PATH. However, two of these species were most dense in MARG, at least as seedlings (*Ulmus americana*, *Vitis vulpina*), and seedlings of box-elder (*Acer negundo*) showed a clear increase from OUTS to MARG to PATH; see further discussion below.

The browsing-associated group of species includes almost all of those with mammalian toxicity or very low palatability (7 versus 1 coded X/x under “Traits”), and all species with thorns or spiny leaves (9 versus 0 coded T/t). Most of this group have either toxicity / unpalatability or thorns / spines (14/16 versus 1/9). It also includes all 10 species with largely mammal dispersed fruits (coded M and N) and none of the 4 species with wind-dispersed fruits (coded W). It includes all 13 species that are clearly intolerant of shade (coded I ), and almost all species with some ability to spread by lateral root suckers or rhizomes (8 versus 1 coded R/r).

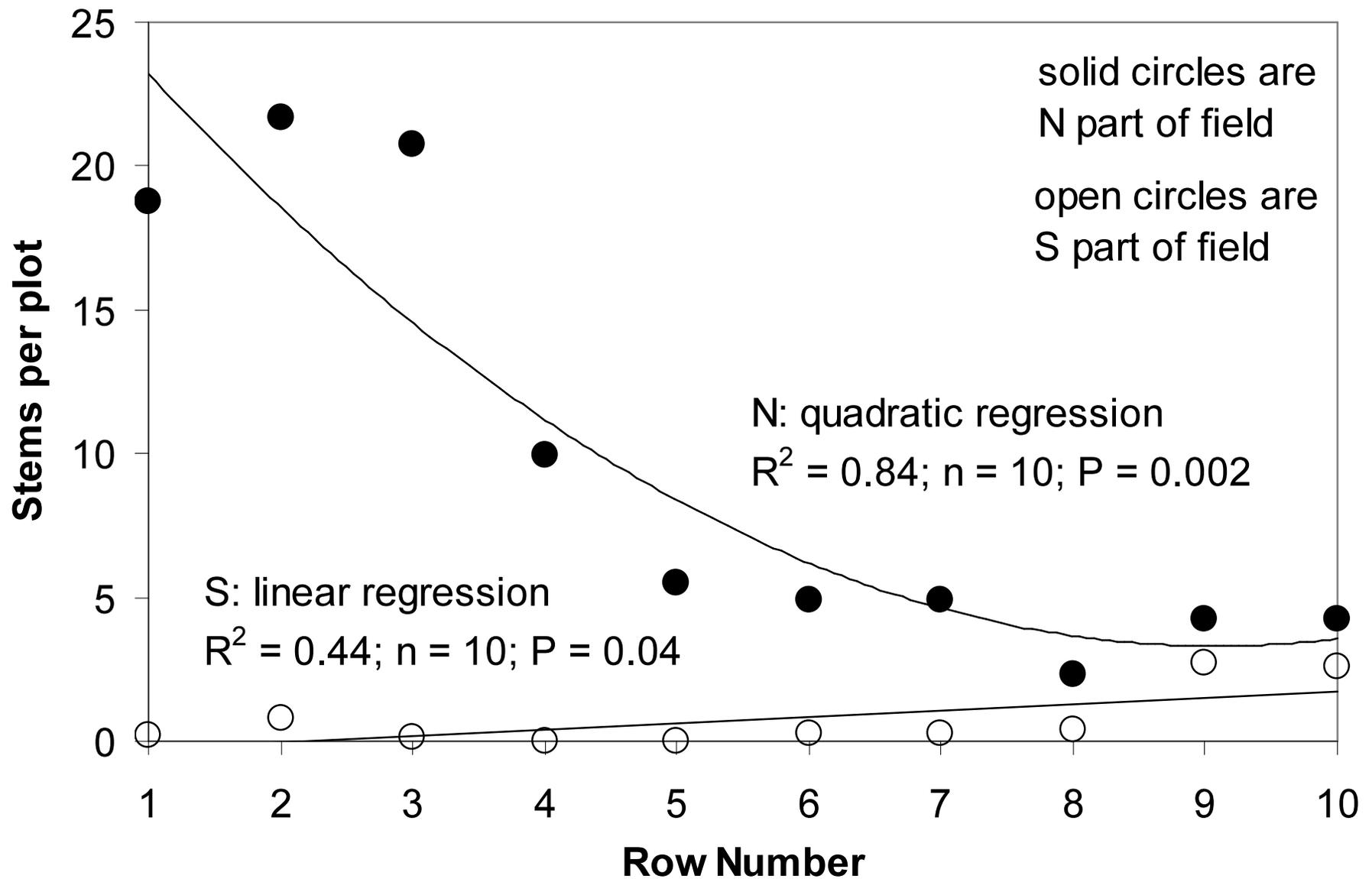
High potential growth rate is generally correlated with intolerance of shade (Valladares & Niinemets 2008), and the browsing-associated group generally had higher percentages of stems  $\geq 1$  m tall (under “Sap” in Table 4). Total percentages  $\geq 1$  m tall were 87% (707 of 814) for the browsing-associated group, and 20% (390 of 1963) for the browsing-sensitive / neutral group;  $P < 0.0001$  with chi-square test. Most browsing-associated species ranged from 17% to 95%; most browsing-sensitive / neutral species ranged from 8% to 34% (excepting infrequent species). The browsing-associated group also had more observed occurrences within the mowed strips between surveyed rows, up to 5 m from each unmowed plot (under “Mow” in Table 4). These mowed stems were mostly resprouts after mowing, and they were probably underestimated. For browsing-associated species, the incidence of mowed stems expressed as a percentage of the total stems surveyed within the unmowed rows was 3.8% (31 of 817). For the remaining browsing-neutral or -sensitive group, the ratio was 0.8% (16 of 1963);  $P < 0.0001$  with chi-square test. For individual species, numbers were generally too small for statistical comparisons, but most browsing-associated trees had percentages of 3-50%, while most of the remainder had percentages of 0-3% (with *Ulmus americana* the only exception).



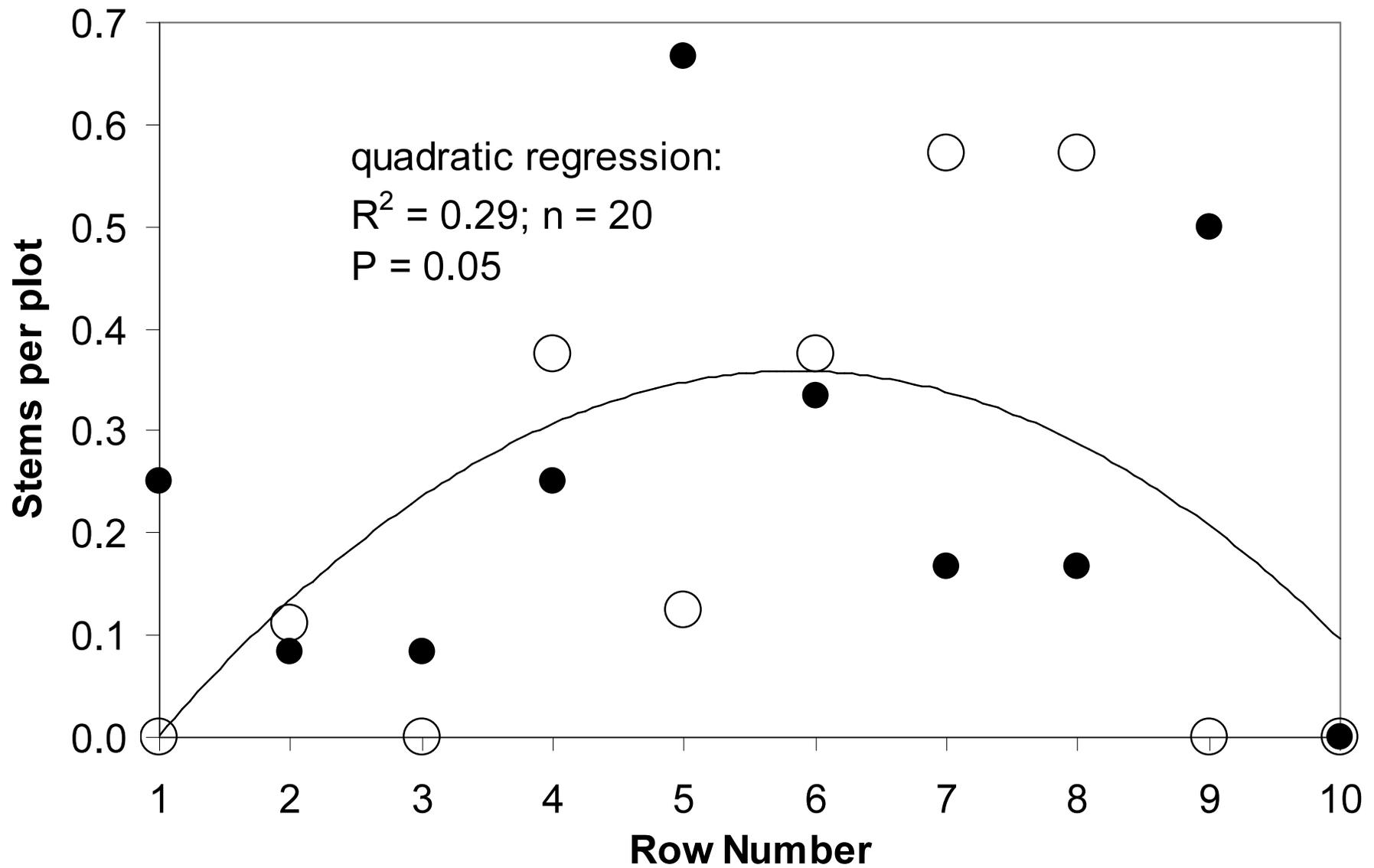
**Figure 4. Mean of total cover score for browsing-associated forbs and subshrubs in each row section. Solid points are from northeastern (N) part of the field; open points are from the southwestern (S) part.**



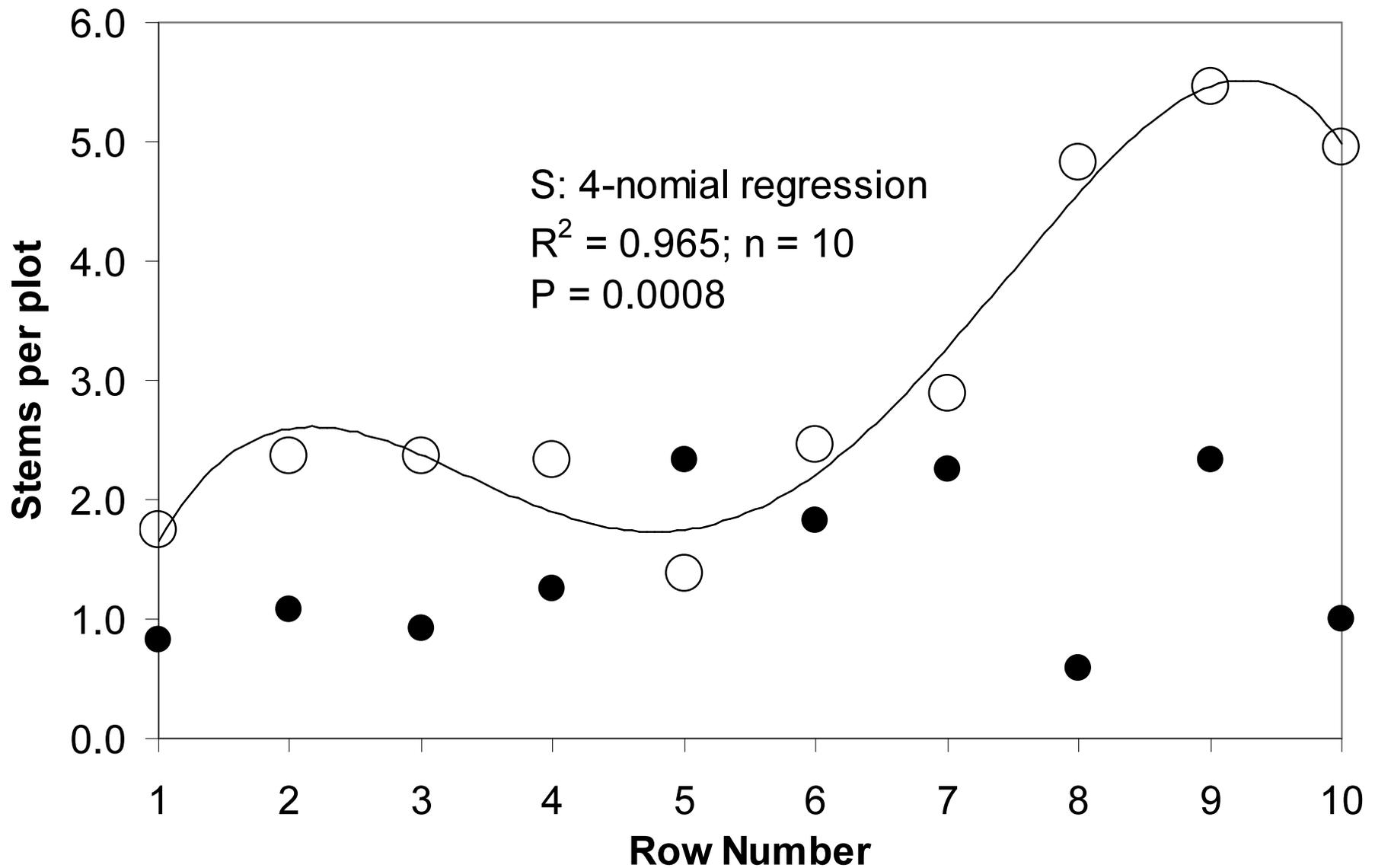
**Figure 5a. Number per plot of all woody stems <1 m tall in each row section, separating northeastern (N) and southwestern (S) parts of the field. Numbers exclude ground-covering vines, subshrubs and clearly connected sprouts from taller individuals (especially *Rosa*).**



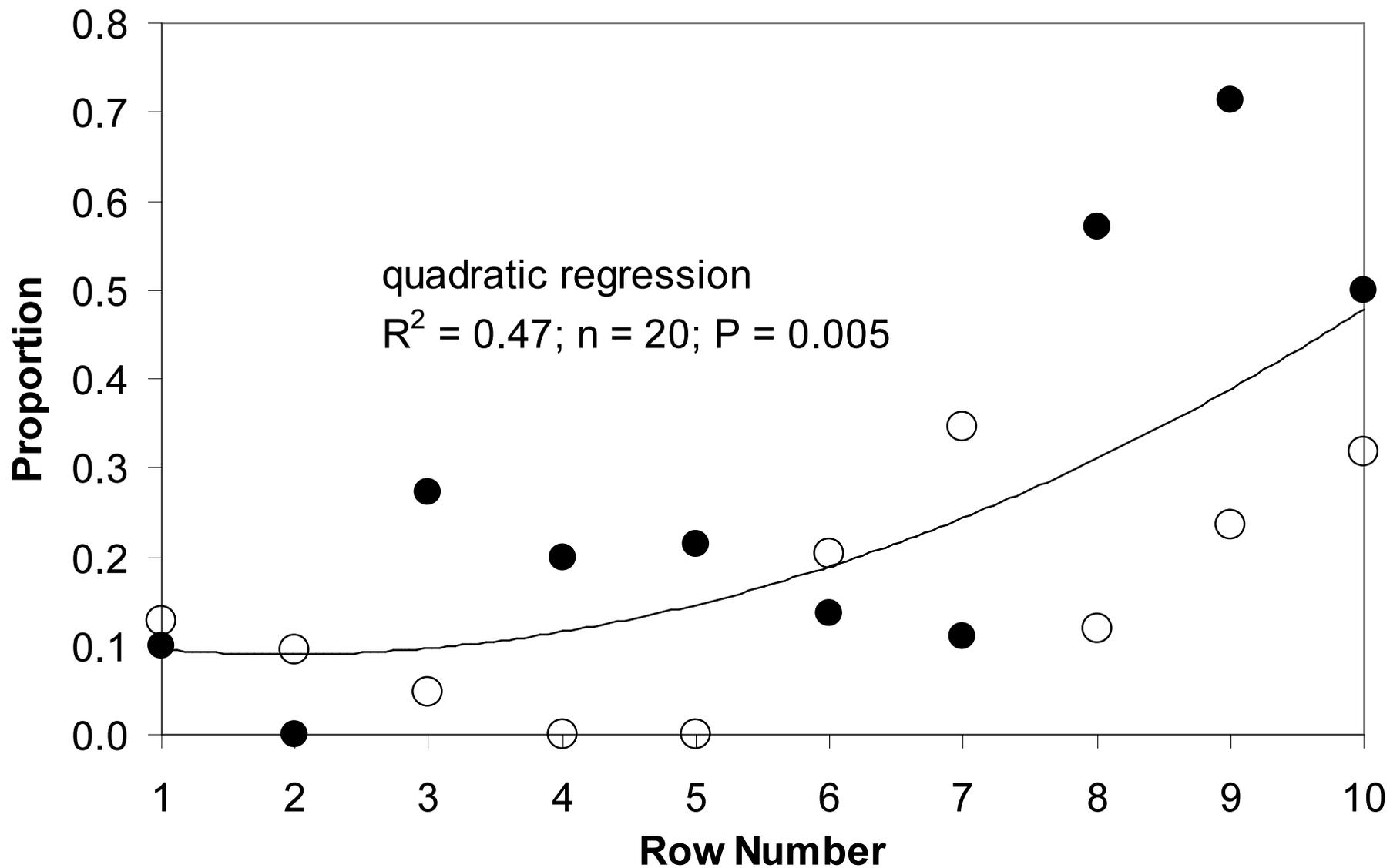
**Figure 5b. Number per plot of white ash stems <1 m tall; all are single stems (not sprouts).**



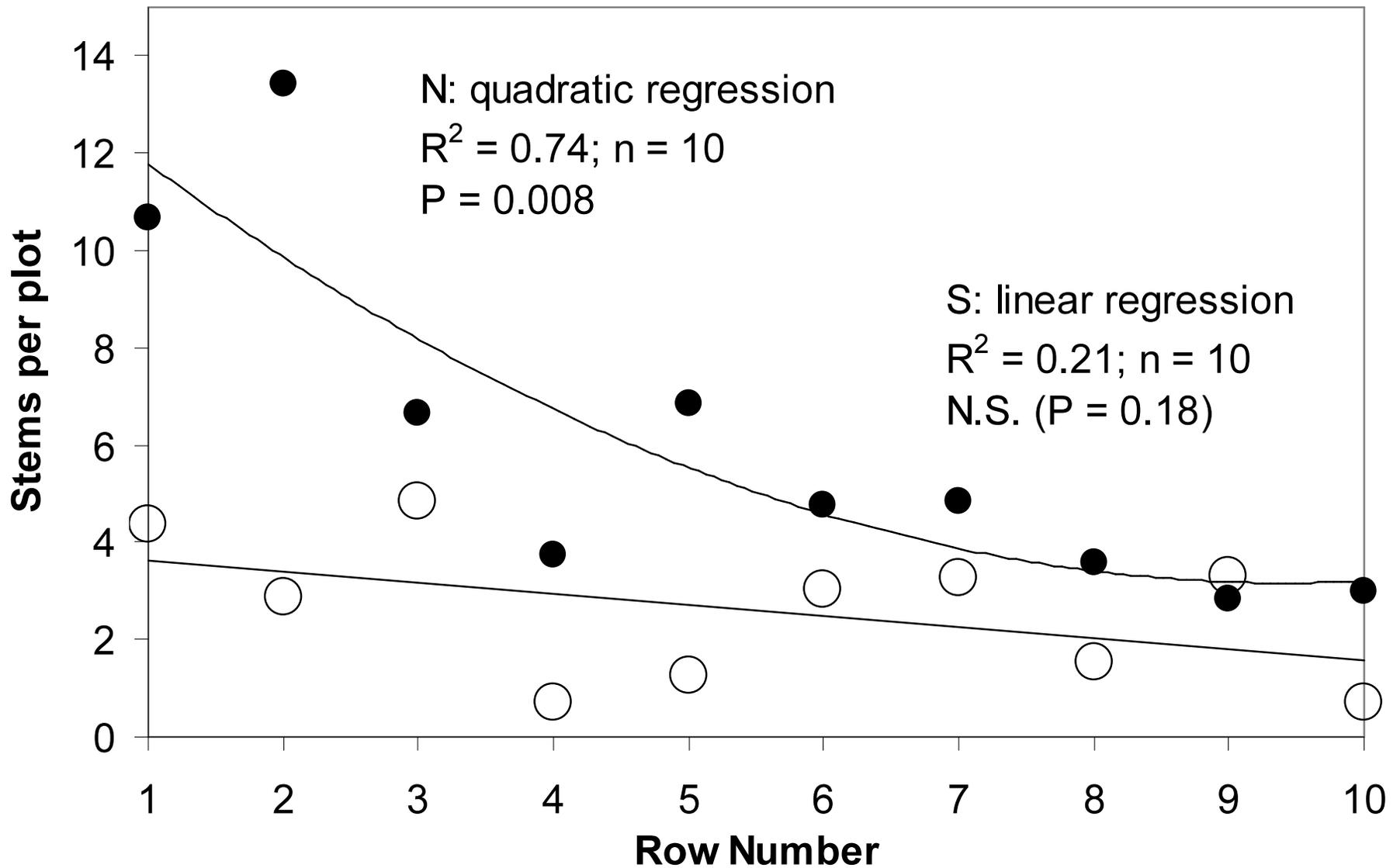
**Figure 5c. Number of stems per plot of multiflora rose plants with all stems <1 m tall.**



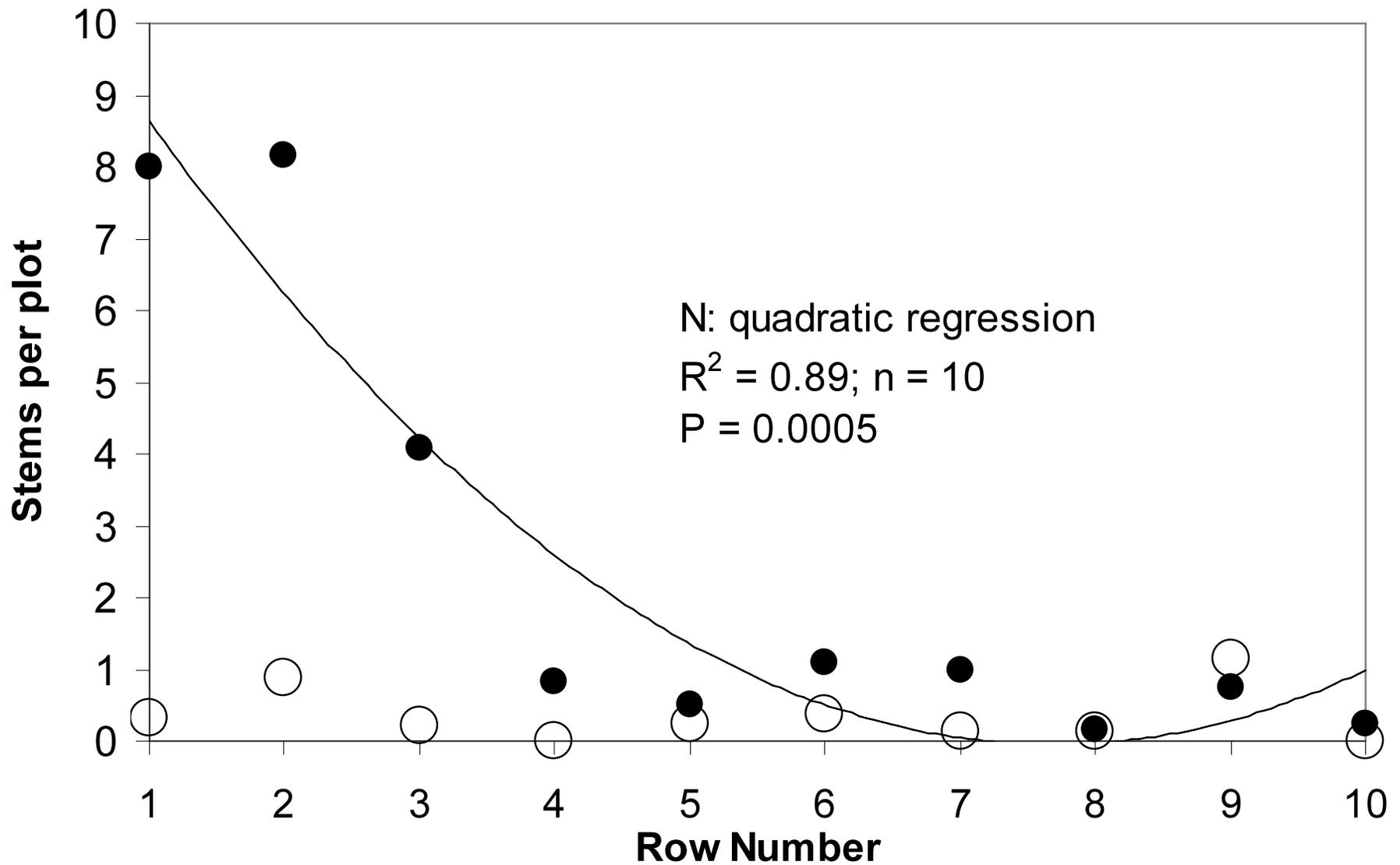
**Figure 5d. Number per plot of all woody stems <1 m tall in each row section, as in Figure 4a but excluding white ash and multiflora rose.**



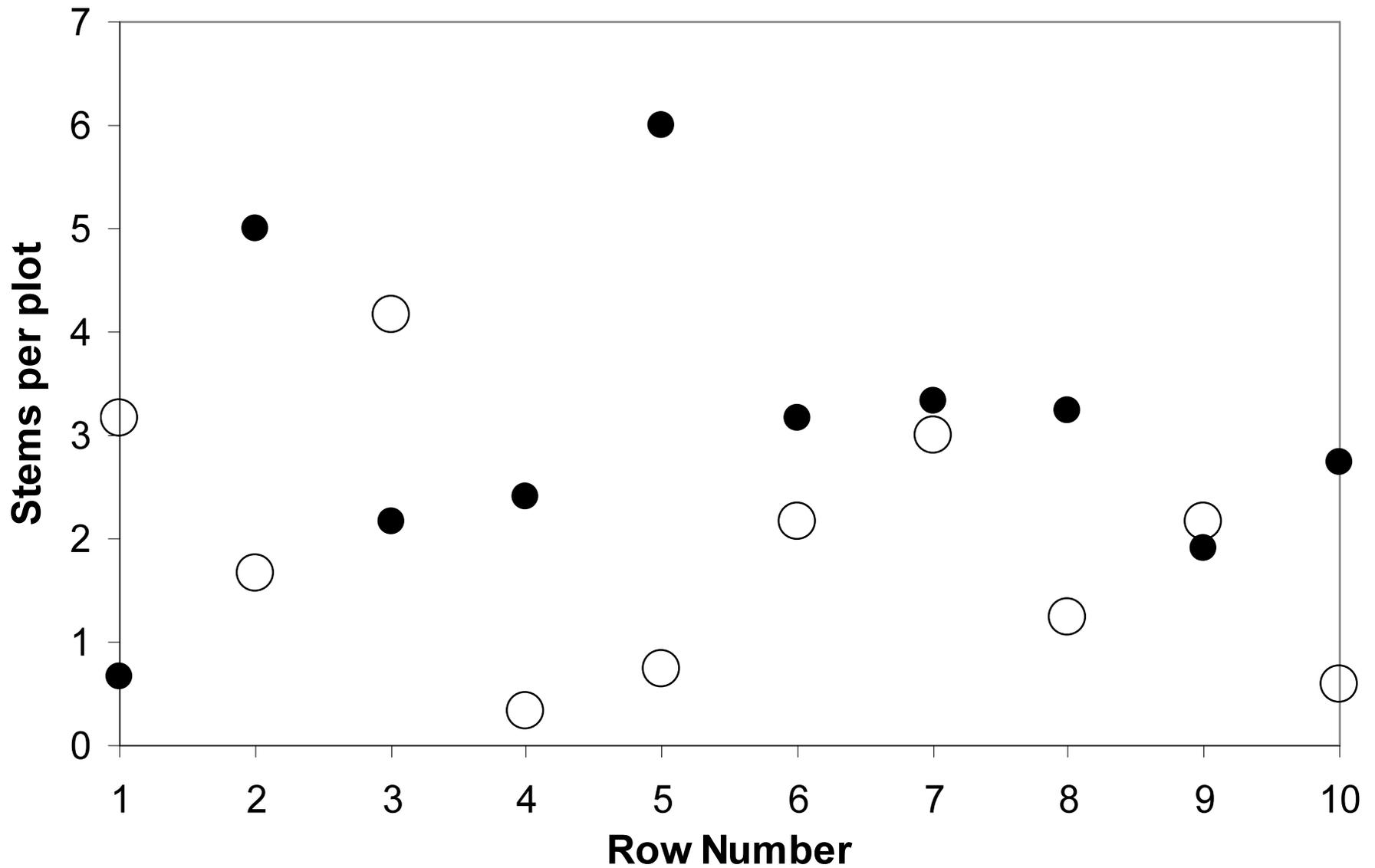
**Figure 5e. Proportion of browsing-associated species among woody plants <1 m tall, as in Figure 5a but excluding white ash and multiflora rose. Regression is for all points.**



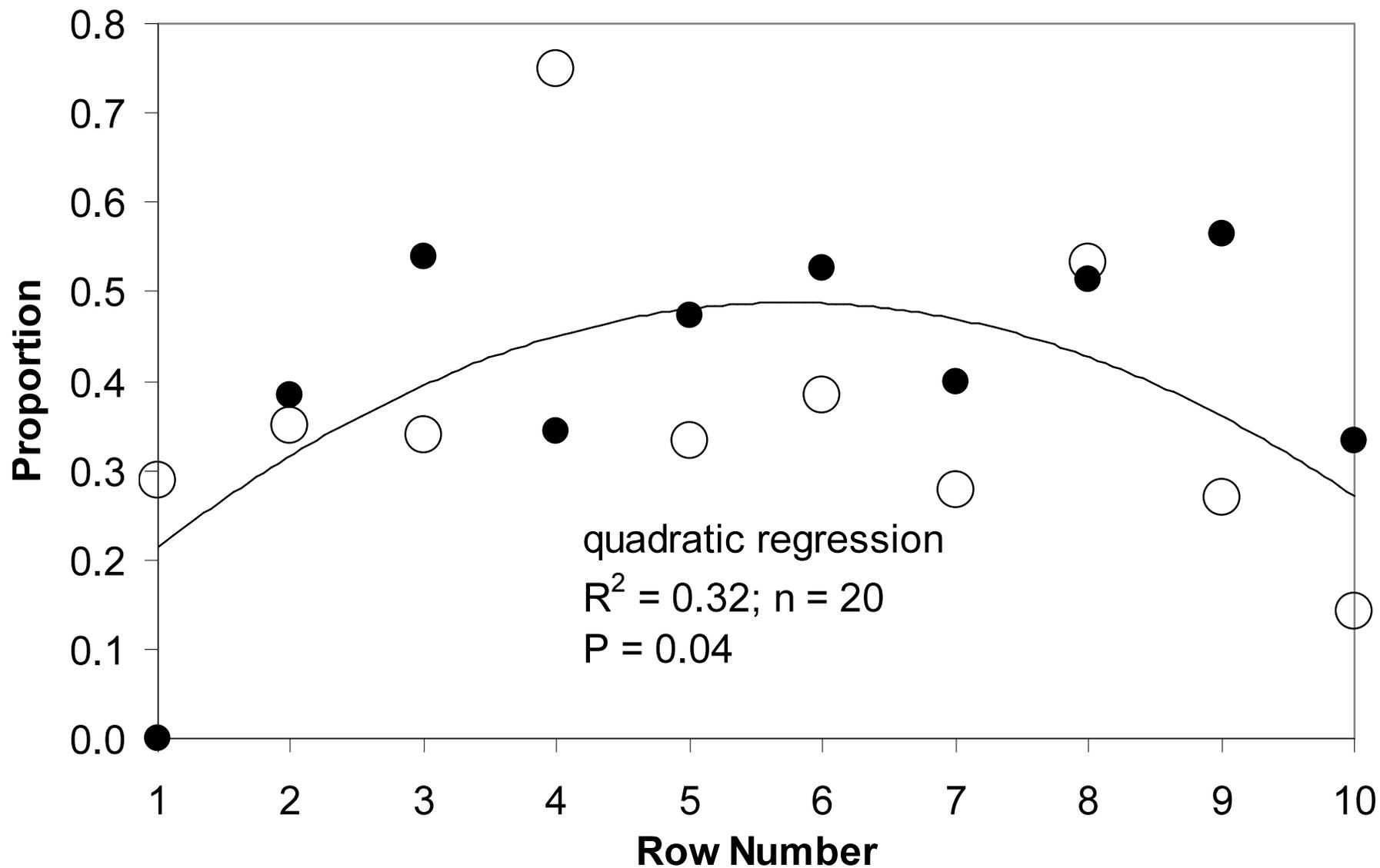
**Figure 6a. Number per plot of all woody stems  $\geq 1$  m tall in each row section, separating northeastern (N) and southwestern (S) parts of the field. Numbers exclude ground-covering vines, subshrubs and clearly connected sprouts from taller individuals.**



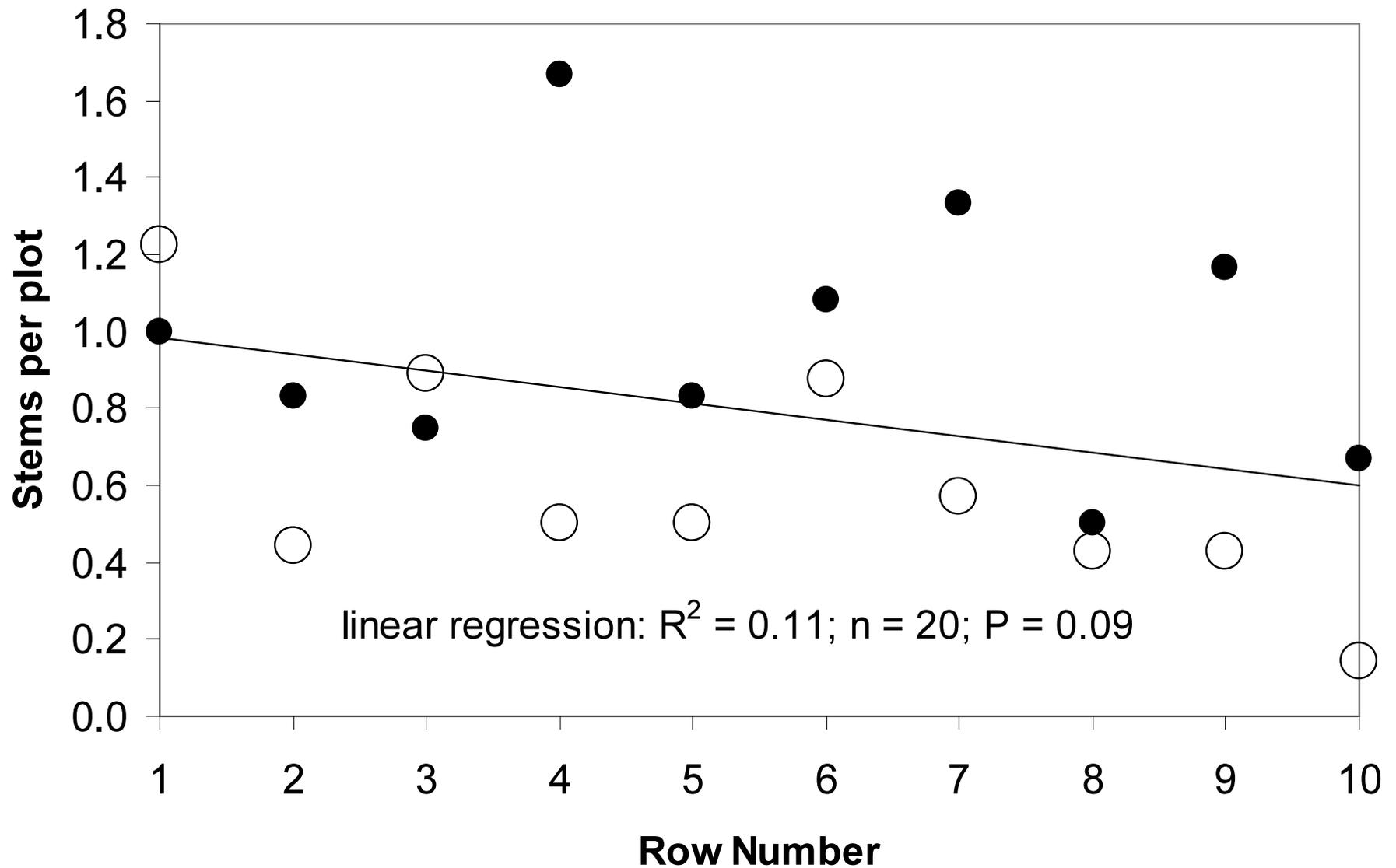
**Figure 6b.** Number per plot of white ash stems  $\geq 1$  m tall. All are single stems (not sprouts).



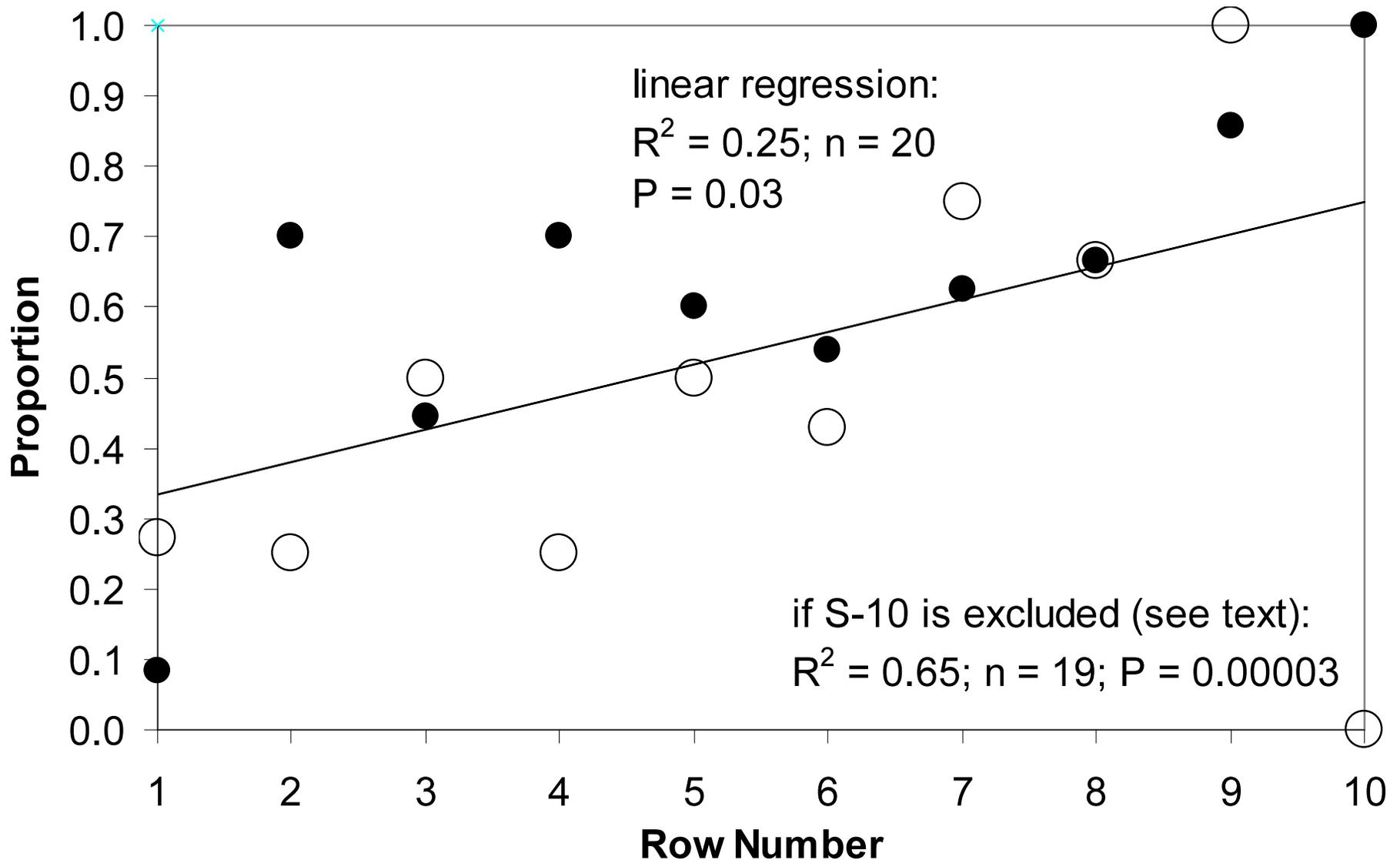
**Figure 6c. Number per plot of multiflora rose plants with at least one stem  $\geq 1$  m long. There are no significant trends.**



**Figure 6d. Proportion of dead or sick stems of multiflora rose plants with a least one stem  $\geq 1$  m long.** “Sick” stems are weighted by half in the numbers. Note: there was also a significantly lower proportion within the “central pathway” of Figure 3 (0.32 versus 0.44).



**Figure 6e. Number per plot of stems of woody plants  $\geq 1$  m tall, as in Figure 6a but excluding white ash, multiflora rose and black locust. [These three species have patches of intense local abundance.]**



**Figure 6f. Proportion of browsing-associated species among woody plants  $\geq 1$  m tall, as in Figure 5a, but excluding white ash, multiflora rose and black locust.**

The outlying point S-10 (back row in southwestern section of field) is based on an unusually small total ( $n = 2$ ), but additional non-counted sprouts of rose (7) do outnumber ash (0).

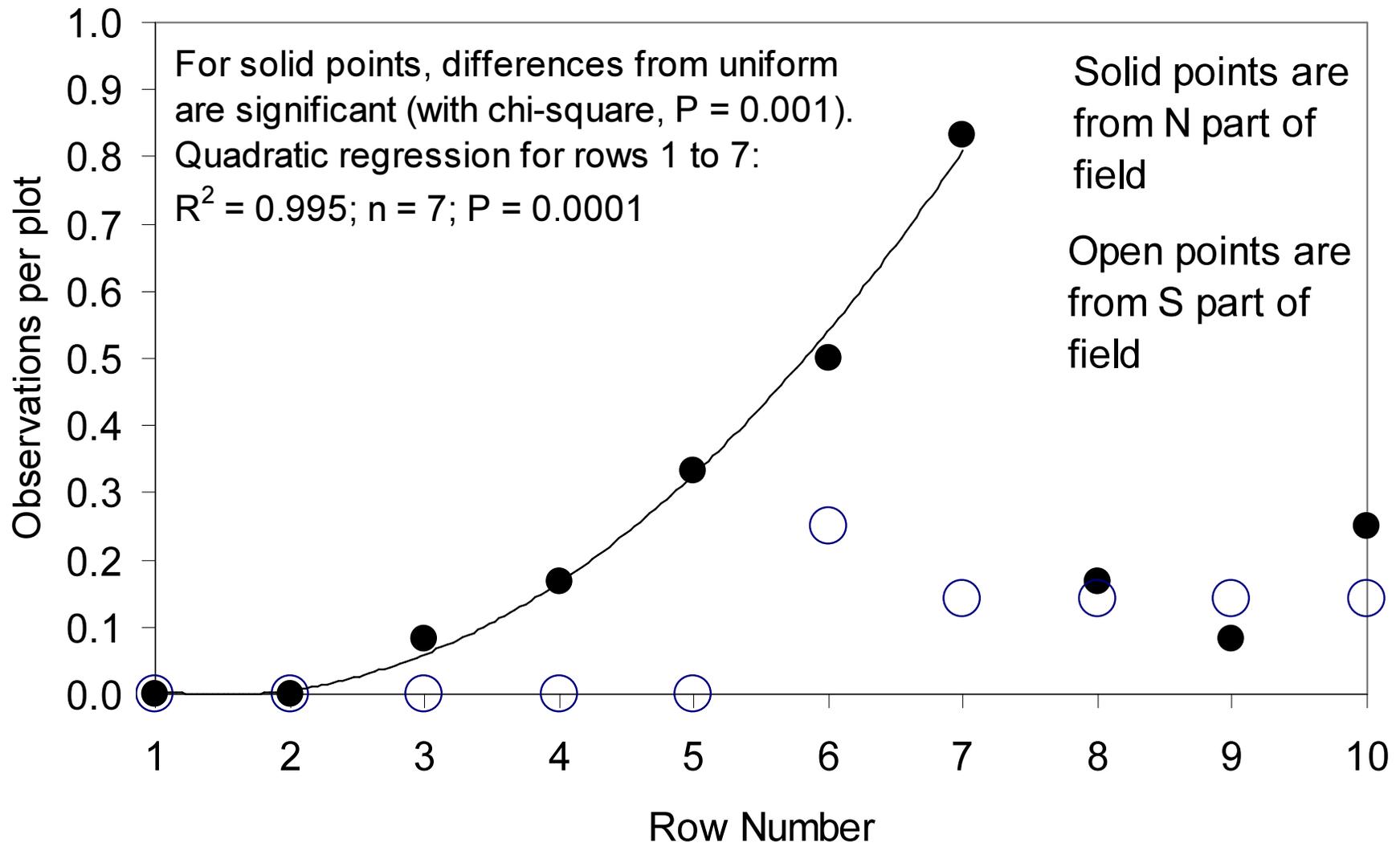
## Direct Signs of Damage by Herbivores, and Correlations among Parameters

About 59 direct signs of recent damage by herbivores were noted in Sep 2007, including 26 on the planted blue ash. Numbers were not sufficient for statistical comparison of plant species, but the most frequently noted species apart from the blue ash were white ash (9 cases) and bush honeysuckle (6 cases); other woody species included box-elder, sugar maple, roughleaf dogwood, red mulberry, Siberian crabapple and elderberry. None of these species are in the ‘browsing-associated’ group except the latter two (Table 4). Curiously, the few forbs with noted damage were among the ‘browsing-associated’ group: *Desmodium perplexum* and *Physalis longifolia*; despite some browsing, these two species may spread readily into browsed zones with seed or rhizomes.

The frequency of these signs increased away from the road but peaked in central to back zones across much of the field (Figures 7, 11b). These signs were concentrated along margins of the broad pathway for deer that was indicated by observations of vegetation composition (Figure 2g). This trend suggests that more palatable forage was relatively abundant along the margins, in contrast to the central pathway—which probably had a history of selection for plants that can resist or tolerate browsing. It is notable that the only signs of damage within the central zone of the indicated pathway were on the planted blue ashes (square symbols in Figure 2g). To avoid confusion, data from these planted blue ashes were excluded from the correlations summarized in Table 6. With observations averaged for each of the 20 row sections, the frequency of signs per plot was loosely correlated with abundances of browsing-associated plants, especially the proportion of these species among trees and shrubs <1 m tall (A with C in Table 6a).

However, there appeared to be some non-linearity in relationships between the incidence of herbivory and varied vegetation parameters: (1) overall abundance of browsing-associated forbs and subshrubs (Figure 8a); (2) proportion of browsing-associated species among all trees and shrubs (Figure 8b); and (3) total density of all trees and shrubs (Figure 8c). For these charts, data from herbivory on blue ash were combined with general observations on the vegetation since numbers were small in some cases. The 199 plots were grouped into classes with increasing values of the vegetation parameters. With quadratic or trinomial regression, maximum frequency of herbivory appeared to be at intermediate parameters in all three relationships. These trends support the general concept that a dynamic balance exists between the incidence of herbivory and response of the vegetation.

Further complexity is indicated by correlations among varied woody densities among the 199 plots (Table 6b). Using Spearman's rank correlation, proportions of browsing-associated trees and shrubs were highly correlated between smaller plants ( $<1$  m) and larger plants ( $\geq 1$  m), as were total densities of smaller and larger plants. Yet while the proportion of browsing-associated trees and shrubs  $\geq 1$  m tall (largely reflecting the ratio of rose to ash) was positively correlated with total density of plants  $\geq 1$  m tall (with more rose), it was negatively correlated with total density  $<1$  m tall (with more ash); see D and E in Table 6b. It is possible that larger woody plants became concentrated in areas which later became more browsed, reducing density of smaller stems, especially white ash. As seen in Figure 8, recent signs of damage from herbivores tended to have non-linear relationships with proportions of browsing-associated species, and with total woody densities. Thus, several rank correlations among all 199 plots provided limited insight (A in Table 6b).



**Figure 7. Signs of herbivory in relation to row section.** These are direct observations of damage by herbivores from the vegetation survey, but excluding damage to the planted blue ash saplings; see Figure 11b for data from blue ash.

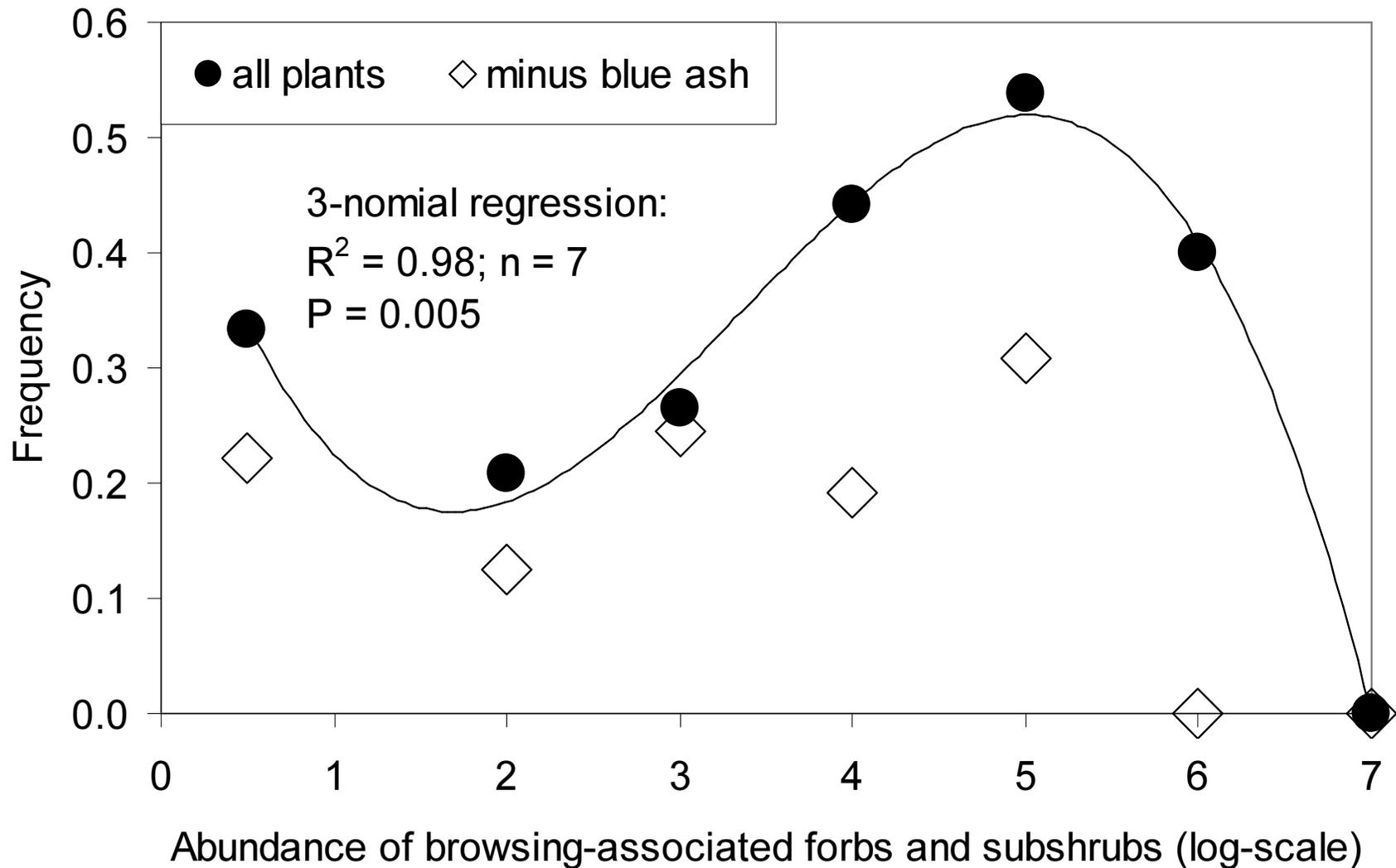
**Table 6a. Spearman’s rank correlations (corrected rho) between potential indices of browsing in each of the rows.** In all correlations, n = 20 for the 20 row sections. See Tables 3 and 4 for lists of “browsing-associated” or presumed “tolerant” species used in the analysis. A: direct signs of herbivory on woody plants or forbs (excluding blue ash): number per plot. B: mean abundances of browsing-associated forbs and subshrubs (Table 3; scale of Table 1).. C: proportions of browsing-associated species among woody plants <1 m tall: mean per row. D: proportions of browsing-associated species among woody plants at least 1 m: mean per row. E: mean stem density per plot (100 m<sup>2</sup>) of woody plants <1 m tall; data are log-transformed. F: mean stem density per plot (100 m<sup>2</sup>) of woody plants ≥1 m tall; data are log-transformed.

<b>INDICATORS</b>	<b>B: tolerant forbs</b>	<b>C: tolerant woody &lt;1m</b>	<b>D: tolerant woody &gt;1m</b>	<b>E: total woodies &lt;1 m</b>	<b>F: total woodies ≥1 m</b>
<b>A: direct signs of herbivory</b>	<b>0.38</b> <b>P = 0.08</b>	<b>0.52</b> <b>P = 0.02</b>	<b>0.39</b> <b>P = 0.08</b>	<b>0.26</b> <b>N.S.</b>	<b>- 0.03</b> <b>N.S.</b>
<b>B: tolerant forbs/subshrubs</b>	<b>X</b>	<b>0.50</b> <b>P = 0.03</b>	<b>0.15</b> <b>N.S.</b>	<b>0.05</b> <b>N.S.</b>	<b>- 0.11</b> <b>N.S.</b>
<b>C: tolerant woody &lt;1 m</b>		<b>X</b>	<b>0.44</b> <b>P = 0.05</b>	<b>0.12</b> <b>N.S.</b>	<b>- 0.06</b> <b>N.S.</b>
<b>D: tolerant woody &gt;1m</b>			<b>X</b>	<b>0.21</b> <b>N.S.</b>	<b>0.18</b> <b>N.S.</b>
<b>E: total woodies ≥1 m</b>				<b>X</b>	<b>0.56</b> <b>P = 0.01</b>

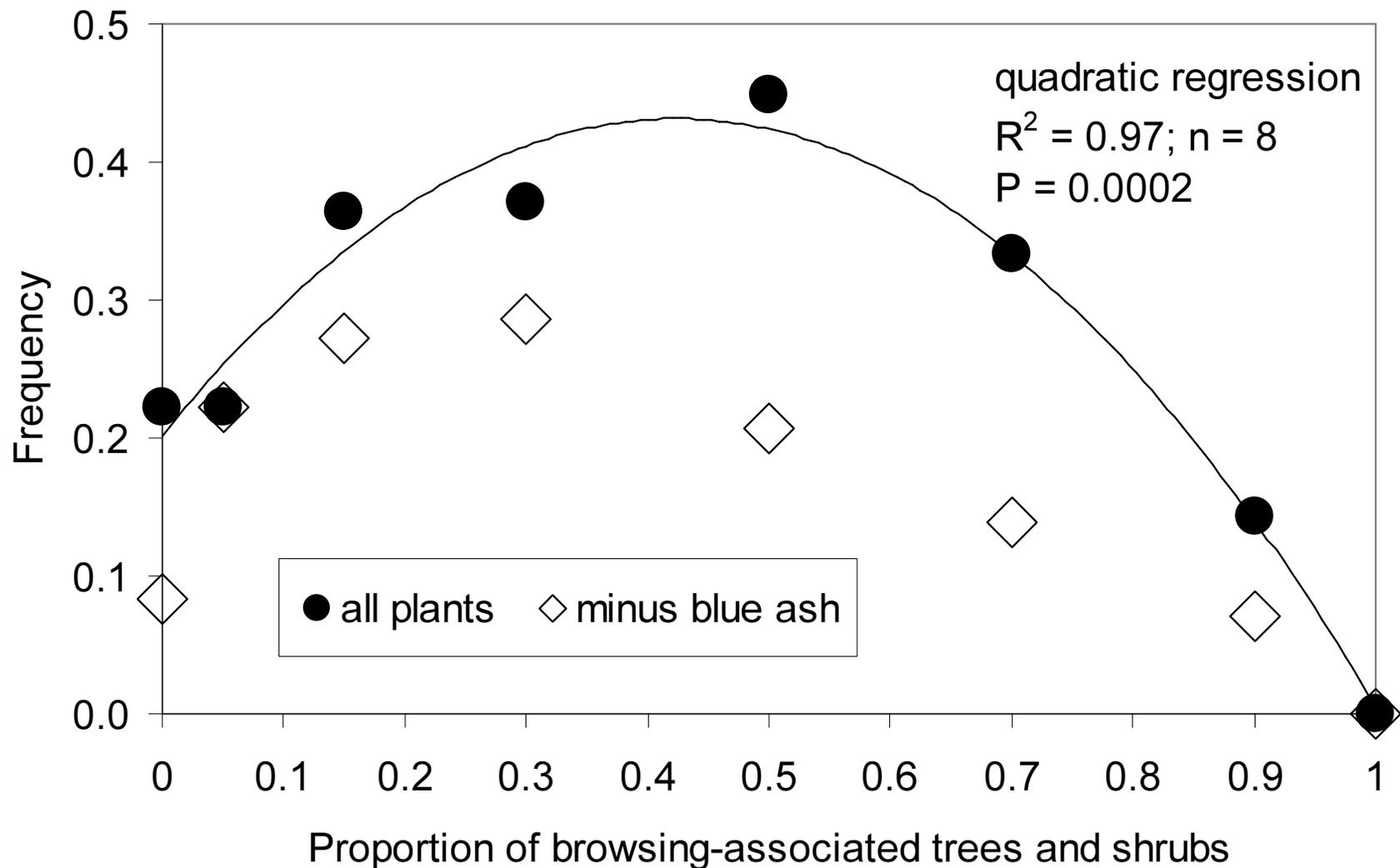
**Table 6b. Spearman’s rank correlations of tolerant forb and subshrub abundance with woody plant parameters.** In all correlations, n = 199 for the 199 vegetation plots. In the proportions, plots with zero woody plants (17 plots for C and 28 for D) were assigned the mean for all remaining plots. Correlations are corrected for ties in all cases. But standard Spearman’s correlations are added in brackets if there are large differences, usually in cases with non-linear relationships (\*).

- A: direct signs of herbivory on woody plants or forbs (excluding blue ash): number per plot.  
 B: mean abundance of browsing-associated forbs and subshrubs (Table 3; scale of Table 1).  
 C: proportion of browsing-associated species among woody plants <1 m tall (Table 4).  
 D: proportion of browsing-associated species among woody plants at least m tall (Table 4)..  
 E: mean stem density per plot (100 m<sup>2</sup>) of woody plants <1 m tall; data are log-transformed.  
 F: mean stem density per plot (100 m<sup>2</sup>) of woody plants ≥1 m tall; data are log-transformed.

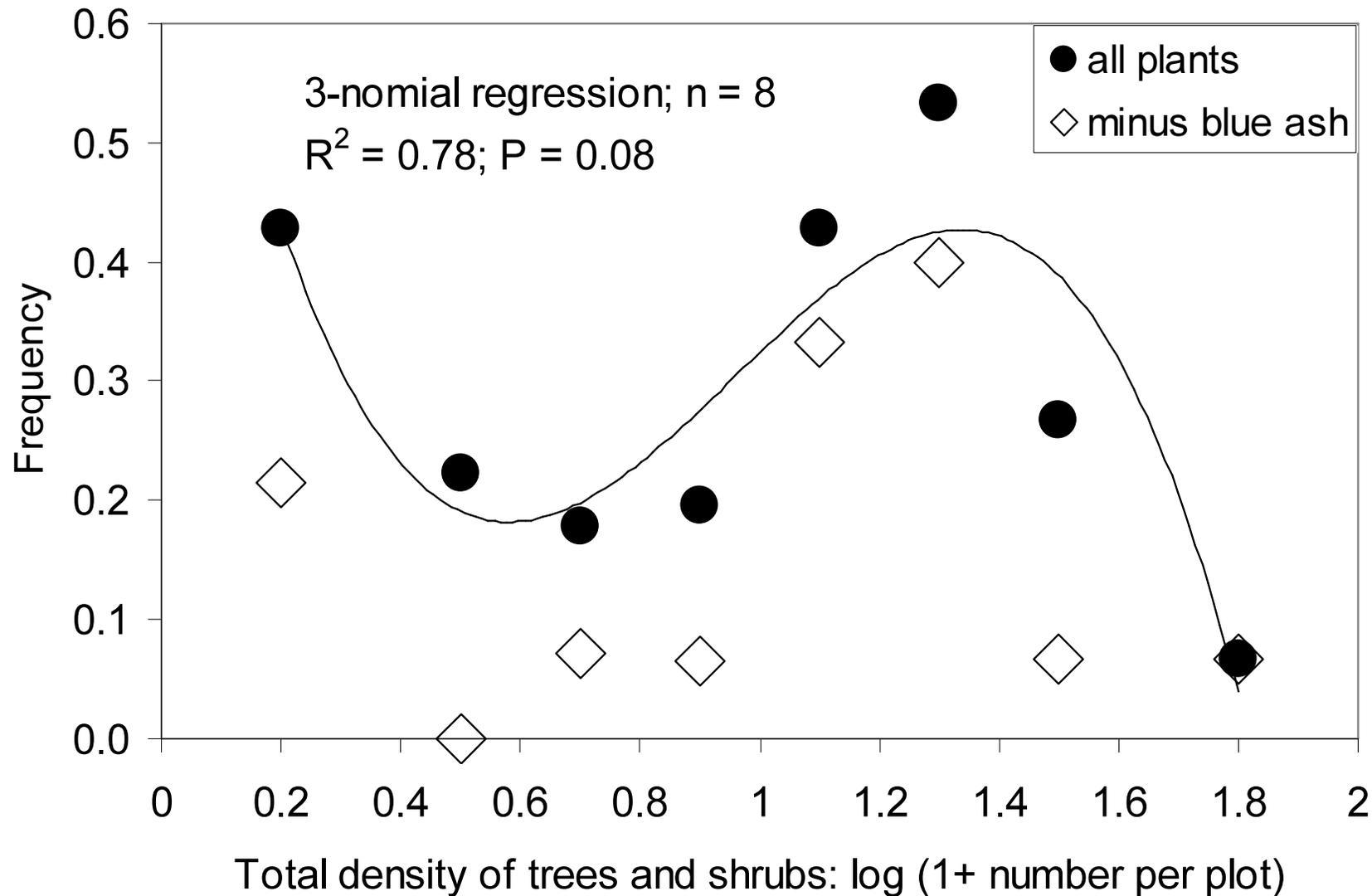
<b>INDICATORS</b>	<b>B: tolerant forbs and subshrubs</b>	<b>C: tolerant woodies &lt;1 m</b>	<b>D: tolerant woodies ≥1 m</b>	<b>E: total woodies &lt;1 m</b>	<b>F: total woodies ≥1 m</b>
<b>A: direct signs of herbivory</b>	<b>0.03 [+0.37] P &lt; 0.0001*</b>	<b>- 0.11 [+0.34] P &lt; 0.0001*</b>	<b>- 0.03 [+0.32] P &lt; 0.0001*</b>	<b>0.18 P &lt; 0.0001*</b>	<b>0.10 P &lt; 0.0001*</b>
<b>B: tolerant forbs and subshrubs</b>	<b>X</b>	<b>0.04 N.S.</b>	<b>0.04 N.S.</b>	<b>- 0.18 P = 0.04</b>	<b>- 0.07 N.S.</b>
<b>C: tolerant woodies &lt;1 m</b>		<b>X</b>	<b>0.23 P &lt; 0.0001</b>	<b>- 0.16 N.S.</b>	<b>- 0.12 N.S.</b>
<b>D: tolerant woodies ≥1 m</b>			<b>X</b>	<b>- 0.25 P = 0.001</b>	<b>0.21 P = 0.001</b>
<b>E: total density of woodies &lt;1 m</b>				<b>X</b>	<b>0.36 P &lt; 0.0001</b>



**Figure 8a. Signs of herbivory on all plants, as frequency per plot, in relation to total abundance of browsing-associated forbs and subshrubs.** Total abundances within each of the 199 plots are scored using the quasi-logarithmic classes of Table 1. Signs of damage include blue ash, since numbers are small; open squares are data without blue ash..



**Figure 8b. Signs of herbivory on all plants, as frequencies per plot, in relation to the proportion of browsing-associated trees and shrubs (seedlings plus saplings, excluding ground-covering vines and subshrubs).** The 199 plots are grouped into classes for sufficient numbers per class: 0,  $>0 < 0.1$ ,  $0.1 < 0.2$ ,  $0.2 < 0.4$ ,  $0.4 < 0.6$ ,  $0.6 < 0.8$ ,  $0.8 < 1$  and 1. Signs of damage include data from blue ash, since numbers are small; open squares are data without blue ash.



**Figure 8c. Signs of herbivory on all plants, as frequencies per plot, in relation to the total density of trees and shrubs.** Densities for all 199 plots are calculated as  $\log(1 + \text{number per plot})$ , then presented as means for classes: 0.1-0.3; 0.3-0.5; 0.5-0.7, etc. Signs of herbivory include data from blue ash, since numbers are small; open squares are data without blue ash.

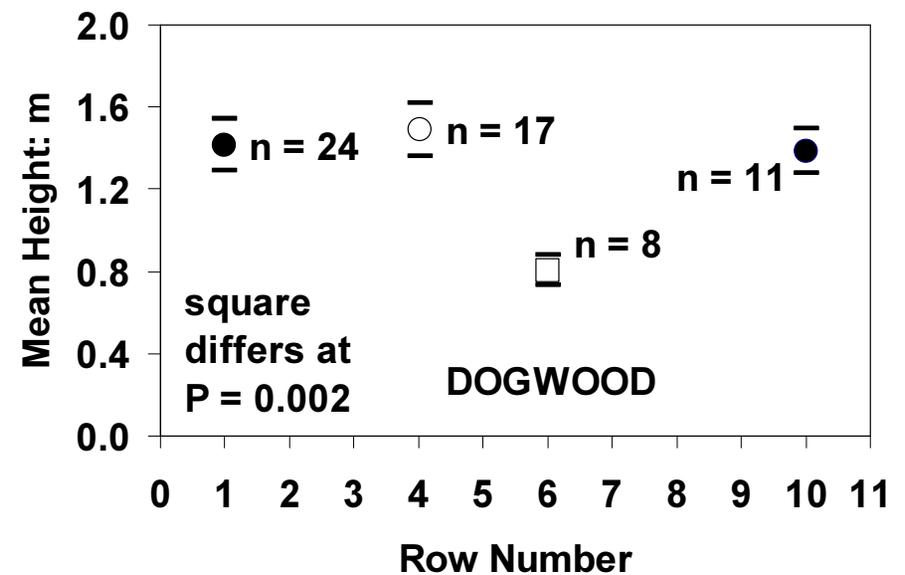
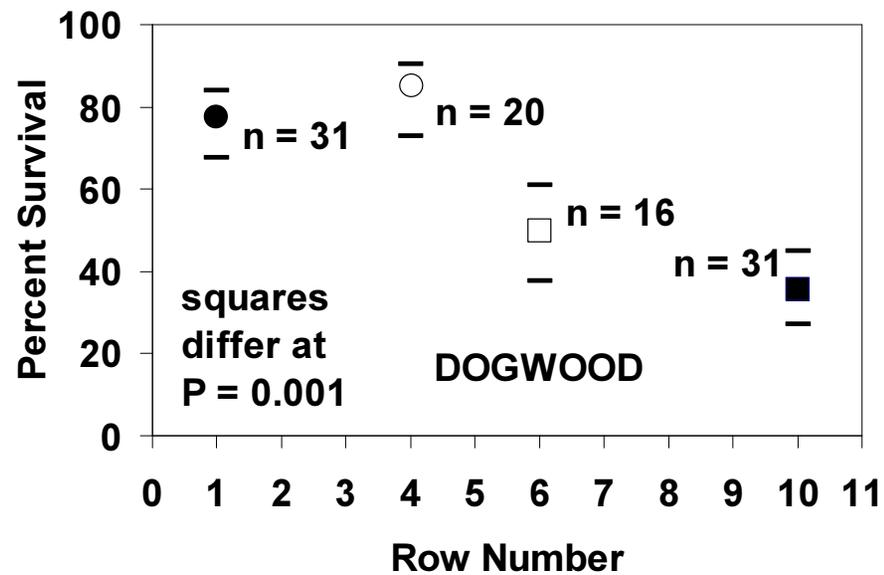
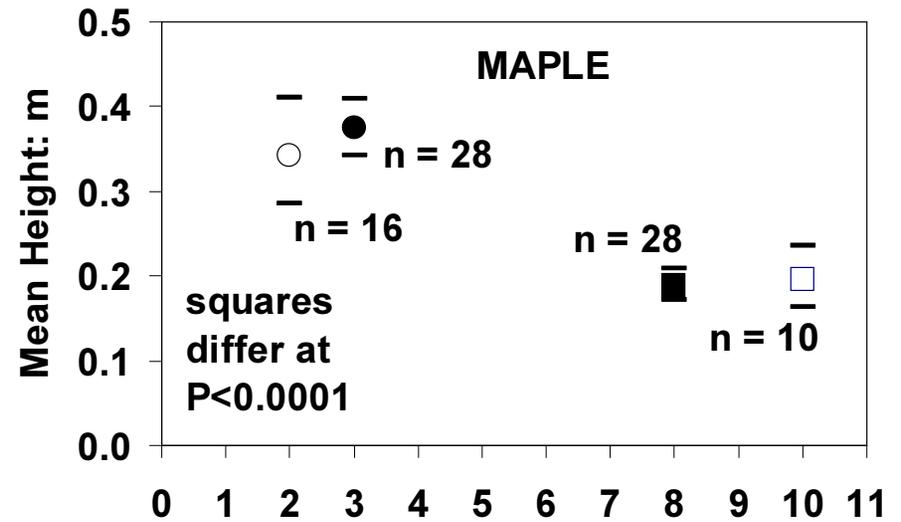
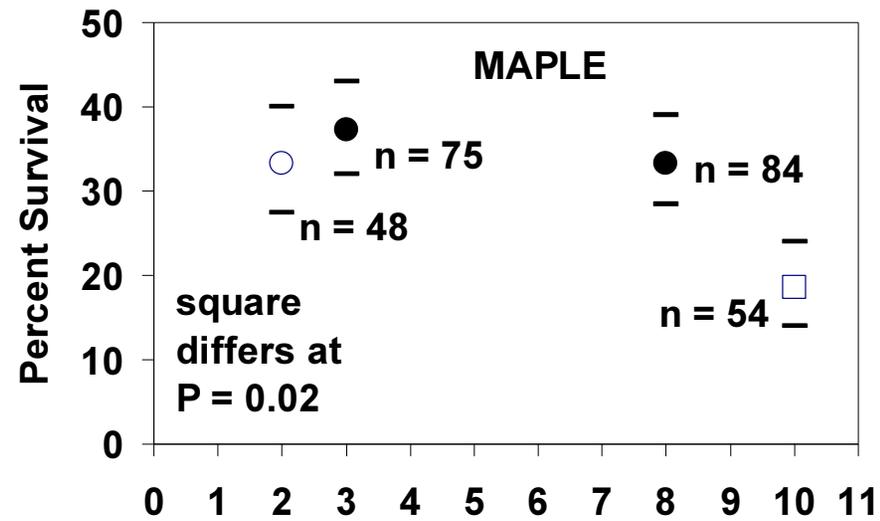
## Survival and Growth of Plantings: Maples and Dogwoods

For both sugar maple (*Acer saccharum* sensu lato) and roughleaf dogwood (100 *Cornus drummondii*), survival percentage and mean height after three growing seasons were lower, by about half, in at least one of the rows in the back half of the field, away from the road (Figure 9). However, surviving dogwoods in the back row (10) did achieve similar height to those near the front. The general decline away from the road was attributable to herbivores, although few direct observations were made. In most cases, there was no sign of dead plants; it is possible that voles and rabbits were more important than deer.

Among all 40 vegetation plots where these plantings occurred, variation in their overall success was indicated by their geometric mean height, with dead individuals counted as zeros (Table 7). For maple, with 69% dead, this index had a marginally significant positive correlation ( $P = 0.06$ ) with density of all woody plants  $\geq 1$  m tall. For dogwood, with 41% dead, this index was not significantly correlated with the vegetation parameters, although there were weak non-significant negative correlations with proportions of browsing-associated species in all three cases.

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**Figure 9a,b,c,d [next page]. Three years after planting, survival percentage ( $\pm$  half of 95% confidence limits) and height of survivors (geometric mean in meters  $\pm$  standard error) among sugar maples and roughleaf dogwoods in their row sections. Solid points (circles and squares) are from the NE part of the field; open points are from the SW part. Numbers on charts (n) are starting totals of in survival charts (a and c), and surviving totals in height charts (b and d). Squares indicate significant differences from circles, using chi-square tests for differences in percentage mortality, and using ANOVA for differences in log-height.**



**Figure 9 [see detailed caption above].**

a: upper left, sugar maple survival.

c: lower left, roughleaf dogwood survival.

b: upper right, sugar maple height..

d: lower right, roughleaf dogwood height.

**Table 7. Spearman’s rank correlations between mean size of planted sugar maple or roughleaf dogwood seedlings and vegetation parameters.** In all correlations,  $n = 40$  for the 40 vegetation plots within which plantings occurred. Parameters for maple and dogwood are the geometric means of height for all planted individuals in each plot, with dead individuals counted as zero. In proportions, the few plots with zero woody plants were assigned the mean for all remaining plots. Correlations are corrected for ties in all cases.

A: abundance of browsing-associated forbs and subshrubs (Table 3a)

B: proportion of browsing-associated woody plants <1 m tall (Table 4a).

C: proportion of browsing-associated woody plants  $\geq 1$  m tall (Table 4a).

D: total density per plot ( $100 \text{ m}^2$ ) of woody plants <1 m tall; data are log-transformed.

E: total density per plot ( $100 \text{ m}^2$ ) of woody plants  $\geq 1$  m tall; data are log-transformed.

<b>PLANTED SPECIES</b>	<b>A: abundance of tolerant forbs/subshrubs</b>	<b>B: proportion of tolerant woody plants &lt; 1 m</b>	<b>C: proportion of tolerant woody plants <math>\geq 1</math> m</b>	<b>D: total density of woody plants &lt; 1 m tall</b>	<b>E: total density of woody plants <math>\geq 1</math> m tall</b>
<b>Maple</b>	<b>0.156</b> N.S.	<b>- 0.164</b> N.S.	<b>- 0.081</b> N.S.	<b>0.126</b> N.S.	<b>0.298</b> P = 0.06
<b>Dogwood</b>	<b>- 0.246</b> N.S.	<b>- 0.293</b> N.S.	<b>- 0.261</b> N.S.	<b>- 0.003</b> N.S.	<b>- 0.105</b> N.S.

## Survival and Growth of Plantings: Blue Ash

After 4 growing seasons (3.5 years), the 167 planted saplings of blue ash had experienced 20% mortality overall. Lower mortality and taller survivors were concentrated in some zones of the field (as shown by blue versus orange in Figure 10), but there was little relationship between survival and distance from the road (Figure 11a). Extension growth rates of leading shoots tended to be higher in the more successful zones, but the trend was not significant (Table 8). Growth rates did decline away from the road, but the trend was less significant if damaged plants were excluded (Figure 11d).

Signs of recent herbivory in 2007, or associated fresh damage such as antler-rubbing, occurred in 19% of the 134 survivors, sometimes with large increases in extension growth of leading shoots or branches. Most of the damage to blue ash could be attributed to deer, although chewing of basal bark probably by voles was noted in three of the 134 survivors. From field notes, it appeared that most breakage from rubbing of antlers occurred at 0.3-1 m above ground, but browsing was often higher. There was a weak tendency for less survival of plants with intermediate initial heights of 1-1.5 m (Figure 13). Among plants with partial or complete resprouting of leaders, indicating damage during 2004-7, 46% (16/35) exhibited signs of recent herbivory or associated damage during 2007. Among plants without partial or complete resprouting, only 11% (11/99) exhibited such signs ( $P = 0.0001$  with Fisher's exact test of difference). The cause of resprouting appeared to be mostly browsing or breakage of stems, possibly due to earlier antler-rubbing in some cases.

Curiously, the overall percentage of plants with signs of herbivory or replacement of leading shoots was almost identical in the two zones with high versus low mortality (Table 8).

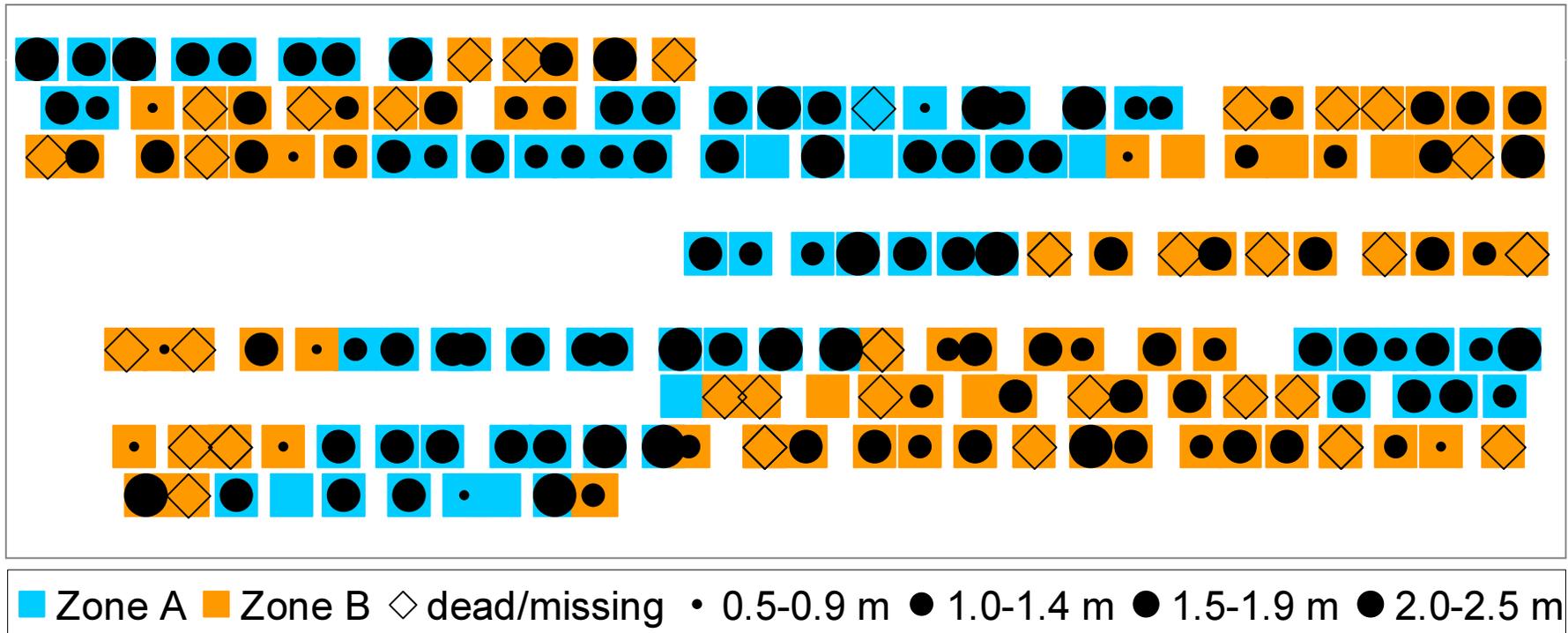
However, there was a significant increase in signs of recent herbivory away from the road within the NE part of the field (Figure 11b), and a weak increase in leader replacement away from the road in the SW part (Figure 11c). Moreover, among the 12 row sections with blue ash plantings, there was a high correlation between the percentage of plants with complete or partial leader replacement (indicating damage in 2004-7) and the percentage of recent damage from herbivores observed in 2007 (Table 9). However, there were no significant correlations between either of these percentages and blue ash mortality, or between any of these three parameters and the frequency of herbivory that was recorded on other species in the vegetation (Table 9). There were almost no significant correlations between these same parameters of blue ash (mortality, signs of herbivory, resprouting of leaders) and parameters of the vegetation. There were weak negative correlations between both mortality or signs of herbivory on blue ash and the total density of woody plants  $\geq 1$  m tall (minus ground-covering vines and subshrubs; column E in Table 10a). There were also relatively high—but non-significant—positive correlations between both mortality or signs of herbivory and the abundance of browsing-associated forbs and subshrubs (column A in Table 10a).

Among the 199 individual plots as well, there were generally small but significant positive correlations between these same parameters of blue ash and indices of browsing-associated species in the vegetation, and there were negative correlations with total woody density (Table 10b). However, frequencies of blue ash per plot were generally insufficient for meaningful correlation coefficients and non-linear relationships also appeared to be involved. For a broader summary of what appeared to be the most significant relationship, plots were grouped into classes based on the logarithmic abundance classes of browsing-associated forbs and subshrubs as the x-axis (as in Figure 9a). There was a significant quadratic regression for  $y =$  [percent of

blue ash with herbivore damage or resprouted leaders] (Figure 12). However, there was no significant regression for  $y = \text{mortality}$ .

A scatter plot of annual extension growth versus final height for all surviving blue ash saplings shows much higher growth rates in plants with damaged or resprouted leaders (Figure 14). Moreover, there is a much stronger relationship of growth to height among plants with replaced leaders, compared to plants without even partial sprouting: in regressions,  $R^2 = 0.75$  versus 0.03. And there was a particularly strong correlation between growth / height ratio, when divided into 10 classes, and the percentage of plants with partial or complete leader replacement (classes b or c noted in methods):  $R^2 = 0.89$ ,  $n = 10$ ,  $P = 0.00004$  (details not displayed here). The correlation of growth / height ratio with complete leader replacement was less strong ( $R^2 = 0.74$ ,  $n = 10$ ,  $P = 0.01$ ), as was that with recent damage from herbivory observed in 2007 ( $R^2 = 0.76$ ,  $n = 10$ ,  $P = 0.001$ ).

Unfortunately, initial height of each blue ash sapling was not recorded, but these heights were estimated by subtraction of  $4 \times$  [annual extension growth of undamaged shoots in 2006-7] for each sapling. With these estimates (results not detailed here), there was still a much stronger relationship of growth to initial height among plants with replaced leaders, compared to plants without even partial sprouting (as in Figure 14). There were significant differences in initial estimated height among the four provenance-groups of planted blue ash (Table 11). However, differences in annual extension growth were less pronounced, and there were no significant differences if growth was expressed as the ratio to initial height, or if browsed or damaged plants were excluded. Plants from the “Alexander” provenance grew and survived more, probably due to having been raised in native soil; the other plants had been grown in pots.



**Figure 10. Map showing variation in height of blue ash saplings (dots of increasing size) and apparent concentrations of mortality (colored zones), from data collected in Sep 2007 after four growing seasons. Blue-versus-orange shows lower mortality and taller survivors.**

**Table 8. Differences in the the fate of blue ash between the two zones of Figure 10.**

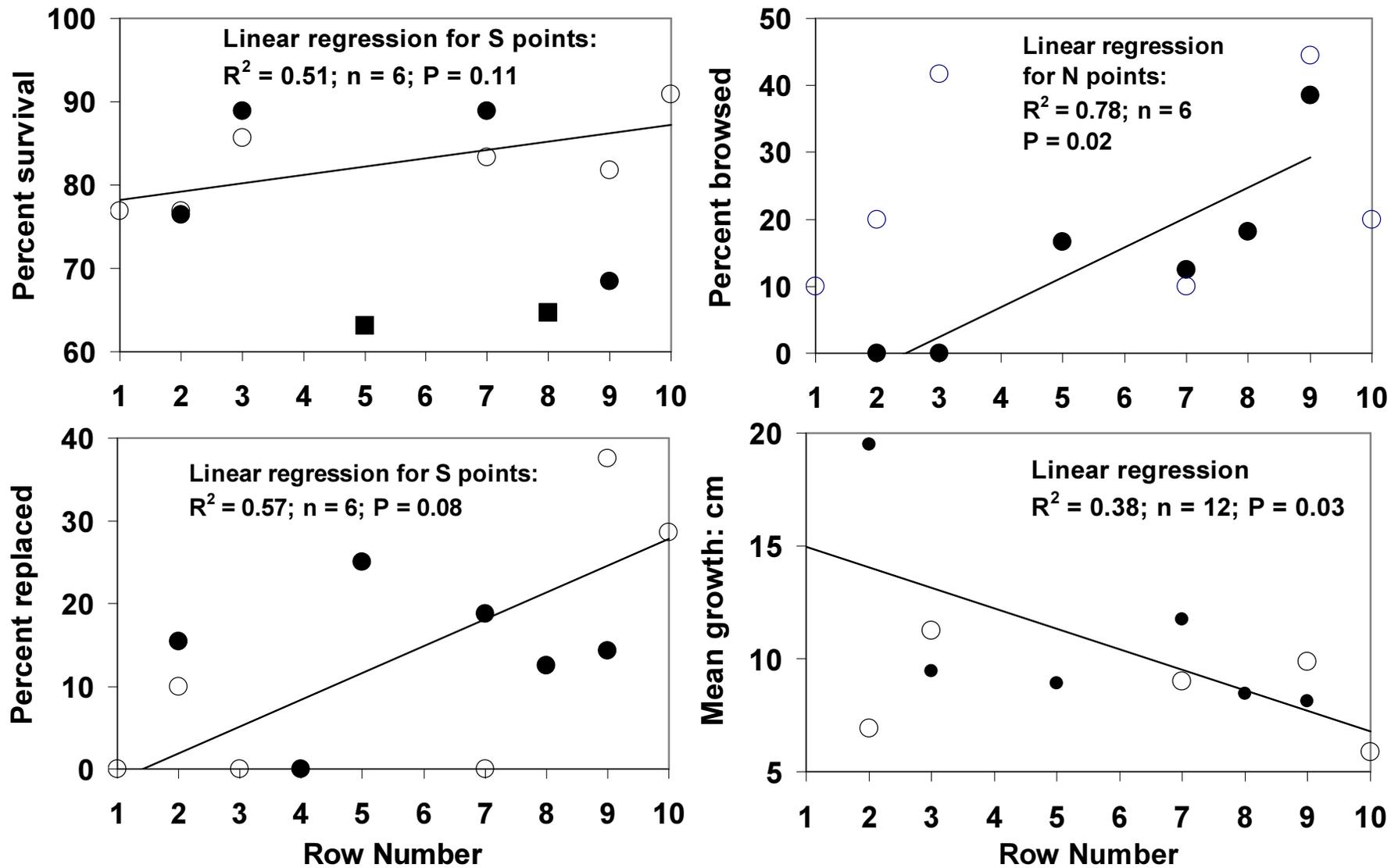
Zones of Figure 10	total trees	died	geometric mean height: m ± S.E.	growth: cm <sup>a</sup>	growth/height: cm/m <sup>b</sup>	browsed, damaged or respouted
A blue	76	1.3%	1.64 [1.60-1.69]	12.25	7.48	34.2%
B orange	89	37.1%	1.35 [1.30-1.42]	8.51	6.12	34.8%

<sup>a</sup> Differences in growth rate are expected but not significant (P = 0.14 with ANOVA of log-data).

<sup>b</sup> Differences in growth/height are expected but not significant (P = 0.11 with ANOVA of log-data).

**Figure 11 [next page]. Trends in blue ash survival, browsing or other damage, and growth rate, averaged for each row section.**

- a. Percent survival of planted blue ash saplings in each row section. Solid points are from northeastern part of field, open points are from southwestern part. Linear regression, with weak significance, is shown only for open points. Among solid points, squares differ from circles with weak significance, at  $P = \text{ca. } 0.1$ .
- b. Percent of planted blue ash saplings in each row section with recent (2006-7) browsing of shoots, breakage of stems, damage from rubbing, or chewing of bark. Linear regression is significant only for points from the northeastern part of field (solid points).
- c. Percent of planted blue ash saplings in each row section with replacement of leading shoots by laterals (largely due to browsing or other damage in 2004-6). Linear regression, with weak significance, is shown only for southwestern part of the field (open points).
- d. Geometric mean annual extension growth (cm on y axis) of planted blue ash saplings within each row section. Linear regression is shown for all points. Slightly less significant regressions (not show here) were found for  $y = \text{growth} / \text{initial height}$  ( $P = 0.04$ ); or  $y = \text{growth}$  but excluding plants with damage or resprouting of leaders ( $P = 0.08$ ); or  $y = \text{growth} / \text{initial height}$  but excluding plants with damage or resprouting of leaders ( $P = 0.06$ ).



**Figure 11: see caption above.**

a: upper left, percent survival.

c: lower left, percent leader replaced.

b: upper right, percent browsed/broke/rubbed/chewed.

d: lower right, geometric mean growth rate.

**Table 9. Spearman’s rank correlation coefficients (corrected for ties) among blue ash mortality, resprouting and signs of herbivory across the 12 row sections with Feb-Mar 2004 plantings.**

A: mortality of blue ash as percentage of dead in each row section.

B: percentage of surviving blue ash with replacement of leading shoots or other major resprouting of branches in each row section (largely due to damage in 2004-2006).

C: direct signs of fresh herbivory, recent breakage, rubbing or chewing of bark in Sep 2007, as percentage of blue ash with these signs for each row section.

D: other direct signs of herbivory on the surrounding vegetation that were observed during the vegetation survey, as number of observations per plot for each row section.

<b>BLUE ASH PARAMETERS</b>	<b>B: resprouting of leaders or major branches</b>	<b>C: direct signs of herbivory or related damage</b>	<b>D: other direct signs of herbivory in the surrounding vegetation</b>
<b>A: mortality</b>	<b>0.16 N.S.</b>	<b>0.03 N.S.</b>	<b>- 0.002 N.S.</b>
<b>B: resprouting</b>	<b>X</b>	<b>0.82 P = 0.007</b>	<b>- 0.20 N.S.</b>
<b>C: signs of herbivory</b>		<b>X</b>	<b>- 0.13 N.S.</b>

**Table 10a. Spearman’s rank correlations (corrected for ties) for blue ash parameters versus vegetation parameters for the 12 whole row sections with Feb-Mar 2004 plantings.** Mortality is the percentage of trees that were dead by Sep 2007. “Resprouting” is the percentage of survivors with replaced leading shoots or other major resprouting of branches due to damage in 2004-7. “Direct signs” of herbivory are the percentages of survivors with clear browsing, fresh breakage or chewing of bark in 2007.

A: abundance of “tolerant” (browsing-associated) forbs and subshrubs (Table 3a)

B: proportion of browsing-associated woody plants <1 m tall (Table 4a).

C: proportion of browsing-associated woody plants at least m tall (Table 4a).

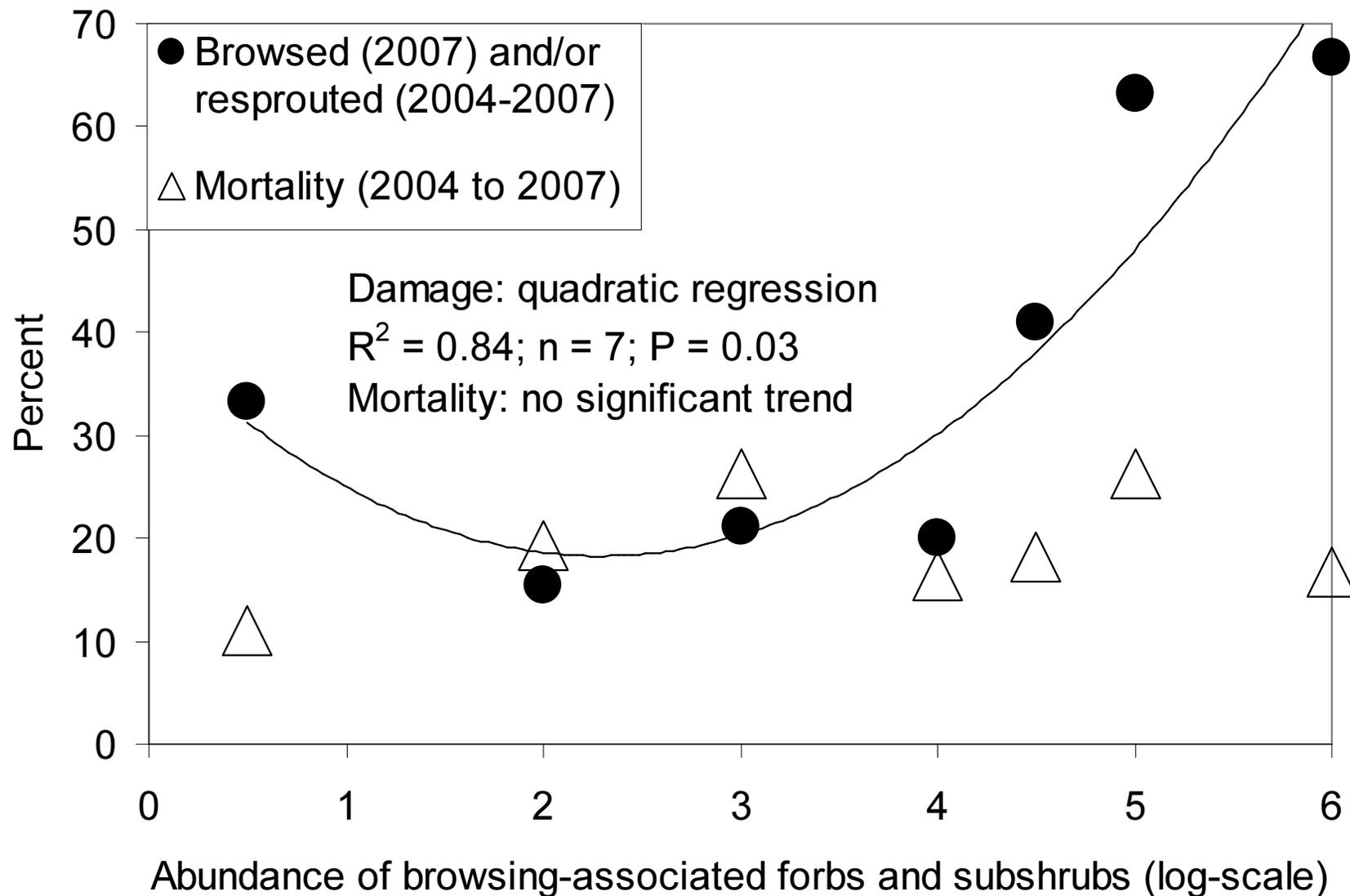
D: total density per plot (100 m<sup>2</sup>) of woody plants <1 m tall; data are log-transformed.

E: total density per plot (100 m<sup>2</sup>) of woody plants <1 m tall; data are log-transformed.

<b>INDICATORS</b>	<b>A: tolerant forbs/subshrubs</b>	<b>B: tolerant woodies &lt;1m</b>	<b>C: tolerant woodies &gt;1m</b>	<b>D: total woodies &lt;1 m</b>	<b>E: total woodies ≥1 m</b>
<b>Direct signs of herbivory</b>	<b>0.42</b> N.S.	<b>0.16</b> N.S.	<b>0.14</b> N.S.	<b>- 0.33</b> N.S.	<b>- 0.53</b> P = 0.08
<b>Resprouting of blue ash</b>	<b>0.40</b> N.S.	<b>- 0.02</b> N.S.	<b>0.04</b> N.S.	<b>- 0.13</b> N.S.	<b>- 0.21</b> N.S.
<b>Mortality of blue ash</b>	<b>0.29</b> N.S.	<b>0.10</b> N.S.	<b>0.36</b> N.S.	<b>- 0.05</b> N.S.	<b>0.21</b> N.S.

**Table 10b. Spearman’s rank correlations (corrected for ties) for blue ash parameters versus vegetation parameters, as in Table 10a but for all 199 individual vegetation plots.** Standard uncorrected correlations are provided in brackets where differences are large. Although some of these initial results provide significant correlations, coefficients are small and some trends appear to be non-linear (\*). Numbers per plot are too small in most cases for good analysis but see Figure 12.

<b>INDICATORS</b>	<b>A: tolerant forbs/subshrubs</b>	<b>B: tolerant woodies &lt;1 m</b>	<b>C: tolerant woodies ≥1 m</b>	<b>D: total woodies &lt;1 m</b>	<b>E: total woodies ≥1 m</b>
<b>Direct signs of blue ash herbivory</b>	<b>0.19</b> <b>P &lt; 0.0001</b>	<b>0.006</b> <b>P = 0.0004*</b>	<b>0.08</b> <b>P = 0.0002*</b>	<b>- 0.03</b> <b>P = 0.007*</b>	<b>- 0.06[+0.23]</b> <b>P = 0.01*</b>
<b>Resprouting of blue ash</b>	<b>0.11</b> <b>P = 0.0006</b>	<b>0.04</b> <b>P = 0.001*</b>	<b>- 0.03 [+0.19]</b> <b>P = 0.04*</b>	<b>- 0.05[+0.19]</b> <b>P = 0.07*</b>	<b>- 0.06[+0.16]</b> <b>P = 0.09*</b>
<b>Mortality of blue ash</b>	<b>0.001</b> <b>P = 0.01</b>	<b>0.07</b> <b>P = 0.0006*</b>	<b>0.11</b> <b>P = 0.001*</b>	<b>- 0.12[+0.11]</b> <b>N.S.</b>	<b>- 0.13[+0.10]</b> <b>N.S.</b>



**Figure 12. Percent damaged (browsed or resprouted) and mortality of planted blue ash saplings in relation to total abundance of browsing-associated forbs and subshrubs.**  
 [Data overlap with Figure 8a, which includes herbivory on blue ash and on other species.]

## DISCUSSION

### Consistency of Results with the ‘Herbivore Hypothesis’

This study is not a general test of the hypothesis (Campbell 2012)—which would require more long-term research, including rigorous experimentation. But it is consistent, and it suggests how investigation might proceed at Griffith Woods. Herbivory, especially from deer, appears to be a major ecological factor controlling the development of vegetation in this old field. Such influence accords with experimental work elsewhere in some grasslands (e.g., Anderson et al. 2007) and old fields (e.g., DiTommaso et al. 2014). Based on general knowledge and review of literature, a group of forb and subshrub species at this site (Table 3), and a group of trees and shrub species (Table 4), are used here as ‘browsing-associated’ indicators. There are no clear relationships of topography to overall species composition, in terms of shifts in dominant species. Instead, patterns in ‘browsing-associated’ species plus observations of damage from herbivory suggest that influence from deer has been concentrated along a broad diagonal pathway across the field (Figures 2 to 7). This path has probably been travelled for many decades, with a concentrated zone of highway-crossing near the western corner of the field plus zones of concentrated browsing towards the back where animals are more sheltered from the road and closer to the ancient woodland.

It is likely that dispersal from local seed sources has enhanced the concentrations of browsing-associated versus -sensitive species within this field. Among tree species at least, there are concentrations of browsing-associated species within the surrounding fencerows and woodland edges (Figure 2h-i). As noted above, there is more frequent dominance of browsing-associated trees adjacent to peripheral plots within the southern zone that appears to have

“concentrated influence” by deer (Figure 2d-g). It is possible that northern sectors of the field have had less influence by larger mammalian herbivores since this old farm was developed out of the wilderness during 1780-1830.

Although deer appear to have obvious spatial effects on the vegetation in this field, smaller mammals may also have significant local effects, based on more detailed research in old fields elsewhere in eastern North America (e.g., Gill & Marks 1991, Ostfeld et al. 1997, Manson et al. 2001, DeJaco 2006). Mice (especially *Peromyscus leucopus* and *P. maniculatus*) and voles (especially *Microtus pennsylvanicus* and *M. ochrogaster*) can consume large numbers of tree seeds and small seedlings, respectively; white ash is a preferred species for voles. Voles tend to be most abundant in grassland rather than shrubby transitions, with *M. ochrogaster* concentrated on drier ground in the central Bluegrass region (Delfino 1993, Schwer 2011; J. Krupa, pers. comm.). Where large herbivores maintain relatively open grassy paths, it is possible that voles enhance the overall damage to woody plants. Such interaction remains speculative, but it seems likely that large herbivores in general do increase effects of rodents on woody vegetation (e.g., Matlack et al. 2001, Zhang et al. 2009). Moreover, meadow voles alone can greatly influence the composition of grasses and forbs within grassland (Hower & Lane 2004, Howe et al. 2006, Fraser & Madson 2006, MacDougall & Wilson 2007). Rabbits can also play a significant role in grassland and old fields, although their effects have been studied much more in Europe than in eastern North America (e.g., Diaz 2000, Delibes-Mateos et al. 2006). In a New Jersey old field, Myster & Pickett (1992) did report that rabbits were the “major seedling predator”—with a somewhat different ranking of preferences than summarized here for deer (Table 4; see also, Myster & McCarthy 1989).

Probable damage from voles and rabbits was noted occasionally during survey of the vegetation in the Collection Field, but there was no effort to search for signs below 1 m in height except on the planted blue ash (see Methods). It is possible that such mammals have relatively high influence close to the highway, where more eutrophic conditions probably prevail (e.g., Truscott et al. 2005), and where escape from predators may be easier in the fencerow. Possibly, such ecological conditions close to the road have enhanced local abundance of poison hemlock (*Conium maculatum*)—which is among the most nitrophilous (Hill et al. 1999) and toxic species in this field (Figure 2a, 2c); see also Farrow (1917). Also, a few large patches of crown-vetch (*Securigera varia*) were located between this hemlock zone and the rest of the field; this species is often browsed by ruminants but avoided by rodents due to toxicity (Tu et al. 2003). Some features of the vegetation (e.g., Figure 2d) suggest a second minor pathway of influence by herbivores just beyond the powerline (Figure 1a) from the road across the northern sector. This pattern could be investigated with more multivariate analysis of the vegetation at this site, as well as survey of soil conditions and small mammals.

The ‘herbivore hypothesis’ revolves around the concept that animals will concentrate their effects in areas with the most accessible productive palatable vegetation, but that these areas then accumulate less palatable and more defended species, leading to shifts in patterns of herbivory. This study provides the following indications of shifting effects by deer—and perhaps other herbivores as well—due to exhaustion of palatable forage in some zones.

1. Although there was a general increase in signs of damage with increasing abundance of browsing-associated forbs and subshrubs, some leveling-off in the increase at higher abundance is suggested by the trinomial regression (Figure 8a). Moreover, there was a highly significant

quadratic relationship of these signs to the proportion of browsing-associated trees and shrubs, with a maximum at ca. 0.4 (Figure 8b).

2. The indicated central pathway itself had little or no sign of recent herbivory or associated damage except on planted blue ash (Figure 2g). This suggests that deer tended to forage at some distance from this pathway for more efficient browsing on palatable plants in the existing non-planted vegetation. Moreover, signs of recent herbivory did extend northeast of the zone with more apparent influence in the vegetation (Figure 2g).

3. Signs of herbivory in the whole vegetation, and damage or resprouting of blue ash, both showed slight rises in frequency at the lowest abundances of browsing-associated forbs and subshrubs (Figures 8a, 12). Although more data are desirable, these features accord with (1) and (2).

4. Recent signs of herbivory or associated damage to the planted blue ash in 2007 tended to increase away from the road in the NE part of the field, but not in the SW part. Partial or complete replacement of leaders, indicating damage as early as 2004, exhibited the opposite trend. This contrast may be explained by deer shifting their concentrated effects from the SW to the NE.

5. The proportion of browsing-associated trees and shrubs  $\geq 1$  m tall was positively correlated with total density of plants  $\geq 1$  m tall, but it was negatively correlated with total density  $< 1$  m tall (Table 6b). Larger woody plants of both types may have become concentrated in areas that later became more browsed, reducing density of smaller stems, especially the potentially abundant and palatable white ash  $< 1$  m tall.

6. There was a weak bimodal trend in signs of recent damage from herbivores (on y-axis) versus total density of woody stems (Figure 8c), which again suggests some complexity in the dynamic relationships. Deer may have shifted some of their browsing into vegetation with a low or moderately high density of woody stems.

Animal behavior is beyond the scope of this paper, but one remarkable study on white-tailed deer is relevant here. In a controlled experiment using enclosures with mixed patches of different forage-depletion, Kohlmann & Risenhoover (1994) found that “feeding patch selection was markedly skewed toward heavily and lightly grazed environments, while moderately depleted patches were selected least. Deer responded to forage depletion by foraging less selectively, reducing movement rates, and increasing average bite size. During the last phase of the trial, biting rates on forbs declined but increased on woody browse in response to declining forage availability.” Their subsequent study (Kohlmann & Risenhoover 1997) compared behavior in artificial patches of poor versus rich forage, and they concluded: “We suggest that the deviation from the predictions of the ideal-free distribution were a necessary consequence of information gathering and processing from continued sampling of patches by deer.” In nature, several other factors might promote repeated use of the same sites: including topographic form, safety from predators, social interactions, cryptic nutritional features, and other physical or chemical features of the vegetation. Like all mammals, deer are ‘creatures of habit’ that will often tend to continue seeking or fleeing in the same manner. But occasional switching to alternative pathways can of course lead to benefits in some cases.

Within this field, it is suggested that deer for many decades have tended to concentrate travel between woodland along the southeastern border and the western corner, crossing the highway near that corner to and from woods further west. The central pathway may be partly

driven by topography, lying close to the 880-884 ft [268-269.5 m] contour just below sight from humans on the road (Figure 1b). But slight variations of this path over the years, with shifts in foraging behavior, have probably contributed dynamic and spatial complexity to the field's vegetation and its borders.

### **Suggested Differences between Plant Species in Responses to Herbivory**

The attempt to identify 'browsing-associated' species of forb and subshrub here is provisional, and deeper analysis is needed. While there have been scattered publications that allow some approximate ranking of mammalian preferences for common plants of eastern North America (e.g., those listed for Table 3), there is little synthesis of relevant ecological or physiological information (e.g., Rodriguez-Iglesias & Kothmann 1998). There have been a few broad simple surveys of palatability to generalist invertebrate herbivores (e.g., Grime et al. 1968, Burt-Smith et al. 2003). It would be fascinating to explore the extent to which such rankings are similar to mammalian preferences.

For woody plants (Table 4), it is important to explore further the suggested distinction of more browsing-associated trees (including species of *Carya*, *Crataegus*, *Juniperus*, *Gleditsia*, *Gymnocladus*, *Juglans*, *Prunus*, *Quercus*, *Platanus* and *Robinia*) versus generally browsing-sensitive trees (including species in *Acer*, *Celtis*, *Fraxinus*, *Morus* and *Ulmus*). Numbers here are too small in some cases for statistical analysis of each species, but general knowledge of preferences by deer across eastern North America does broadly support the adopted classification (Table 4). Yet while the browsing-associated group of species generally have reported 'low' usage by deer—sometimes 'none' and sometimes 'moderate'—the browsing-sensitive group mostly have variable usage from 'low' to 'high' and almost none have

consistently ‘high’ ranking—perhaps only the alien *Morus alba*. Many environmental factors, including seasonal changes and edaphic effects, are known to influence the selection of plants by deer (e.g., Halls 1975, McCullough 1985, Nudds 1980, Tripler et al. 2002).

A deeper review and synthesis of data on preferences for tree species by mammals of eastern North America would be valuable, including larger animals that have disappeared from the wild. Bison—and several larger herbivores now extinct—are known to have been concentrated in the Bluegrass region during some post-glacial periods. Bones of bison dating from about 400-600 years ago indicate that these animals consumed more woody browse, and more C3 versus C4 plants, in this region compared to the Great Plains (Widga 2006). The few studies of browsing preferences or other effects of bison and (especially) cattle tend to accord with the classification adopted here (Day & DenUyl 1932, Biswell & Hoover 1945, Hopkins et al. 1972, Campbell et al. 1978, Dennis 1997, Coppedge & Shaw 1997, Coppedge et al. 1998, Lehmkuhler et al. 2008). However, highland cattle (Hedtcke et al. 2009), elk (*Lupardus* 2005, Schneider et al. 2006, Roberts et al. 2014) and red deer (Katona et al. 2013) appear to have broader preferences, sometimes including *Elaeagnus*, *Juniperus*, *Robinia*, *Sambucus* and other plants with relatively high protein content plus deterrent chemistry (tannins, terpenoids, saponins, alkaloids); such plants are generally not preferred by white-tailed deer (Table 4). The tannin-rich oak species (especially red oaks) in general also tend to be consumed by these larger animals with more preference, although some oaks occasionally have moderate to high reported use by white-tailed deer as well (as in literature cited for Table 4).

Smaller mammals can have quite distinct preferences than deer. It is remarkable, for example, that beaver consistently avoid boxelder, *Acer negundo*, and select bitternut hickory, *Carya cordiformis* (e.g., Nixon & Ely 1969, Barnes & Dibble 1988, Dieter & McCabe 1989;

and personal observations in Kentucky). The unusual success of *A. negundo* seedlings within more browsed parts of the field studied here remains inexplicable (Figure 3); voles can cause significant damage to saplings of this tree at woodland edges (J. Lempke, Univ. of Ky. Arboretum, pers. comm.). But even for deer, *A. negundo* does have widely reported preference; for example, Dahlberg & Guettinger (1956) showed unusually low usage in Wisconsin. It may be relevant that *A. negundo* has distinctive secondary chemistry and lepidopteran consumers, compared to other North American species in the genus *Acer* (Ricklefs 2008).

The woody species planted here (*Acer saccharum* sensu lato, *Cornus drummondii*, *Fraxinus quadrangulata*) can be added to the more sensitive group, based on their apparent decline from herbivory in some sections of the field, and based on further review of the literature. Although *Acer saccharum* is often considered less preferred by deer than *A. rubrum* and even *Quercus alba* in some northeastern states (Strohmayer & Warren 1997, Wakeland & Swihart 2009), the species can become intensively browsed, especially on fertile soils in shade (Russell et al. 2001, Tripler et al. 2002, Horsley et al. 2003, Long et al. 2007). Little published data are available for *Cornus drummondii*: Littlefield et al. (2011) indicated a low to moderate preference by deer for this species, which had an unusually low protein content and also low tannin content; but Gubanyi et al. (2008) found 90% less of this species in areas browsed by deer intensively for two decades.

The effects of deer on blue ash (*Fraxinus quadrangulata*) have been largely undocumented until now. Slater & Anderson (2014) recently noted low use and a small increase in seedling density with intense browsing. However, from personal observation, frequent browsing on blue ash is evident in the forests of central Kentucky, with about as much preference for this species as for white ash (*F. americana*). In the collection field, 19% of the

planted saplings showed signs of herbivory or associated damage during 2007; an additional 14% had partial or complete replacement of leaders, perhaps largely due to damage during 2004-2006; and an additional 20% had died or disappeared, probably due in part to herbivory or associated damage. Only about a half of the saplings survived in good condition. Moreover, it is remarkable that zero self-sown blue ash seedlings were discovered within the field, given that large trees dominate the 25 acres [10 ha] of old growth adjacent to the field on the southeast side (Table 5), where scattered saplings and patches of seedlings have been observed. This virtually complete absence of blue ash seedlings from open areas at Griffith Woods and elsewhere in the region is at least partly attributable to small mammals (Wallingford 2006).

### **Need for Refinement of Distinctions in Responses to Herbivory**

The classification of plant species here into two groups will need to be refined. Complexity of factors affecting herbivore preferences and their variation through space and time presents great problems for initial understanding of overall interactions with vegetation. In review of the literature, it is important to distinguish studies that focus on direct selection of different plants versus studies that focus on the results over time within particular areas—from controlled exclosures to uncontrolled patterns attributed to free-ranging animals. The latter deserve much more attention in eastern North America. As noted in the introduction, some studies of patterns in old fields or across woodland edges have produced results relevant to the potential effects of herbivory that are suggested at Griffith Woods. For example, Flory and Clay (2006) found that *Lonicera maackii* increased in forested sites sharply close to roads while *Rosa multiflora* showed no trend, and they suggested that herbivory was one of several potential causes; a similar distinction is indicated here (Figure 3). However, it is difficult to synthesize such results without a more refined analysis of interactions with herbivores.

Lack of consistent relationships at intensively browsed sites between distributional patterns and preferences of mammalian herbivores (e.g., Table 4) may be partly attributed to additional processes, not just environmental or ecological ‘noise’.

1. Patterns of seed dispersal, germination and establishment could enhance or obscure the effects of herbivory. For example, several of the ‘browsing-associated’ species indicated here (Fabaceae, Rosaceae) have fruits that may often be dispersed internally by larger mammals (Table 4a), which would be expected to deposit seeds along trails. In contrast, birds tend to concentrate droppings under perches, especially shrubs (e.g., McDonnell & Stiles 1983, McDonnell 1986), but seed predation can be faster under forbs or shrubs than in more open grassy areas, at least for more palatable trees (e.g., Gill & Marks 1991, Myster & Pickett 1993, Meiners 2007, Dutra et al. 2011).

2. Some relatively palatable woody species exhibit ‘compensatory growth,’ resprouting more vigorously from stem bases and lateral buds after browsing (or burning), in some cases increasing overall growth rates and even increasing palatability. Among small herbaceous species, there are many examples of highly palatable species that have become generally browsing- or grazing-associated due to vigorous resprouting or clonal spreading, in some cases with dependence on regular disturbance: for example, several species of clover (Table 3a). Among trees, species of *Celtis*, *Fraxinus* and *Ulmus* may provide good examples of compensatory growth (e.g., Hopkins et al. 1972, George & Powell 1977, Morrissey et al. 2008), as also indicated here for *F. quadrangulata*. Such responses may explain some observed increases of these species within forest understories that have been browsed, especially if more unpalatable species are lacking (e.g., Rossell et al. 2005, Asani et al. 2006, Gubanyi et al. 2008). In contrast, some unpalatable to toxic woody species such as thick-twigged trees like *Gymnocladus dioica* have less ability for rapid resprouting of leafy shoots (e.g., Janzen 1976);

instead, several of these species tend to resprout from the ground, often with lateral runners (Table 4a). However, other trees that are relatively unpalatable but sometimes browsed can resprout vigorously from roots and damaged stems, as in most oaks (*Quercus* spp.). This spectrum of responses by different tree species needs more careful analysis.

3. Interactions of disturbance, soil chemistry and secondary chemistry within plants could explain much of the variation in responses to herbivores. This is a complex subject that deserves broader review and application than possible here (Bryant et al. 1991, Herms & Mattson 1992, Milchunas & Lauenroth 1993, Augustine & McNaughton 1998)—“Even the sprouts from unpalatable plants such as hickory (*Carya* sp.) may be readily consumed after a fire” (Halls 1984).

4. Differences in effects of varied mammalian herbivores, as noted in the previous section.

5. Interaction of mammalian herbivory with invertebrate pests and pathogens. This is another complex subject that deserves more review than possible here (e.g., Epstein & Hill 1999, Bailey & Whitham 2005, Yamazaki 2010).

### **Notes on Methods and Future Tests**

This paper relies partly on an ‘indicator species’ approach, using abundances of ‘browsing-associated’ species-groups as parameters in the analysis. Although general knowledge and literature review support the assignments of species to these groups (Tables 3 and 4), this approach is open to charges of ‘circular reasoning’ since ‘general knowledge’ does include knowledge of this farm and this field. In a subsequent paper, patterns of species

distribution within this field will be analyzed using standard multivariate methods, for an objective test of the hypothesis that the major gradient in composition here is attributable to patterns of herbivory rather than topography and soil.

Another limitation of this paper is the superficial recording of damage from herbivores, which was conducted only as part of a general vegetation survey. These observations were not designed as an intensive study of deer browsing patterns, and there was little effort to search for clear signs of damage by rabbits and voles closer to the ground. Future work at Griffith Woods could adopt much more detailed methods for direct measurement of browsing by deer and other animals (e.g., Bergstrom & Guillet 2002, Dumont et al. 2005, Bilyeu et al. 2007, Crimmins et al. 2010). Indeed, Shaffer (2013) has already initiated observations of distinct damage from deer, rabbits and voles on planted trees in some other fields at Griffith Woods.

This study has shown the value of planted ‘phytometers’ for indicating spatial patterns of herbivory: setting out plants in transects or other systematic designs and then measuring how growth and survival varies across the site. Such research has sometimes been advocated for more rigorous measurement of influences from deer in eastern North America (e.g., Rooney & Waller 2002), but it has rarely been implemented (e.g., Zenker 2012, Waller & Maas 2013). With multiple replications into small plots, the approach has potential for special insight to how herbivory varies in space and time at fine scales (e.g., Scherber et al. 2006, Crain 2008).

The Collection Field at Griffith Woods—where this initial study has been conducted—offers a microcosm for local conservation science, where fundamental questions can be explored in a preliminary manner on a relatively small scale. In addition to repeated survey of the vegetation and more detailed assessment of herbivory, in order to test the reality of trends

indicated by this paper, a truly experimental approach is needed. For example, with use of small exclosures (especially to control deer) or experimental browsing with amenable livestock (especially goats and sheep), one could examine directly how larger herbivores influence the vegetation. Experimental designs with sets of phytometers could compare groups of planted species with differences in palatability or other functional characteristics. And after small blocks are established with different planted composition (perhaps requiring exclosures), one could then observe ecological trajectories when different types of planted block are exposed to free-ranging herbivores. The rest of Griffith Woods Wildlife Management Area is, of course, available for more large-scale and long-term research using some sections of the fields and woods for designed comparisons. Cooperative progress along these lines was initially conceived, with a focus on the most urgent and important questions for conservation and restoration at this site. An ultimate dream would be to use elk and bison for some of this work.

Given that eutrophic soils may have originally enhanced the role for larger herbivores in this region (Campbell 2012, 2013), it will also be important to conduct a detailed soil survey within this field and to compare other fields nearby. Preliminary work has suggested that significant differences in nitrogen level, from field to field, are associated with some species. In particular, poison hemlock (*Conium maculatum*) is locally abundant on the farm—especially where cattle were recently stocked—and this species is known to require high nitrogen for growth (Hill et al. 1999, Mamolos & Veresglou 2000). Old hayfields such as the Collection Field have much less of this alien weed. It is also likely that the ratio of fescue (*Festuca arundinacea*) to bluegrass (*Poa pratensis*) is related to soil fertility, as well as to associated past disturbance from livestock. The diagonal alternating bands of these two dominant grasses in the Collection Field (Figure 2b) might be explained in terms of 100-150 year old driveways for

livestock into this corner of the farm, exiting here towards market at Cynthiana (northeast along US 62)—this hypothesis could be tested by looking for zones of higher N in the soil.

One particular native species would be quite useful as a phytometer for assessment of gross soil fertility (N, P and K) and herbivory in these fields: *Urtica gracilis* Ait. [= *U. dioica* L. ssp. *gracilis* (Ait.) Selander]. The genus *Urtica* is known to have high demand for N and P, and has been used for associated experimental work in Europe (e.g., Taylor 2009) and East Asia (e.g., Kato et al. 2008). However, given its high palatability to most mammalian herbivores despite stinging hairs (see also: Kirby 2001), small cages might be needed for its establishment, and comparison of its fate inside versus outside cages could become another valuable parameter for mapping herbivory. “Nettles” (*Laportea* in deeper woods and *Urtica* in more open) used to be locally abundant within Bluegrass Woodland, but these plants have become uncommon to absent, presumably due to intensive continual browsing by livestock for 230 years (Campbell 2013).

Ultimately, complete tests and developments of the ‘herbivore hypothesis’ could be based on dynamic computer models. Patches of vegetation could be treated as cells for generic models (e.g., Adler et al. 2001), and zones of vegetation could be related to distances from essential resources or pathways for animals (e.g., Adler & Hall 2005). Central questions could then be addressed concerning the roles of herbivores in enhancing or reducing heterogeneity of vegetation and in overall modification of succession (e.g., Seagle & Liang 2001). In western North America, initial applications of such models are leading to a revolution in ecological thinking about management of rangeland (e.g., Fuhlendorf et al. 2012, Herrick et al. 2012).

## Relevance to Current Management and Future Restoration

**Ecological Goals.** Original vegetation of the central Bluegrass uplands appears to have been largely wooded (Campbell 1985, 1989, 2013a), with relatively deep shade at mid-storey in the sugar-maple/bitternut type (20-40%), intermediate shade in ash/elm, walnut/buckeye plus oak/hickory types (50-70%), and partial to full sun in canebrakes plus associated thickets among the woods (1-10%). Openings were probably concentrated along major trails and around licks, glades, campsites and villages maintained by animals and native people. Despite the strong evidence for this interpretation, it has been overwhelmed in some accounts by the concept that “savanna” or “savanna-woodland” was the major original type, dominated by open-grown blue ash and and oaks. This savanna concept was based largely on the condition and composition of old woodland-pastures, such as those at Griffith Woods (Bryant et al. 1980). But evidence from tree-rings confirms that the old trees in these pastures only became open-grown after settlement in 1780-1800, when their growth rates increased greatly as the woods were thinned out for use by livestock (McEwan & McCarthy 2008). Unfortunately, the ash-oak savanna concept has been perpetuated in several recent reports, including the newsletter of Kentucky State Nature Preserves Commission (Yahn 2006) and some master’s theses from the University of Kentucky (Wallingford 2006, Adkins 2007, Schaffer 2013).

The herbivore hypothesis, when applied to Bluegrass Woodland, suggests that concentrations of browsing within the original woods caused partial segregation of the walnut/buckeye type and (especially on drier sites) the oak/hickory type from the ash/elm type (Campbell 2012, 2013a). But the Collection Field—and most other old fields in the region—has relatively little colonization by oaks, hickories and buckeyes, trees with large seeds and seedlings that tend to be clustered close to parents (Campbell et al. 1978). For scientific interest

and general restoration, it will be useful to implement further experimental plantings of all typical tree species in Bluegrass Woodland, especially the large-seeded *Aesculus glabra*, *Carya laciniosa* and *Quercus macrocarpa*. From measurement of browsing effects on different plant species, plus comparisons with effects of burning, mowing or other management, we will gain much deeper ecological understanding of the native vegetation.

Controlled browsing by deer or livestock has rarely been used for restoration of native vegetation in eastern North America. As the science of conservation developed over a century ago, both browsing and burning in forests became viewed in a negative light, as exemplified by Sargent's statement (1884, Part III, p. 490): "Two causes, however, are constantly at work destroying the permanence of the forests of the country and threatening their total extermination as sources of national prosperity—fire and browsing animals inflict greater permanent injury upon the forests of the country than the ax, recklessly and wastefully as it is generally used against them." Paradoxically, Sargent was also a specialist on the taxonomy of *Crataegus* (hawthorns), a diverse genus that appears intimately associated with ungulates (Vera 2000, Smit & Ruifrok 2011, Phipps 2013), as illustrated here by *C. mollis* (Figure 3).

In addition to practical concerns about difficulties with management of ungulates, there has been a general assessment that livestock are bad for the woods in east-central states (e.g., Dambach 1944, Johnson 1952, Apsley et al. 1985), and that deer populations are now too high in the region (e.g., Rooney 2001, Russell et al. 2001). Yet a more balanced view deserves to emerge, based on the potential for management of ungulates to simulate the original naturalistic ecology, to help restore ungulate-associated rare plants (especially along trails), to reduce more palatable alien plants, and to provide some economic return from restored vegetation (e.g.,

Dennis 1997, Williams 1997, Garrett et al. 2004, Arbuckle 2009, Harrington & Kathol 2009, Burkhart et al. 2013, Campbell 2013b).

In contrast, fire does not appear to have had a general influence in woods of the central Bluegrass during the 100-200 years before settlement. There are virtually no accounts of fire before or after settlement (Campbell 2013a and citations), and there are no fire-scars in the older tree sections studied by McEwan & McCarthy (2008). Yet there is certainly ecological interest in the potential effects of fire, and a central theme for research at Griffith Woods should be to compare effects of burning versus browsing, plus varied combinations. Prescribed burning in native vegetation now has many proponents across east-central states, with much federal support (e.g., Nowacki & Abrams 2008, Spetich et al. 2011). But it is important that the momentum of interest in prescribed burning does not lead to exaggerated claims and excessive applications. A more balanced objective assessment is needed, taking account of all relevant data (e.g., McEwan et al. 2011, Matlack 2013).

A most egregious recent example of misinformation about Bluegrass Woodland comes from the LANDFIRE project of US Forest Service. Within a detailed treatment of “oak-ash-woodland” in the central Bluegrass region, Frost (2005) made the following largely erroneous statements: “The original woodland-savanna aspect, especially on drier uplands of the Inner Bluegrass is believed to have been dominated by fire-resistant oaks, especially chinquapin oak (*Quercus muhlenbergii*) and burr oak (*Quercus macrocarpa*), but also with a variety of other species... Central Kentucky grasslands were maintained by fire but we could expect that woody succession was also retarded by the heavy, clayey soils originating from the limestone substrate. The first approximation map of presettlement fire regimes of the U.S. (Frost 1998) indicated fire regimes of 4-6 and 7-12 years in the model area... Lightning and Native

Americans likely provided roughly equal influence as ignition sources in presettlement Kentucky, with Indian influence being the dominant factor locally... Recent examination of early surveys [has] suggested that the landscape might more appropriately be described as oak or oak-ash woodland, having an open, fire-maintained understory and perhaps with a lower fire frequency than that previously suggested (Campbell, pers. comm.)... Openings had patches of cane (mesic sites) or calciphilic prairie graminoids and forbs...and possibly other prairie grasses that have been extirpated by grazing and elimination of fire. Little bluestem and a variety of other prairie grasses do well on high pH soils elsewhere and could be candidates for inclusion in the original herb layer..." There is no mention of native herbivores. I (JC) am listed as a reviewer of this document, but I did not review anything like the final draft, I do not agree with it, and I do not want my name associated with it. There is a danger that lack of good critical review based on existing information—and lack of careful new research attuned to the needs of this region—will delay or even interrupt the restoration of something like the original ecosystem.

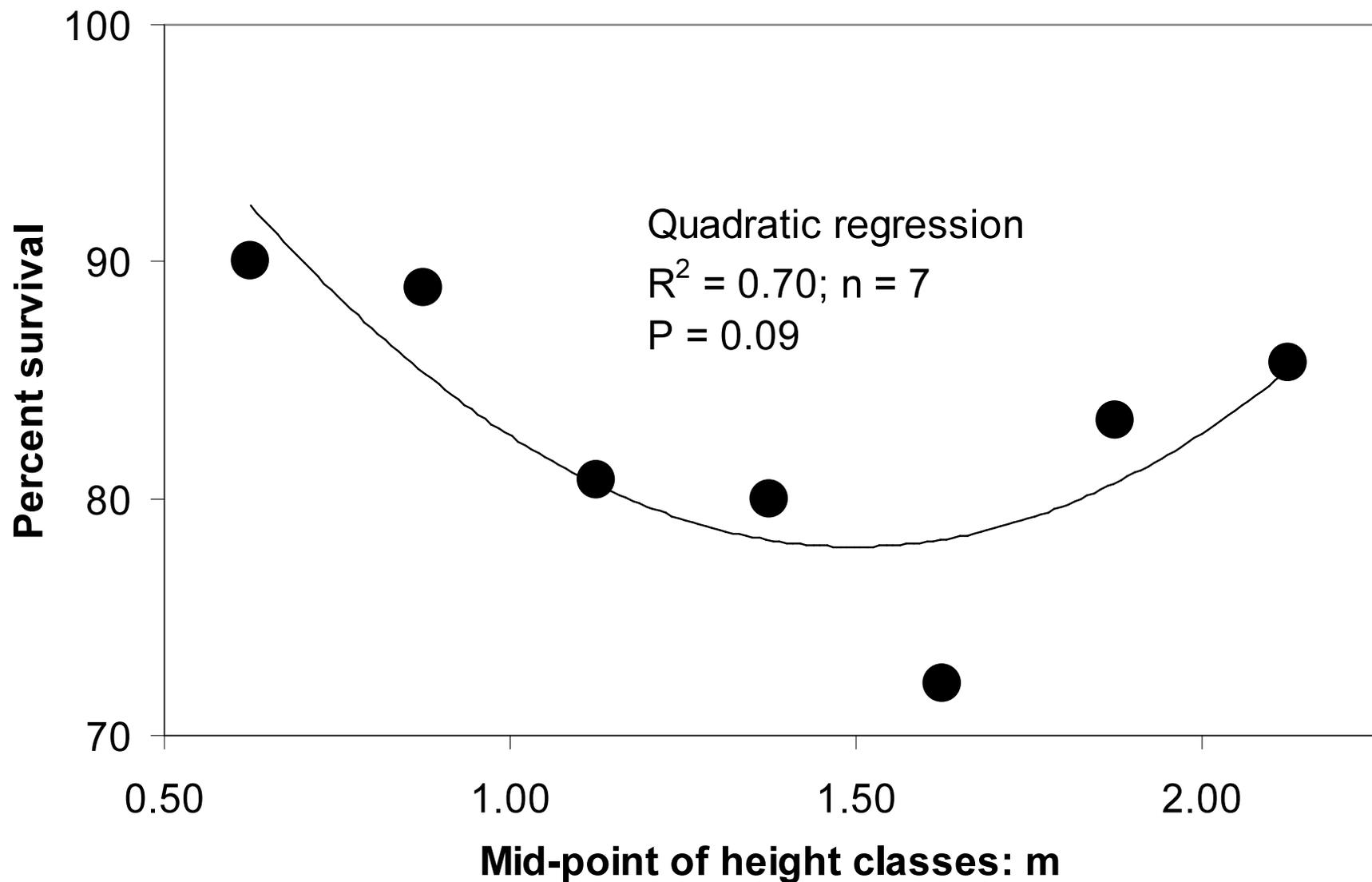
**Biological Goals.** In addition to restoring or simulating prehistoric ecological processes, a broad goal for management at this site is to conserve native biological diversity. Ideally, this biological interest would be advanced by ecological management. It is encouraging that, even within this one field, browsing appears to have promoted a spatially heterogeneous mix among the two provisional groups of plant species (Figure 2c-i). Moreover, spatial heterogeneity among tree species along surrounding fencerows and woodland edges may be interpreted in terms of previous browsing influence, perhaps for 100-200 years during development of this farm: decreasing from south to north (lower left to upper right in Figure 2h-i). This trend is not related to woodland age (ancient along all of SE border, youngest along all of NW and NE borders). The southern sections of these fencerows and edges have much less dominance by

white ash and (to a lesser extent) hackberry, with a more species-rich tree composition (Table 5). This trend parallels the developing pattern among seedlings and saplings within the field (Figure 3).

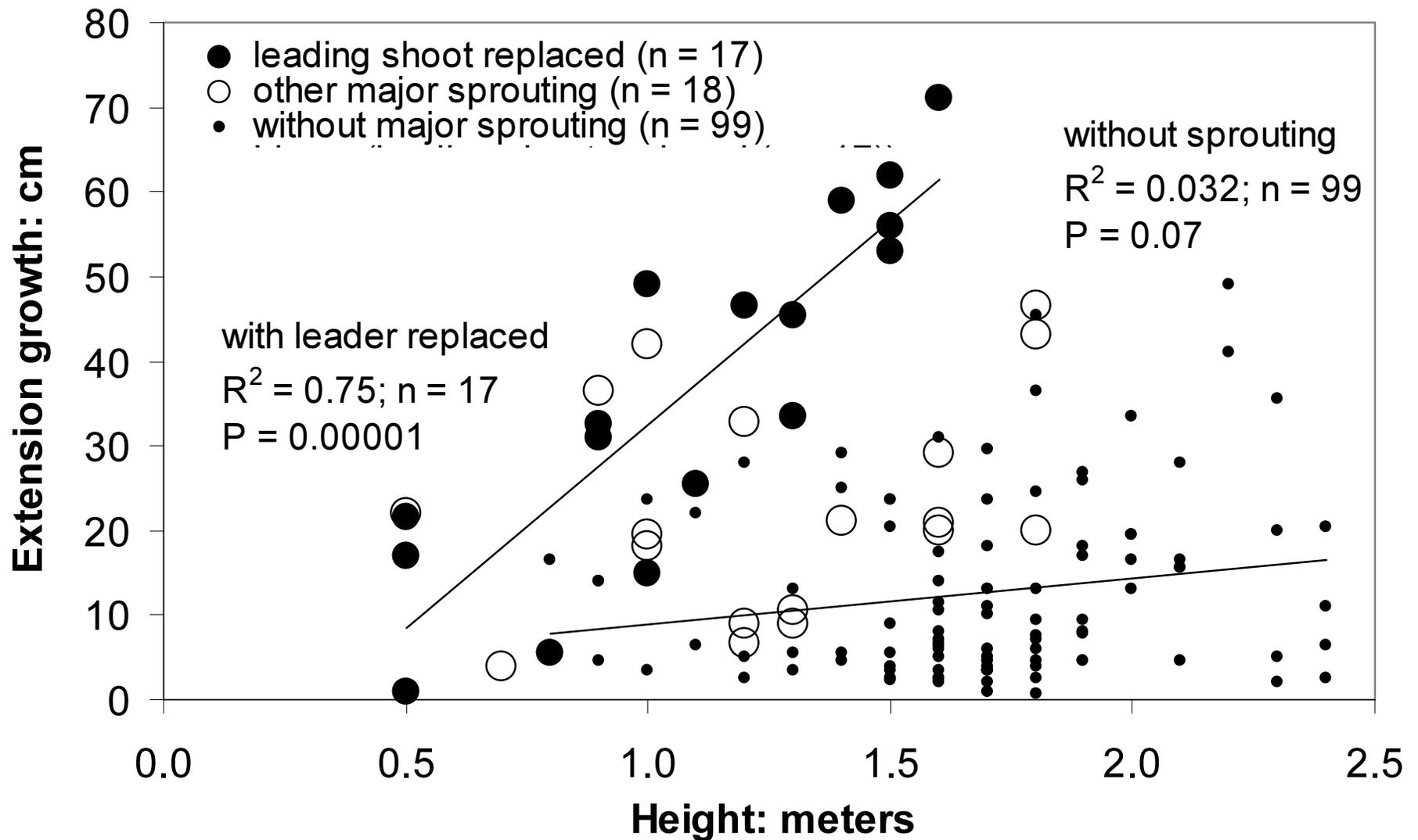
Alien trees and shrubs in this field include several browsing-associated species—mostly Rosaceae—and two browsing-sensitive species—with many plants of *Lonicera maackii* plus a few *Morus alba*. Thus control of browsing by livestock or deer, with fencing, cannot be a simple panacea for reducing aliens. However, continued seasonally intense browsing combined with shade may become increasingly useful as the vegetation develops. All of the browsing-associated aliens in this field are intolerant of shade, but *L. maackii* is by far the most common invasive woody species in forests and fencerows of this region. More mature closed forests with oaks, hickories and sugar maple tend to have less invasion by *L. maackii* (Wilson et al. 2013). But, paradoxically, Hutchinson & Vankat (1998) showed that: “Large expanses of agricultural land apparently act as a barrier to the dispersal of this naturalized shrub”—it is most successful in suburban areas with no browsing. Although invasion of *L. maackii* is not prevented by dense deer populations, evidence assembled here indicates that browsing may reduce it somewhat (Table 4; Figure 3). Species of *Lonicera*, in general, are often preferred by ruminants and can be greatly reduced by them under some conditions (e.g., Nelle 1996, Luginbuhl et al. 1999, Turner et al. 2000, Asani et al. 2006, Shrestha & Wegge 2008, Poppe & Scheibe 2013). The potential negative effect of ruminants on *L. maackii*, especially in shade, deserves much more experimental investigation.

Other alien species include most of the browsing-associated forbs in this field, and a smaller proportion of the browsing-neutral or -sensitive forbs (Table 3). They also include most of the grasses (all cool-season/C3 species), which were not classified as browsing-associated

here but do generally withstand the varied effects of ungulates. If more open zones of grassy vegetation are to be promoted in a naturalistic restoration that includes the effects of ungulates, how can these alien plants be reduced? One simple approach is to kill the dominant pasture grasses with selective herbicides to see what comes up instead; initial trials produced varied results, with alien thistles increasing in some plots but native wild ryes in others (Adkins 2007, Adkins & Barnes 2013). Another approach is to kill the fields completely with herbicides and then replant warm-season/C4 grasses, as already conducted in several fields at Griffith Woods, but those species do not generally appear to have formed a significant component of the original openings within woodland of the central Bluegrass (Campbell 2005). A third approach is to let these aliens become gradually suppressed by replanted cane (*Arundinaria gigantea*)—which was formerly dominant in the original openings. Deeper analysis of these issues will be addressed in future papers, based partly on extensive plot data from the several fields planted with cane at Griffith Woods.



**Figure 13. Percent survival of blue ash saplings (y-axis) in relation to initial height classes (meters on x-axis).** Quadratic regression, with weak significance, is shown for these seven points. Even the lowest point (at 72%) does not differ significantly in percent survival from the remainder using chi-square test.



**Figure 14. Scatter plot of blue ash plants with annual extension growth (mean of 2006 and 2007) versus final height (Sep 2007), showing segregation of plants with leading shoots replaced since planting (solid points). Plants with “other major sprouting” of lower branches but not leaders (open points) had intermediate growth but no significant regression ( $R^2 = 0.10$ ).**

**Table 11. Comparison of blue ash growth and survival from the four provenances (mixed systematically along the planted rows).** Names are landowner-based with counties in parentheses. Differences are tested using ANOVA on log-transformed data for height and extension growth. In addition to complete data from all surviving trees, data are provided that exclude clearly damaged or resprouted stems; these rows are marked with asterisks (\*).

<b>Means</b>	<b>Kern (Fayette)</b>	<b>Wilson (Jessamine)</b>	<b>Alexander (Woodford)</b>	<b>Griffith (Harrison)</b>	<b>Significance of differences</b>
<b>Initial height, estimated (m)</b>	<b>1.209</b>	<b>1.255</b>	<b>1.293</b>	<b>1.591</b>	<b>P = 0.003</b>
<b>Final height, all data (m)</b>	<b>1.453</b>	<b>1.605</b>	<b>1.584</b>	<b>1.661</b>	<b>P = 0.03</b>
<b>* Final height excluding (m)</b>	<b>1.577</b>	<b>1.642</b>	<b>1.732</b>	<b>1.985</b>	<b>P = 0.003</b>
<b>Annual growth, all data (cm)</b>	<b>9.82</b>	<b>8.69</b>	<b>16.41</b>	<b>11.99</b>	<b>N.S. (P = 0.1)</b>
<b>* Annual growth excluding (cm)</b>	<b>8.23</b>	<b>6.56</b>	<b>7.56</b>	<b>9.88</b>	<b>N.S. (P= 0.7)</b>
<b>Annual growth / final ht. (cm/m)</b>	<b>5.33</b>	<b>4.47</b>	<b>6.11</b>	<b>3.37</b>	<b>N.S. (P = 0.4)</b>
<b>Mortality (percent)</b>	<b>20.9</b>	<b>27.5</b>	<b>10.0</b>	<b>25.9</b>	<b>N.S. (P = 0.4)</b>

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## LITERATURE CITED

[\*Asterisks indicate that only summaries have been seen; many other sources remain to check.]

- Adkins, J.K. 2007. Efficacy of herbicides to restore understory cool season grassland communities in central Kentucky. M.Sc. thesis, University of Kentucky (Department of Forestry), Lexington. 96 pages.
- Adkins, J.K., & T.G. Barnes. 2013. Herbicide treatment and timing for controlling Kentucky bluegrass (*Poa pratensis*) and tall fescue (*Festuca arundinacea*) in cool season grasslands of central Kentucky, USA. *Natural Areas Journal* 33: 31–38.
- Adler, P.B., D.A. Raff & W.K. Lauenroth. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465–479.
- \*Allen, E.O. 1968. Range use, foods, condition, and productivity of white-tailed deer in Montana. *Journal of Wildlife Management* 32: 130–141

- Anderson, R.C., E.A. Corbett, M.R. Anderson, G.A. Corbett & T.M. Kelley. 2001. High white-tailed deer density has negative impact on tallgrass prairie forbs. *Journal Torrey of the Botanical Societies* 128: 381–392.
- Anderson, R.C., B. Dorick & T. Crispino. 2007. Impacts of initial species richness and deer browsing on the quality of restored prairie in Central Illinois. *Ecological Restoration*. 25: 99–101.
- Apsley, D.K., D.J. Leopold & G.R. Parker. 1985. Tree species response to release from domestic livestock grazing. *Proceedings of the Indiana Academy of Science* 94: 215–226.
- Arbuckle, J.G. 2009. Cattle and trees don't mix!?! Competing agri-environmental paradigms and silvopasture agroforestry in the Missouri Ozarks. Pages 116–133 in A.J. Franzluebbbers (ed). *Farming with Grass: Achieving Sustainable Mixed Agricultural Landscapes*. Soil and Water Conservation Society. Ankeny, Iowa.
- Asnani, K.M., R.A. Klips & P.S. Curtis. 2006. Regeneration of woodland vegetation after deer browsing in Sharon Woods Metro Park, Franklin County, Ohio. *Ohio Journal of Science* 106: 86–92.
- Ashton, I.W., & T.M. Ler dau. 2008. Tolerance to herbivory, and not resistance, may explain differential success of invasive, naturalized, and native North American temperate vines. *Diversity and Distributions* 14: 169–178.
- Atwood, E.L. 1941. White tailed deer foods of the United States. *Journal of Wildlife Management* 5: 314-332.
- \*Augustine, D.J., & S.J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62: 1165–1183.

- Bakker, E.S., H. Olf, C. Vandenberghe, K. de Maeyer, R. Smit, J.M. Gleichman & F.W.M. Vera. 2004. Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. *Journal of Applied Ecology* 41: 571–582.
- Bailey, J.K., & T.G. Whitham. 2003. Interactions among elk, aspen, galling sawflies and insectivorous birds. *Oikos* 101: 127–134.
- Barnes, W.J., & E. Dibble. 1988. The effects of beaver in riverbank forest succession. *Canadian Journal of Botany* 66: 40–44.
- Benavides, J.E. 2002. Utilization of mulberry in animal production systems. Pages 291–327 in: M.D. Sánchez (ed). *Mulberry for Animal Production*. FAO Animal Production and Health Paper 147 [Proceedings of an electronic conference carried out between May and August 2000]. Food and Agriculture Organization, Rome.
- Bergstrom, R., & C. Guillet. 2002. Summer browsing by large herbivores in short-rotation willow plantations. *Biomass and Bioenergy* 23: 27–32.
- Berry, A.I. 2007. Creation of a geodatabase for Griffith Woods. M.Sc. thesis, University of Kentucky (School of Biological Sciences). 193 pages.
- Bilyeu, D.M., D.J. Cooper, & N.T. Hobbs. 2007. Assessing impacts of large herbivores on shrubs: tests of scaling factors for utilization rates from shoot-level measurements. *Journal of Applied Ecology* 44: 168–175.
- Biswell, H.H., & M.D. Hoover. 1945. Appalachian hardwood trees browsed by cattle. *Journal of Forestry* 43: 675–676.
- \*Blair, R.M. 1960. Deer forage increased by thinnings in a Louisiana loblolly pine plantation. *Journal of Wildlife Management* 24: 401–405.
- \*Blyth, L.H., L.J. Ouborg, D.M. Johnson & L.J. Anderson. 2013. The short-term germination and establishment success of deer-dispersed seeds in mesic temperate forests. *Journal of the Torrey Botanical Society* 140: 334–348.

- Bressette, J.W., H. Beck & V.B. Beauchamp. 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. *Oikos* 121: 1749–1760.
- Bryant, F.C., C.A. Taylor & L.B. Merrill. 1981. White-tailed deer diets from pastures in excellent and poor range condition. *J. Range. Manage.* 34: 93–200.
- Bryant, J.P., F.D. Provenza, J. Pastor, P.B. Reichardt, T.P. Clausen & T. DuToit. 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics* 22: 31–446.
- Bryant, W.S., M.E. Wharton, W.H. Martin & J.B. Varner. 1980. The Blue Ash-Oak Savannah Woodland, a remnant of presettlement vegetation in the Inner Bluegrass of Kentucky. *Castanea* 45: 149–165.
- Bryson, C.T., & M.S. DeFelice (ed). 2009. *Weeds of the South*. University of Georgia Press, Athens. 468 pages.
- Burkhart, J.Q. J.R. Rentch & T.M. Schuler. 2013. Effects of forest management on running buffalo clover (*Trifolium stoloniferum* Muhl. ex A. Eaton) distribution and abundance in the Fernow Experimental Forest. *Natural Areas Journal* 33: 156–162.
- Bullock, J., C.B. Hill & J. Silvertown. 1994. Demography of *Cirsium vulgare* in a grazing experiment. *Journal of Ecology* 82: 101–111.
- Burnett, W.C., S.B. Jones & T.J. Mabry. 1977. Evolutionary implications of herbivory on *Vernonia* (Compositae). *Plant Systematics and Evolution* 128: 277–286.
- Burrows, G., & R. Tyrl. 2001. *Toxic Plants of North America*. Ames, Iowa State University. 1390 pages.
- Burt-Smith, G.S., J.P. Grime & D. Tilman. 2003. Seedling resistance to herbivory as a predictor of relative abundance in a synthesised prairie community. *Oikos* 101: 345–353.

- Buttenschøn, R.M., & J. Buttenschøn. 1998. Population dynamics of *Malus sylvestris* stands in grazed and ungrazed, semi-natural grasslands and fragmented woodlands in Mols Bjerger, Denmark. *Annales Botanica Fennica* 35: 233–246.
- Cadenasso M.L., & S.T.A. Pickett. 2000. Linking forest edge structure to edge function: mediation of herbivore damage. *Journal of Ecology* 88: 31–44.
- Cain, N., S.J. Darbyshire, A. Francis, R.E. Nurse & M.-J. Simard. 2010. The Biology of Canadian weeds. 144. *Pastinaca sativa* L. *Canadian Journal of Plant Science* 90: 217–240.
- Campbell, J.J.N., D.B. Richards & L.R.F. Crowley. 1978. Regression analysis of sapling abundance in the Inner Bluegrass of Kentucky, with special reference to seed source. Pages 258-268 in: P.E. Pope (ed). *Proceedings of the Second Central Hardwood Forest Conference*. Purdue University, West Lafayette, Indiana.
- Campbell, J.J.N. 1985. *The Land of Cane and Clover: Presettlement Vegetation in the So-called Bluegrass Region*. Report from the Herbarium, University of Kentucky. 93 pages.
- Campbell, J.J.N., M. Evans, M.E. Medley & N.L. Taylor. 1988. Buffalo clovers in Kentucky (*Trifolium stoloniferum* and *T. reflexum*): historical records, presettlement environment, rediscovery, endangered status, cultivation and chromosome number. *Rhodora* 90: 399–418.
- Campbell, J.J.N. 1989. Historical evidence of forest composition in the Bluegrass region of Kentucky. Pages 231–246 in: G. Rink & C. A. Budelsky (eds). *Proceedings of the Seventh Central Hardwoods Forest Conference*. Southern Illinois University, Carbondale, Illinois.
- Campbell, J.J.N. 2005. Comparative ecology of warm-season (C4) versus cool-season (C3) grass species in Kentucky, with special reference to Bluegrass Woodlands. Pages 95–115 in: T.G. Barnes (ed). *Proceedings of the 4th Eastern Native Grass Symposium*. University of Kentucky, Department of Forestry. Lexington, Kentucky.
- Campbell, J.J.N. 2012. *The Herbivore Hypothesis for Bluegrass Woodland*. Posted at [http://www.bluegrasswoodland.com/uploads/Herbivore\\_Hypothesis.pdf](http://www.bluegrasswoodland.com/uploads/Herbivore_Hypothesis.pdf). 6 pages.

- Campbell, J.J.N. 2013a. Bluegrass Woodland and its eutrophic nature. Posted at [http://www.bluegrasswoodland.com/uploads/Bluegrass\\_Woodland\\_and\\_Its\\_Eutrophic\\_Nature.pdf](http://www.bluegrasswoodland.com/uploads/Bluegrass_Woodland_and_Its_Eutrophic_Nature.pdf). 40 pages.
- Campbell, J.J.N. 2013b. Evergreen woody vines in deciduous mid-temperate forests: a review of habit, habitat, mammalian herbivory, secondary chemistry and biogeographic context. Posted at [http://www.bluegrasswoodland.com/uploads/Evergreen\\_Vines\\_in\\_Deciduous\\_Woods.pdf](http://www.bluegrasswoodland.com/uploads/Evergreen_Vines_in_Deciduous_Woods.pdf). 263 pages.
- \*Castleberry, S.B., W.M. Ford, K.V. Miller & W.P. Smith, W.P. 1999. White-tailed deer browse in a southern bottomland hardwood forest. *Southern Journal of Applied Forestry* 23: 78–82.
- \*Castellano, S.M., & D.L. Gorchov. 2013. White-tailed deer (*Odocoileus virginianus*) disperse seeds of the invasive shrub, Amur Honeysuckle (*Lonicera maackii*). *Natural Areas Journal* 33: 78–80.
- Chantal, M. de, & A. Granström. 2007. Aggregations of dead wood after wildfire act as browsing refugia for seedlings of *Populus tremula* and *Salix caprea*. *Forest Ecology and Management* 250: 3–8.
- Chapel, K.J., & M.A. Vincent. 2013. *Trifolium kentuckiense* (Fabaceae, Papilionoideae), a new species from Franklin and Woodford counties, Kentucky. *Phytoneuron* 2013-63: 1–6.
- \*Cheplick, G.P., & K. Clay. 1988. Acquired chemical defenses in grasses: the role of fungal endophytes. *Oikos* 52: 309–18
- Chmielewski, J.G., & J.C. Semple. 2001. The biology of Canadian weeds. 114. *Symphyotrichum pilosum* (Willd.) Nesom (*Aster pilosus* Willd.). *Canadian Journal of Plant Science* 81: 851–865.
- \*Christopher, C.C., S.F. Matter, & G.N. Cameron. 2014. Individual and interactive effects of Amur honeysuckle (*Lonicera maackii*) and white-tailed deer (*Odocoileus virginianus*) on

- herbs in a deciduous forest in the eastern United States. *Biological Invasions* (2014). 15 pages..
- Cipollini, K. A., E. Ames & D. Cipollini. 2009. Amur honeysuckle (*Lonicera maackii*) management method impacts restoration of understory plants in the presence of white-tailed deer (*Odocoileus virginiana*). *Invasive Plant Science and Management* 2: 45–54.
- Cogger, B.J., N.R.D. Jager, M. Thomsen & C.R. Adams. 2014. Winter browse selection by white-tailed deer and implications for bottomland forest restoration in the Upper Mississippi River Valley, USA. *Natural Areas Journal* 34: 144-153 [see also thesis].
- Comisky, L., A.A. Royo & W.P. Carson. 2005. Deer browsing creates rock refugia gardens on large boulders in the Allegheny National Forest, Pennsylvania. *American Midland Naturalist* 154: 201–206.
- Conover, M.R., & G.S. Kania. 1988. Browsing preference of white-tailed deer for different ornamental species. *Wildlife Society Bulletin* 16: 175–179.
- Cooke, A.S., & L. Farrell. 2001. Impact of muntjac deer (*Muntiacus reevesi*) at Monk's wood nature reserve, Cambridgeshire, eastern England. *Forestry* 74: 241–250.
- Coppedge, B.R., & J.H. Shaw. 1997. Effects of horning and rubbing by bison (*Bison bison*) on woody vegetation in a tallgrass prairie landscape. *American Midland Naturalist* 138: 189–196.
- Coppedge, B.R., D.M. Leslie & J.H. Shaw. (1998b) Botanical composition of bison diets on tallgrass prairie in Oklahoma. *Journal of Range Management* 51: 379–382.
- Corrigan, E.E. 2003. *Calystegia spithamea* (L.) Pursh ssp. *spithamea*, Low Bindweed. Conservation and Research Plan for New England. New England Wildflower Society, Framingham, Massachusetts. 27 pages.
- Crain, C.M. 2008. Interactions between marsh plant species vary in direction and strength depending on environmental and consumer context. *Journal of Ecology* 96: 166–173.

- Crimmins, S.M., J.W. Edwards, W.M. Ford, P.D. Keyser & J.M. Crum. 2010. Browsing patterns of white-tailed deer following increased timber harvest and a decline in population density. *International Journal of Forestry Research* (2010). 7 pages.
- Curtis, R.O., & F.M. Rushmore. 1958. Some effects of stand density and browsing on reproduction in an Adirondack hardwood stand. *Journal of Forestry* 56: 116–121.
- Cutulle, M.A., J.F. Derr, D. McCall, B. Horvath & A.D. Nichols. 2013. Impact of hybrid bluegrass and tall fescue seeding combinations on brown patch severity and weed encroachment. *HortScience* 48: 493–500.
- \*Dahlberg, B.L., & R.C. Guettinger. 1956. The white-tailed deer in Wisconsin. Pittman-Robertson Project W-4-R, Technical Wildlife Bulletin 14. Wisconsin Conservation Department, Madison, Wisconsin. 282 pages.
- Dale, J.M. 1974. The biology of Canadian weeds. 5. *Daucus carota*. *Canadian Journal of Plant Science* 54: 673–685.
- Dambach, C.A. 1944. A ten-year ecological study of adjoining grazed and ungrazed woodlands in northeastern Ohio. *Ecological Monographs* 14: 255–270.
- Day, R.K., & D. Den Uyl. 1932. The natural regeneration of farm woods following the exclusion of livestock. Purdue University, Agricultural Experiment Station Bulletin No. 368, Lafayette, Indiana. 47 pages.
- DeJaco, C.E. 2006. The effects of mammalian herbivores on successional grasslands in central Illinois. Ph.D. thesis, University of Illinois at Urbana-Champaign. 175 pages.
- \*Delfino, J.C. 1993. Importance of cover and food in habitat choice by *Microtus ochrogaster*: a tailoring experiment. Ph.D. dissertation, University of Kentucky. 267 pages.
- Deliberto, T.J. 1987. Nutritional ecology of white-tailed Deer in southcentral Oklahoma. M.Sc. thesis, Texas Tech University. 88 pages.

- Delibes-Mateos, M., M. Delibes, P. Ferreras & R. Villafuerte. 2008. Key role of European rabbits in the conservation of the western Mediterranean basin hotspot. *Conservation Biology* 22: 1106–1117.
- Dennis, A. 1997. Effects of livestock grazing on forest habitats. Pages 313–341 in: M.W. Schwartz (ed). *Conservation in Highly Fragmented Landscapes*. Chapman & Hall, New York.
- Desrochers, A.M., J.F. Bain & S.I. Warwick. 1988. The biology of Canadian weeds.89. *Carduus nutans* L. and *Carduus acanthoides* L. *Canadian Journal of Plant Science* 68: 1053–1068.
- Diaz, A., & Ford, M.A. 2000. Can palatability trials be used to predict the effect of rabbit grazing on the flora of ex-arable land? *Agriculture Ecosystems and Environment* 78: 249–259.
- Dieter, C.D., & T.R. McCabe. 1989. Habitat use by beaver along the Big Sioux River in eastern South Dakota. Pages 135–140 in: R.E. Gresswell, B.A. Barton & J.L. Kerschner (eds). *Practical Approaches to Riparian Resource Management, an Educational Workshop*. U.S. Bureau of Land Management, Billings, Montana.
- DiTommaso, A., F.M. Lawlor & S.J. Darbyshire. 2005. The biology of invasive alien plants in Canada. *Cynanchum rossicum* (Kleopow) Borhidi (= *Vincetoxicum rossicum* (Kleopow) Barbar.) and *Cynanchum louiseae* (L.) Kartesz & Gandhi (= *Vincetoxicum nigrum* (L.) Moench) *Canadian Journal of Plant Science* 85: 243–263.
- DiTommaso, A., S.H. Morris, J.D. Parker, C.L. Cone & A.A. Agrawal. 2014. Deer browsing delays succession by altering aboveground vegetation and belowground seed banks. *PloS One* 9: e91155. 9 pages.
- Dostaler, S., J-P. Ouellet, J.F. Therrien & S.D. Côté. 2011. Are feeding preferences of white-tailed deer related to plant constituents? *Journal of Wildlife Management* 75: 913–918.

- Dumont, A., J-P. Ouellet, M. Crête & J. Huot. 2005. Winter foraging strategy of white-tailed deer at the northern limit of its range. *Écoscience* 12: 476–484.
- Dutra, H.P., K. Barnett, J.R. Reinhardt, R.J. Marquis & J.L. Orrock. 2011. Invasive plant species alters consumer behavior by providing refuge from predation. *Oecologia* 166: 649–657
- Ehrlén, J., & O. Eriksson. 1993. Toxicity in fleshy fruits – a non-adaptive trait? *Oikos* 66: 107–113.
- English, E.I., & M.A. Bowers. 1994. Vegetational gradients and proximity to woodchuck (*Marmota monax*) burrows in an old field. *Journal of Mammalogy* 75: 775–780.
- Englund, J., & W. Meyer. 1986. The impact of deer on 24 species of prairie forbs. *Proceedings of the North American Prairie Conference* 9: 210–212.
- Epstein, A.H., & J.H. Hill. 1999. Status of rose rosette disease as a biological control for multiflora rose. *Plant Disease* 83: 92–101.
- Etzenhouser, M.J., M.K. Owens, D.E. Spalinger & S.B. Murden, S.B. 1998. Foraging behaviour of browsing ruminants in a heterogeneous landscape. *Landscape Ecology* 13: 55–64.
- Fargione, M.J., P.D. Curtis & M.A. Richmond. 1991. Resistance of woody ornamental plants to deer damage. Cornell Cooperative Extension Fact Sheet 800.00, Cornell University, Ithaca, New York. 4 pages.
- Farrow, E.P. 1917. On the ecology of the vegetation of Breckland. III. General effects of rabbits on the vegetation. *Journal of Ecology* 5: 1–18.
- Fedriani, J.M., & M. Delibes. 2009. Seed dispersal in the Iberian pear, *Pyrus bourgaeana*: a role for infrequent mutualists. *Ecoscience* 16: 311–321.
- Fernald, M.L. 1950. *Gray's Manual of Botany*. 8th edition. Van Nostrand, New York.

- Finder, R.A., J.L. Roseberry & A. Woolf. 1999. Site and landscape conditions at white-tailed deer/vehicle collision locations in Illinois. *Landscape and Urban Planning* 44: 77–85.
- Fletcher, J. 2007. The rise of British deer parks: their raison d'être in a global and historical perspective. *Landscape Archaeology and Ecology* 6: 31–44.
- Flory, S.L., & Clay, K., 2006. Invasive shrub distribution varies with distance to roads and stand age in eastern deciduous forests in Indiana, USA. *Plant Ecology* 184:131–141.
- \*Forrester, J. A., D.J. Leopold, & H. B. Underwood. 2006. Isolating the effects of white-tailed deer on the vegetation dynamics of a rare maritime American holly forest. *American Midland Naturalist* 156: 135–150.
- Fowells, H.A. (ed) 1965. *Silvics of Forest Trees of the United States*. U.S.D.A. Agricultural Handbook 271. 762 pages.
- Fraser, L.H., & E.B. Madson. 2008. The interacting effects of herbivore exclosures and seed addition in a wet meadow. *Oikos* 117: 1057–1063
- Frost, C. 2005. Rapid Assessment Reference Condition Model. Potential Natural Vegetation Group (PNVG): R8OKAW Oak-Ash-Woodland. Posted at [http://www.fs.fed.us/database/feis/pdfs/PNVGs/S\\_Appalachians/R8OKAW.pdf](http://www.fs.fed.us/database/feis/pdfs/PNVGs/S_Appalachians/R8OKAW.pdf). 6 pages.
- Frost, R.A., J.C. Mosley & B.L. Roeder. 2013. Recovery and viability of sulfur cinquefoil seeds from the feces of sheep and goats. *Rangeland Ecology & Management* 66: 51–55.
- Fuhlendorf, S.D., D.M. Engle, R.D. Elmore, R.F. Limb & T.G. Bidwell. 2012. Conservation of pattern and process: developing an alternative paradigm of rangeland management. *Rangeland Ecology & Management* 65:579–589.
- Garrett, H.E., M.S. Kerley, K.P. Ladyman, W.D. Walter, L.D. Godsey, J.W. Van Sambeek & D.K. Brauer. 2004. Hardwood silvopasture management in North America. *Agroforestry Systems* 61: 21–33.

- George, J.F., & J. Powell. 1977. Deer browsing and browse production of fertilized elm sprouts. *Journal of Range Management* 30: 357–360.
- Gill, D.S., & P.L. Marks. 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecological Monographs* 61: 183–205.
- Gleason, H.A., & A. Cronquist. 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*. 2nd edition. New York Botanical Garden, Bronx. 910 pages.
- Grime, J.P., S.F. McPherson-Stewart & R.S. Dearman. 1968 An investigation of leaf palatability using the snail *Cepaea nemoralis*. *Journal of Ecology* 56: 405–420.
- Grove, A.T., & O. Rackham. 2001. *The Nature of Mediterranean Europe: an Ecological History*. Yale University Press, London. 384 pages.
- Gubanyi, J.A., J.A. Savidge, S.E. Hygnstrom, K.C. VerCauteren, G.W. Garabrandt & S.P. Korte. 2008. Deer impact on vegetation in natural areas in southeastern Nebraska. *Natural Areas Journal* 28: 121–129.
- \*Halls, L.K., & T.R. Dell. 1966. Trail of ranked set sampling for forage yield. *Forest Science* 12: 22–26.
- Halls, L.K. 1975. Browse use by deer in an east Texas forest. *Proceedings of the Annual Conference of Southeastern Association of Game and Fish Commissioners (1974)* 28: 557–562.
- Harrington, J.A., & E. Kathol. 2009. Responses of shrub midstory and herbaceous layers to managed grazing and fire in a North American savanna (oak woodland) and prairie landscape. *Restoration Ecology* 17: 234–244.
- Hedtcke J, J. Posner, M. Rosemeyer & K. Albrecht. 2009. Browsing for conservation: Springtime forage value of midstory shrubs of degraded oak savannas in Southern Wisconsin. *Renewable Agriculture and Food Systems* 24: 293–299.

- \*Heinen, J.T., & R.C. Currey. 2000. A 22-year study on the effects of mammalian browsing on forest succession following a clearcut in northern lower Michigan. *American Midland Naturalist* 144: 243-252.
- Heinrich, H., & S. Predl. 1995. Can we landscape to accommodate deer? The Tracy Estate Research Garden. Page 102-112 in: *Proceedings of the Sixth Eastern Wildlife Damage Control Conference (1993)*, Asheville, North Carolina. University of Nebraska, School of Natural Resource Science, Lincoln.
- Herms, D.A., & W.J. Mattson. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology* 67: 283–335.
- Herrick, J.E., J.R. Brown, B.T. Bestelmeyer, S.S. Andrews, G. Baldi, J. Davies, M. Duniway, K.M. Havstad, J.W. Karl, D.L. Karlen, D.P.C. Peters, J.N. Quinton, C. Riginos, P.L. Shaver, K.M. Steinaker & S. Twomlow. 2012. Revolutionary land use change in the 21st century: Is (rangeland) science relevant? *Rangeland Ecology and Management* 65: 590–598.
- Hickman K.R., & D.C. Hartnett 2002. Effects of grazing intensity on growth, reproduction, and abundance of three palatable forbs in Kansas tallgrass prairie. *Plant Ecology* 159: 23–33.
- Hill, M.O., J.O. Mountford, D.B. Roy & R.G.H. Bunce. 1999. *Ellenberg's Indicator Values for British Plants: ECOFACT. Vol. 2. Technical Annex*. HMSO, London, UK. 46 pages.
- Hilty, J. 2012. Illinois Wildflowers. Posted at <http://www.illinoiswildflowers.info/index.htm>.
- Hochwender, C.G., R.J. Marquis & K.A. Stowe. 2000. The potential for and constraints on the evolution of compensatory ability in *Asclepias syriaca*. *Oecologia* 122: 361–70.
- Hopkins, C.O., & W.E. Hopkins. 1972. Importance per cent values of a browsed southeastern Indiana forest. *Proceedings of the Indiana Academy of Science* 81: 160-164.
- Horsley, S.B., S.L. Stout & D.S. deCalesta DS. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications* 13: 98–118

- Howe, H.F., & D. Lane. 2004. Vole-driven succession in experimental wet-prairie restorations. *Ecological Applications* 14: 1295–1305.
- Howe, H. F., B. Zorn-Arnold, A. Sullivan & J. S. Brown. 2006. Massive and distinctive effects of meadow voles on grassland vegetation. *Ecology* 87: 3007–3013.
- Howery, L.D., D.L. Nolte, M. Sullivan & M.W. Kilby. 1999. Sensory attributes, phytotoxicity, and production of grape cultivars after treatment with two deer repellents. *Horticultural Technology* 9: 429–432.
- Hutchings, M.J., & E.A.C. Price. 1999. Biological Flora of the British Isles. *Glechoma hederacea* L. (*Nepeta glechoma* Benth., *N. hederacea* (L.) Trev.). *Journal of Ecology* 87: 347–364.
- Hutchinson, T.J., & J.L. Vankat. 1998. Landscape structure and spread of the exotic shrub *Lonicera maackii* (Amur honeysuckle) in southwestern Ohio forests. *American Midland Naturalist* 139: 383–390.
- Inouye, R.S., T.D. Allison & N.D. Johnson, N.D. 1994. Old field succession on a Minnesota sand plain – effects of deer and other factors on invasion by trees. *Bulletin of the Torrey Botanical Club* 121: 266–276.
- Iravani, M., M. Schütz, P.J. Edwards, A.C. Risch, C. Scheidegger & H.H. Wagnerd. 2011. Seed dispersal in red deer (*Cervus elaphus* L.) dung and its potential importance for vegetation dynamics in subalpine grasslands. *Basic and Applied Ecology* 12: 505–515.
- Janzen, D.H. 1976. Effects of defoliation on fruit-bearing branches of the Kentucky coffee-tree *Gymnocladus dioicus* (Leguminosae). *American Midland Naturalist* 95: 474–478.
- \*Janzen, D.H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. *American Naturalist* 123: 338–353.

- Johnson, A.S., P.H. Hale, W.M. Ford, J.M. Wentworth, J.R. French, O.F. Anderson & G.B. Pullen. 1995. White-tailed deer foraging in relation to successional stage, overstory type and management of southern Appalachian forests. *American Midland Naturalist* 133: 18–35.
- Johnson, C.N. 2009. Ecological consequences of late quaternary extinctions of megafauna. *Proceedings of the Royal Society B* 276: 2509–19.
- Johnson, E.A. 1952. Effect of farm woodland grazing on watershed values in the Southern Appalachian Mountains. *Journal of Forestry* 50: 109–113.
- Jull, J.G. 2001. Plants not favored by deer. University of Wisconsin Extension Publication A3727. 4 pages.
- Kato, T., K. Ishida & H. Sato. 2008. The evolution of nettle resistance to heavy deer browsing. *Ecological Research* 23: 339–345.
- Katona, K., M. Kiss, N. Bleier, J. Székely, M. Nyeste, V. Kovács, A. Terhes, Á. Fodor, T. Olajos, E. Rasztovits & L. Szemethy. 2013. Ungulate browsing shapes climate change impacts on forest biodiversity in Hungary. *Biodiversity Conservation* 22. 14 pages.
- Kindscher, K, Q. Long, S. Corbett, K. Bosnak, H. Loring, M. Cohen & B.N. Timmerman. 2012. The ethnobotany and ethnopharmacology of wild tomatillos, *Physalis longifolia* Nutt., and related *Physalis* species: a review. *Economic Botany* 66: 298–310.
- Kirby, K.J., 2001. The impact of deer on the ground flora of British broadleaved woodland. *Forestry* 74: 219–229.
- Knapp, L.B., J.H. Fownes & R.A. Harrington, R.A. 2008. Variable effects of large mammal herbivory on three non-native vs. three native woody plants. *Forest Ecology and Management* 255: 92–98.
- Kohlmann, S.G., & K.L. Risenhoover. 1994. Spatial and behavioral-response of white-tailed deer to forage depletion. *Canadian Journal of Zoology* 72: 506–513.

- Kohlmann, S.G., & K.L. Risenhoover. 1997. White-tailed deer in a patchy environment: a test of the ideal-free-distribution theory. *Journal of Mammalogy* 78: 1261–1272.
- \*Kohn, B.E., & J.J. Mooty. 1971. Summer habitat of white-tailed deer in north-central Minnesota. *Journal of Wildlife Management* 35: 476–487.
- Korschgen, L.J. 1962. Foods of Missouri deer, with some management implications. *Journal of Wildlife Management* 26: 164–172.
- Korschgen, L.J., W.R. Porath & O. Torgerson. 1980. Spring and summer foods of deer in the Missouri Ozarks. *Journal of Wildlife Management* 44: 89–97.
- Krueger, L.M., & C.J. Peterson. 2009. Effects of woody debris and ferns on herb-layer vegetation and deer herbivory in a Pennsylvania forest blowdown. *Ecoscience* 16: 461–469.
- Lehmkuhler, J.W., E.E.D. Felton & D.A. Schmidt. 2004. Tree protection methods during the silvopastoral-system establishment in Midwestern USA: cattle performance and tree damage. *Agroforestry Systems* 59: 35–42.
- Leif, J. 2013. Plant guide for Dillenius' ticktrefoil (*Desmodium glabellum*). USDA, Natural Resources Conservation Service, East Lansing, Michigan. 2 pages.
- Littlefield, K.A., J.P. Mueller, J.P. Muir & B.D. Lambert. 2011. Correlation of plant condensed tannin and nitrogen concentrations to white-tailed deer browse preferences in the Cross Timbers. *Texas Journal of Agriculture and Natural Resource* 24: 1–7.
- Long, Z.T., T.H. Pendergast & W.P. Carson. 2007. The impact of deer on relationships between tree growth and mortality in an old-growth beech–maple forest. *Forest Ecology and Management* 252: 230–238.
- Luginbuhl, J.M., T.E. Harvey, J.T. Green, M.H. Poore & J.P. Mueller. 1999. Use of goats as biological agents for the renovation of pastures in the Appalachian region of the United States. *Agroforestry Systems* 44: 241–252.

- Lupardus, J.L. 2005. Seasonal forage availability and diet of reintroduced elk in the Cumberland Mountains, Tennessee. M.Sc. thesis, University of Tennessee. 98 pages.
- MacDonald, M.A., & P.B. Cavers. 1991. The biology of Canadian weeds. 97. *Barbarea vulgaris* R. Br. Canadian Journal of Plant Science 71: 149–166.
- MacDougall, A.S., & S.D. Wilson. 2007. Herbivory limits recruitment in an old-field seed addition experiment. Ecology 88: 1105–1111.
- Mamolos, A.P., & D.S. Veresoglou. 2000. Patterns of root activity and responses of species to nutrients in vegetation of fertile alluvial soil. Plant Ecology 148: 245–253.
- Manson, R.H., R.S. Ostfeld & C.D. Canham. 2001. Longterm effects of rodent herbivores on tree invasion dynamics along forest-field edges. Ecology 82: 3320–3329.
- Masters, R., P. Mitchell & S. Dobbs. 1991. Ornamental and garden plants: controlling deer damage. Oklahoma Cooperative Extension Service Fact Sheet F-6427. Oklahoma State University, Stillwater. 8 pages.
- Matlack, G.R. 2013. Reassessment of the use of fire as a management tool in deciduous forests of eastern North America. Conservation Biology 27: 916-926.
- Matlack, R.S., D.W. Kaufman & G.A. Kaufman. 2001. Influence of grazing by bison and cattle on deer mice in burned tallgrass prairie. American Midland Naturalist 146: 361–368.
- McCullough, D.R. 1985. Variables influencing food habits of white-tailed deer on the George Reserve. Journal of Mammalogy 66: 682–692.
- McEwan, R.W., & B.C. McCarthy. 2008. Anthropogenic disturbance and the formation of oak savanna in central Kentucky, USA. Journal of Biogeography 35: 965–975.
- Meiners, S.J. 2007. Apparent competition: an impact of exotic shrub invasion on tree regeneration. Biological Invasions 9: 849–855.
- Meiners, S. J. and Martinkovic, M. J. 2002. Survival of and herbivore damage to a cohort of *Quercus rubra* planted across a forest- old-field edge. Am. Midl. Nat. 147: 247–256.

- Milchunas, D.G., & W.K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63: 327–366
- Mitchell, F.J.G. 2005. How open were European primeval forests? Hypothesis testing using palaeoecological data. *Journal of Ecology* 2005, 93: 168–177.
- Morellet, N., & B. Guibert. 1999. Spatial heterogeneity of winter forest resources used by deer. *Forest Ecology and Management* 123: 11–20.
- Morrissey, R.C., D.F. Jacobs & J.R. Seifert. 2008. Response of northern red oak, black walnut, and white ash seedlings to various levels of simulated summer deer browsing. *Proceedings of the Central Hardwood Forest Conference* 16: 59–69.
- Muenschler, W.C. 1961. *Poisonous plants of the United States*, 2nd edition. Macmillan Co., New York. 277 pages.
- Myers, J.A., M. Vellend, S. Gardescu & P.L. Marks. 2004. Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* 139: 35–44.
- Myster, R.W., & B.C. McCarthy. 1989. Effects of herbivory and competition on survival of *Carya tomentosa* (Juglandaceae) seedlings. *Oikos* 56: 145–148.
- Myster, R.W., & S.T.A. Pickett. 1992. Effects of palatability and dispersal mode on spatial patterns of trees in old fields. *Bulletin of the Torrey Botanical Club* 119: 145–151.
- Myster, R.W., & S.T.A. Pickett. 1993. Effects of litter, distance, density and vegetation patch type on postdispersal tree seed predation in old fields. *Oikos* 66: 381–388.
- Nelle, S.A. 1996. Management and use of browse in the Edwards Plateau of Texas. Pages 151–155 in: J.R. Barrow, E.D. McArthur, R.E. Sosebee & R.J. Tausch (eds). *Shrubland Ecosystem Dynamics in a Changing Environment*. U.S.D.A. Forest Service, General Technical Report INT-GTR-338. Ogden, Utah.

- Nixon, C.M., & J. Ely. 1969. Foods eaten by a beaver colony in southeast Ohio. *Ohio Journal of Science* 69: 313–319.
- Nowacki, G.J., & M.D. Abrams. 2008. The demise of fire and “mesophication” of forests in the eastern United States. *Bioscience* 58: 123-138.
- Nudds, T. D. 1980. Forage “preference”: theoretical considerations of diet selection by deer. *Journal of Wildlife Management* 44: 735–740.
- Odor, H., B.C. Weisenberger, R.L. Blevins & J.L. Taylor. 1968. Soil survey of Harrison County, Kentucky. U.S.D.A. Soil Conservation Service. 59 pages.
- Ortega, I.M., S. Soltero-Gardea, D.L. Drawe & F.C. Bryant. 1997. Evaluating grazing strategies for cattle: deer and cattle food partitioning. *Journal of Range Management* 50: 622–630.
- Ostfeld, R.S., R.H. Manson & C.D. Canham, C.D. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78: 1531–1542.
- \*Panter, C.J., & P.M. Dolman. 2012. Mammalian herbivores as potential seed dispersal vectors in ancient woodland fragments. *Wildlife Biology* 18: 292–303
- Parks Canada Agency. 2011. Recovery Strategy for the Red Mulberry (*Morus rubra*) in Canada. Species at Risk Act Recovery Strategy Series. Parks Canada Agency. Ottawa, Ontario. 47+ pages.
- Parks, C.G., B.A. Endress, M. Vavra, M.L. McInnis & B.J. Naylor. 2008. Cattle, deer, and elk grazing of the invasive plant sulfur cinquefoil. *Natural Areas Journal* 28: 404–409.
- Petrides, G.A. 1941. Observation of the relative importance of winter deer browse species in Central New York. *Journal of Wildlife Management* 5: 416–422.
- Phipps, J.B. 2013. *Crataegus*. Pages 871-917 in G. Yatskievytch (ed.). Steyermark’s Flora of Missouri. Volume 3. Missouri Dept. of Conservation and Missouri Botanical Garden Press, St. Louis, Missouri.

- Pitcher, D. 1989. Element Stewardship Abstract for *Conium maculatum* L. The Nature Conservancy, Arlington, Virginia. 9 pages.
- Pogge, F.L. 1967. Elm as deer browse. *Journal of Wildlife Management* 31: 354–356.
- Poppe, A., & K.M. Scheibe. 2013. The importance of groves for cattle in semi-open pastures. *Agriculture* 3: 147–156.
- \*Porto, L.C.S., J. Silva, A.B.F. Ferrazc, D.S. Corrêac, M.S. Santosc, C.D.L. Porto & J.N. Picada, 2013. Evaluation of acute and subacute toxicity and mutagenic activity of the aqueous extract of pecan shells [*Carya illinoensis* (Wangenh.) K. Koch]. *Food and Chemical Toxicology* 59: 579–585.
- Rawinski, T.J. 2008. Impacts of white-tailed deer overabundance in forest ecosystems: an overview. U.S. Forest Service, Newton Square, Pennsylvania. 8 pages.
- Richens, R. 1947. Biological Flora of the British Isles. *Allium vineale* L. *Journal of Ecology* 34: 209–226
- \*Ricklefs, R.E. 2008. Foliage chemistry and the distribution of Lepidoptera larvae on broad-leaved trees in southern Ontario. *Oecologia* 157: 53–67.
- Riemenschneider, V., T.B. Cordell & B. Allison. 1995. Impact of white-tailed deer on plant cover and biomass in Potato Creek State Park, St. Joseph County, Indiana. *Proceedings of the Indiana Academy of Science* 104: 35–41.
- \*Roberts, C.P., C.J. Mecklin & H.H. Whiteman. 2014. Effects of browsing by captive elk (*Cervus canadensis*) on a midwestern woody plant community. *American Midland Naturalist* 171: 219–228.
- Rodriguez-Iglesias, R.M., & M.M. Kothmann. 1998. Best linear unbiased prediction of herbivore preferences. *Journal of Range Management* 51: 19–28.
- Rooney, T.P. 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. *Plant Ecology* 202: 103–111.

- Rosas, C.A., D.M. Engle, J.H. Shaw & M.W. Palmer. 2008. Seed dispersal by bison in a tallgrass prairie. *Journal of Vegetation Science* 19: 769–778.
- Rose, J., & J.D. Harder. 1985. Seasonal feeding habits of an enclosed high density white-tailed deer herd in northern Ohio. *Ohio Academy of Science* 85: 184–190.
- \*Rossell, C., B. Gorsira & S. Patch. 2005. Effects of white-tailed deer on vegetation structure and woody seedling composition in three forest types on the Piedmont Plateau. *Forest Ecology and Management* 210: 415–424.
- Russell, F.L., D.B. Zippin & N.L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *American Midland Naturalist* 146: 1–26
- Ruzicka, K.J., J.W. Groninger & J.J. Zaczek. 2010. Deer browsing, forest edge effects, and vegetation dynamics following bottomland forest restoration. *Restoration Ecology* 18: 702–710.
- Sanderson, M.A., M. Labreveux, M.H. Hall & G.F. Elwinger. 2003. Nutritive value of chicory and English plantain forage. *Crop Science* 43: 1797–1804.
- Sargent, C.S. 1884. Report on the forests of North America. United States Department of the Interior, Census Office, Washington, D.C. 612 pages.
- Sauer, P.R., J.E. Tauck & C.W. Severinghaus. 1969. Herbaceous food preferences of white-tailed deer. *New York. Fish and Game Journal* L6: 145–157.
- Scherber, C., A. Milcu, S. Partsch, S. Scheu & W.W. Weisser. 2006. The effects of plant diversity and insect herbivory on performance of individual plant species in experimental grassland. *Journal of Ecology* 94: 922–931.
- Schneider, J., D.S. Maehr, K.J. Alexy; J.J. Cox, J.L. Larkin & B.C. Reeder. 2006. Food habits of reintroduced elk in southeastern Kentucky. *Southeastern Naturalist*. 5: 535–546.

- Schwer, L.J.M. 2011. Small mammal populations in switchgrass stands managed for biomass production compared to hay and corn fields in Kentucky. M.Sc. thesis, University of Kentucky (College of Agriculture), Lexington. 79 pages.
- Seagle, S.W., & Liang S-Y. 2001. Application of a forest gap model for prediction of browsing effects on riparian forest succession. *Ecological Modeling* 144: 213–229.
- Shaffer, J. 2013. Factors influencing the establishment and survival of native hardwood tree seedlings of the Kentucky Inner Bluegrass blue ash-oak savanna-woodland. M.Sc. thesis, University of Kentucky (School of Biological Sciences), Lexington. 103 pages.
- Shang X., Pan H., Li M., Miao X. & Ding H. 2011. *Lonicera japonica* Thunb.: ethnopharmacology, phytochemistry and pharmacology of an important traditional Chinese medicine. *Journal of Ethnopharmacology* 138: 1–21.
- \*Shi, H., E. Laurent, J. LeBouton, L. Racevskis, K. Hall, M. Donovan, R. Doepker, M. Walters, F. Lupi & J. Liu. 2006. Local spatial modeling of white-tailed deer distribution. *Ecological Modeling* 190: 171–189.
- Shrestha, R., & P. Wegge. 2008. Wild sheep and livestock in Nepal Trans-Himalaya: coexistence or competition? *Environmental Conservation* 35: 125–136.
- \*Slater, M.A., & R.C. Anderson. 2014. Intensive selective deer browsing favors success of *Asimina triloba* (paw-paw), a native tree species. *Natural Areas Journal* 34: 178–187.
- Smit, C., & J.L. Ruifrok. 2011. From protege to nurse plant: establishment of thorny shrubs in grazed temperate woodlands. *Journal of Vegetation Science* 22: 377–386.
- Sommer, R.S., N. Benecke, L. Lougas, O. Nelle & U. Schmölcke. 2011. Holocene survival of the wild horse in Europe: a matter of open landscape? *Journal of Quaternary Science* 26: 805–812.
- Sotala, D.J., & C.M. Kirkpatrick. 1973. Foods of white-tailed deer, *Odocoileus virginianus*, in Martin County, Indiana. *American Midland Naturalist* 89: 281–286.

- Spetich, M.A., P.W. Roger, C.A. Harper & S.L. Clark. 2011. Fire in eastern hardwood forests through 14,000 years. Pages 41–58 in: C. Greenberg, B. Collins & F. Thompson, F. (eds), *Managing Forest Ecosystems, Sustaining Young Forest Communities, Ecology and Management of early successional Habitats in the Central Hardwood Region USA*, Vol. 21. Springer, New York.
- Stewart-Wade, S.M., S. Neumann, L.L. Collins & G.J. Boland. 2002. The biology of Canadian weeds. 117. *Taraxacum officinale* G.H. Weber ex Wiggers. *Canadian Journal of Plant Science* 82: 825–853.
- \*Stromayer, K.A.K., & R.J. Warren. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildlife Society Bulletin* 25: 227–34
- Taylor, W.P. 1956. *The Deer of North America*. Stackpole Company, Harrisburg, Pennsylvania and the Wildlife Management Institute, Washington, D.C.
- Taylor, K. 2009. Biological Flora of the British Isles: *Urtica dioica* L. *Journal of Ecology* 97: 1436–1458.
- Thanabhorn, S., K. Jaijoy, S. Thamaree, K. Ingkaninan & A. Panthong. 2006. Acute and subacute toxicity study of the ethanol extract from *Lonicera japonica* Thunb. *Journal of Ethnopharmacology* 107: 370–373.
- \*Tilghman, N.G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management* 53: 524–532.
- Torgenson, O., & W.H. Pfander. 1971. Cellulose digestibility and chemical composition of Missouri deer foods. *Journal of Wildlife Management* 35: 221–231.
- Tripler, C.E., C.D. Canham, R.S. Inouye & J.L. Schnurr. 2002. Soil nitrogen availability, plant luxury consumption, and herbivory by white-tailed deer. *Oecologia* 133: 517–524.

- Truscott, A.M., S.C.F. Palmer, G.M. McGowan, J.N. Cape & S. Smart. 2005. Vegetation composition of roadside verges in Scotland: the effects of nitrogen deposition, disturbance and management. *Environmental Pollution* 136: 109–118.
- Tu, M., J.M. Randall & B.A. Rice. 2003. Element stewardship abstract for *Coronilla varia* [*Securigera varia*]. The Nature Conservancy, Arlington, Virginia. 11 pages.
- \*Turner, K.E., & J.G. Foster, 2000. Nutritive value of some common browse species. Pages 241–245 in: Proceedings/Reports of the American Forage and Grassland Council, 37th North American Alfalfa Improvement Conference, July 16–19; Madison, Wisconsin. American Forage and Grassland Council, Georgetown, Texas.
- Valladares, F., & Ü. Niinemets. 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Systematics and Evolution* 39: 237–257.
- Vera, F.W.M. 2000. *Grazing Ecology and Forest History*. CABI Publishing, Wallingford, England. 506+ pages.
- Viehoever, A., C.O. Johns & C.L. Alsberg 1916. Cyanogenesis in plants. Studies on *Tridens flavus*. *Journal of Biological Chemistry* 25: 141–150.
- Vilà, M., J.L. Maron & L. Marco. 2005. Evidence for the enemy release hypothesis in *Hypericum perforatum*. *Oecologia* 142: 474–479
- Wallace, L.L., M.G. Turner, W.H. Romme, R.V. O’Neill & Wu Y-G. 1995. Scale of heterogeneity of forage production and winter foraging by elk and bison. *Landscape Ecology* 10: 75–83.
- Waller, D.M., & L.I. Maas. 2013. Do white-tailed deer and the exotic plant garlic mustard interact to affect the growth and persistence of native forest plants? *Forest Ecology and Management* 304: 296–302.

- Wallingford, K.D. 2006. Restoration of blue ash (*Fraxinus quadrangulata*) in the Inner Bluegrass of Kentucky. M.Sc. thesis, University of Kentucky (School of Biological Sciences). 101 pages.
- Warren, R.J., & L.J. Krysl. 1983. White-tailed deer food habits and nutritional status as affected by grazing and deer-harvest management. *Journal of Range Management* 36: 104–109.
- Watling, J.I., C.R. Hickman, E. Lee, K. Wang & J.L. Orrock. 2011. Extracts of the invasive shrub *Lonicera maackii* increase mortality and alter behavior of amphibian larvae. *Oecologia* 165: 153–159.
- Webster, C.R., M.A. Jenkins & J.H. Rock. 2005. Long-term response of spring flora to chronic deer herbivory and deer exclusion in Great Smoky Mountains National Park, USA. *Biological Conservation* 125: 297–307.
- Weakley, A.S. 2015. Flora of the Southern and Mid-Atlantic States. University of North Carolina Herbarium, University of North Carolina, Chapel Hill. [This is a working draft available at <http://www.herbarium.unc.edu/flora.htm>.]
- Widga, C. 2006. Niche variability in late Holocene bison: a perspective from Big Bone Lick, KY. *Journal of Archaeological Science* 33: 1237–1255.
- Williams, A.H. 1997. In Praise of Grazing. *Restoration & Management Notes [Ecological Restoration]* 15: 116–118. [See also letters: 1998. 16: 5–6. 7–8.]
- Williams, S.C., & J.S. Ward. 2006. Exotic seed dispersal by white-tailed deer in southern Connecticut. *Natural Areas Journal*. 26: 383–390.
- \*Willson, M.F. 1993. Mammals as seed-dispersal mutualists in North America. *Oikos* 67: 159–176.
- Wilson, H.N., M.A. Arthur, A. Schörgendorfer, R.D. Paratley, B.D. Lee & R.W. McEwan. 2013. Site Characteristics as predictors of *Lonicera maackii* in second-growth forests of Central Kentucky, USA. *Natural Areas Journal* 33: 189–198.

- Yahn, B. 2006. Bluegrass Savanna-woodland Project. Naturally Kentucky [KSNPC Newsletter] 50: 2.
- Yamazaki, K. 2010. Leaf mines as visual defensive signals to herbivores. *Oikos* 119: 796–801
- Yatskievytch, G. 1999, 2006, 2013. Steyermark's Flora of Missouri. 3 volumes. Missouri Botanical Garden Press, St. Louis.
- Zhang, H., Wang Y. & Zhang Z.. 2009. Domestic goat grazing disturbance enhances tree seed removal and caching by small rodents in a warm-temperate deciduous forest in China. *Wildlife Research* 36: 610–616.
- Zenker, K. 2012. Predator-mediated effects on deer browsing behavior. Posted at <http://www3.nd.edu/~underc/east/education/documents/Zenker.pdf>. 5 pages.