The association of two invasive shrubs, common buckthorn (*Rhamnus cathartica*) and Tartarian honeysuckle (*Lonicera tatarica*), with oak communities in the midwestern United States

Lisa A. Schulte, Erik C. Mottl, and Brian J. Palik

Abstract: Oak forests throughout North America are declining due to changes in disturbance regimes that have led to increased competition from other tree and shrub species. We evaluated associations between oak regeneration, the occurrence of two common invasive shrubs (common buckthorn (*Rhamnus cathartica* L.) and Tartarian honeysuckle (*Lonicera tatarica* L.)), and forest edges in oak forests in a portion of the midwestern United States where bur (*Quercus macrocarpa* Michx.), red (*Quercus rubra* L.), and white oak (*Quercus alba* L.) were historically dominant. We found poor recruitment of oaks in comparison to other, more shade-tolerant tree species. Results further revealed a strong stand-scale association between bur oak, open canopy conditions, high soil nutrient levels, and the presence of common buckthorn and Tartarian honeysuckle; these same site characteristics were disassociated with red and white oak. Within red and white oak stands, however, the presence of the invasive shrubs was more pronounced near forest edges. While oak recruitment is hampered throughout stands, our research suggests that predominant constraints may vary based on soil and light gradients found along forest edges.

Résumé : Les forêts de chêne dépérissent, partout en Amérique du Nord, à cause de changements dans les régimes de perturbation qui ont entraîné une augmentation de la compétition d'autres espèces d'arbre et d'arbuste. Nous avons évalué les liens entre la régénération du chêne, la présence de deux arbustes invasifs (le nerprun cathartique (*Rhamnus cathartica* L.) et le chèvrefeuille de Tartari (*Lonicera tatarica* L.)) et la lisière de la forêt dans les forêts de chêne d'une partie du Midwest des États-Unis, où les chênes à gros fruits (*Quercus macrocarpa* Michx.), rouge (*Quercus rubra* L.) et blanc (*Quercus alba* L.) étaient historiquement les espèces dominantes. Nous avons trouvé que le recrutement des chênes était faible comparativement à d'autres espèces d'arbre plus tolérantes à l'ombre. Les résultats révèlent de plus qu'il y a une relation étroite à l'échelle du peuplement entre le chêne à gros fruits, un couvert clairsemé, une teneur élevée en nutriments dans le sol et la présence du nerprun cathartique et du chèvrefeuille de Tartari; ces même caractéristiques étaient négativement associées aux chênes rouge et blanc. Dans les peuplements de chênes rouge et blanc cependant, la présence des arbustes invasifs était plus prononcée près de la lisière de la forêt. Tandis que le recrutement du chêne blanc est entravé dans l'ensemble des peuplements; nos travaux indiquent que les contraintes prédominantes peuvent varier selon les gradients de sol et de lumière le long de la lisière de la forêt.

[Traduit par la Rédaction]

Introduction

Oak forests across North America are undergoing dramatic changes as dominance shifts to more shade-tolerant later-successional species (Nowacki and Abrams 2008; Knoot et al. 2010*a*; McEwan et al. 2011), prompting concern among scientific and practitioner communities over the loss of this resource. Causal factors of changes in oak forests remain difficult to elucidate and quantify (Lorimer 2003; Knoot et al. 2010*a*; McEwan et al. 2011), but Lorimer (2003) suggested that some major reasons include changes in fire regimes, high rates of deer herbivory on oak seedlings, increased consumption of acorns by burgeoning mammal populations, and competition with invasive species. Nowacki and Abrams (2008) provided strong support for a positive feedback cycle of "mesophication," which begins with the suppression of fire within oak ecosystems and leads to ultimate dominance by mesophytic, mid- and later-successional hardwoods (e.g., sugar maple (*Acer saccharum* Marsh.) and black cherry (*Prunus serotina* Ehrn.)).

The large amount of edge habitat associated with the remaining, often small patches of oak forest may be further

Received 10 April 2011. Accepted 5 August 2011. Published at www.nrcresearchpress.com/cjfr on 27 September 2011.

L.A. Schulte and E.C. Mottl.* Department of Natural Resource Ecology and Management, 339 Science II, Iowa State University, Ames, IA 50011-3221, USA.
B.J. Palik. US Forest Service Northern Research Station, 1831 Highway 169 E, Grand Rapids, MN 55744, USA.

Corresponding author: Lisa A. Schulte (e-mail: lschulte@iastate.edu).

*Current address: Department of Biology, 1116 8th Avenue, Grinnell College, Grinnell, IA 50112-1690, USA.

doi:10.1139/X11-112

contributing to shifts away from dominance by oak species (López-Barrera et al. 2006; Ward et al. 2007; Knoot et al. 2010*a*). While the specific characteristics of edge habitat vary according to edge orientation (e.g., north versus south), degree of contrast between forestland and its surrounding land cover (e.g., an abrupt versus gradual transition to the adjacent contrasting land cover), and distance from forest edge (Cadenasso et al. 2003), plant establishment and growth are generally expected to be different than in forest interior conditions (Ross and Harper 1972; Matlack 1994; Oliver and Larson 1996). Wind speeds, air and soil temperatures, and light availability decrease, while soil moisture and relative humidity tend to increase from forest edges to interiors (Palik and Murphy 1990; Murcia 1995; Cadenasso et al. 1997). These differences can in turn directly or indirectly affect litter fall, decomposition, nutrient cycling, and nutrient availability (Didham 1998; Vasconcelos and Luizão 2004; Vasconcelos and Laurance 2005). Edge effects may have important implications for oak forest management because of known relationships among distance from edge, competition, and the survivability of oak seedlings (Lorimer et al. 1994; Meiners and Martinkovic 2002; López-Barrera et al. 2006). “Soft” (low-contrast) edges have been shown to produce vigorous oak seedling development in comparison with abrupt or “hard” edges (López-Barrera et al. 2006); however, hard edges have been shown to have higher oak seedling survival than forest interiors (Meiners and Martinkovic 2002; López-Barrera et al. 2006).

In terms of potential competitors, numerous studies document higher occurrences of invasive plants at forest edges (Hester and Hobbs 1992; Flory and Clay 2006; Honu and Gibson 2006) and higher invasive plant diversity on warmer, south-facing edges than on cooler, north-facing edges (Brothers and Spingarn 1992; Honnay et al. 2002). Several studies have shown that that exotic invasive plants can have a negative long-term impact on oak regeneration (Meekins and McCarthy 1999; Williams et al. 2006; Hartman and McCarthy 2008), although the effect may initially be facilitative through the protection of advance regeneration from herbivory (Williams et al. 2006).

Oak forest decline in the Driftless Area of the Upper Midwest, where bur (*Quercus macrocarpa* Michx.), red (*Quercus rubra* L.), and white oak (*Quercus alba* L.) were historically dominant species (Grubh 2010), exemplifies the general concern for this resource in other regions (Knoot et al. 2010*a*). Oaks are foundational species in Driftless Area forests (sensu Ellison et al. 2005), affecting populations and community dynamics and modulating ecosystem processes (Rodewald and Abrams 2002; Fralish 2004; Lovett et al. 2004). They also constitute an important timber resource. While some of the factors leading to oak forest decline in the region are being addressed (e.g., forest management and harvest practices, competition from other tree species, predation from animals, and changes in fire regimes: Lorimer et al. 1994; Knoot et al. 2010*a*), interactions with invasive plants largely remain unexplored. Specifically, there is little to no information on the role that two common exotic invasive shrubs, common buckthorn (*Rhamnus cathartica* L.) and Tartarian honeysuckle (*Lonicera tatarica* L.), may play in the decline. These species are commonly found in the Upper Midwest and are known to be highly invasive in forest ecosystems (Woods 1993; Knight et al. 2007).

To understand potential relationships between invasive shrubs and oak forest decline, we evaluated associations between oak regeneration and the occurrence of common buckthorn and Tartarian honeysuckle within oak forests in a portion of the US Midwest Driftless Area. Although the Driftless Area is geologically unique for the upper Midwest, the forests are similar to those throughout the central hardwoods region; thus, our results can have wide application. Due to the prominence of agricultural fields adjacent to remaining oak forests in the study region, we framed our study around the role of edge habitat as a mediator of oak regeneration success and exotic shrub invasion through its influence on light availability and soil nutrient levels. Specific study objectives were to (*i*) quantify the composition and structure of oak forests and assess whether these forests were in a state of decline based on abundance of in different structural layers, (*ii*) examine the spatial relationship of oak regeneration and invasion by common buckthorn and Tartarian honeysuckle as related to agricultural edges, and (*iii*) evaluate differences in topographic, soil, and canopy characteristics from forest edges to interiors that might relate to exotic invasion or oak decline.

Study area

This study was conducted in oak forests of the Whitewater Wildlife Management Area (WMA) in Minnesota, USA, which lies within the Midwest Driftless Area. The Driftless Area ecoregion encompasses over 4 million hectares in southeastern Minnesota, southwestern Wisconsin, northeastern Iowa, and northwestern Illinois and has a high proportion of forest cover in comparison with surrounding ecoregions (Vogelmann et al. 2001). It is colloquially referred to as the Driftless Area because it was not covered by ice during Late Wisconsin glaciation of the Quaternary Period; however, evidence of pre-Illinoian glacial drift over 500 000 years old has been identified in parts of the area (Hobbs 1999). The region’s topography is typified by deep valleys with steep hillsides and flat topped bluffs and possesses a distinct dendritic drainage pattern consistent with older, eroded landscapes. Lowlands and bluff tops have largely been cleared for agriculture, but approximately 33% of the region remains in forest, primarily located on steep hillsides (Albert 1995; Knoot et al. 2010*a*). Many of these forests have been grazed to various degrees during the past century.

Whitewater WMA is an 11 100 ha area located in Winona, Wabasha, and Olmsted Counties, Minnesota, owned and managed by the state. The climate of Whitewater WMA and surrounding areas is continental in character, with growing seasons ranging from 130 to 170 days and an average annual precipitation of 80 cm (Albert 1995). Major soil classifications include Udalfs on ridgetops and sideslopes and Aquents on flood plains (Albert 1995). Loess thickness can vary from <30 cm on valley walls to up to 6 m on ridgetops. The area’s steep hillsides are covered with mixed hardwood forests, punctuated by small bluff prairies on south- and southwest-facing slopes (MDNR 2010). Ridgetops are covered by either row-crop agricultural fields, hayfields, or prairies.

Methods

Field methods

Edge and fragmentation studies have generally suffered from a number of methodological shortcomings, as outlined by Murcia (1995). Our field sampling protocols were specifically designed to overcome several of these problems, including (*i*) selection of appropriate replicates based on forest age, stand size, and composition, (*ii*) circumvention of certain topographic features (e.g., streams and large depressions), and (*iii*) careful delineation of transect start points based on the location of canopy tree trunks.

Between mid-June and August 2005, we sampled 17 dry to mesic oak forest stands in Whitewater WMA. All stands were designated as "mature oak forest" by the Minnesota Department of Natural Resources and were located adjacent to an agricultural edge. Agricultural edges were defined as the boundary between a forest stand and either a crop field (e.g., corn, soybean, alfalfa, hay) or a filter strip adjacent to a crop field. To minimize effects from any adjacent edges, stands were selected only if they were at least 250 m long and 200 m wide. As a group, stands covered all topographic aspects, with two or three stands facing each of the following directions: north, northeast, east, south, southwest, west, and northwest; southeasterly facing stands were not sampled because the few available did not fulfill our size criteria. Aspect was subsequently converted to heat load index, according to McCune and Keon (2002), as solar radiation plays a key role in determining strength and depth of edge effects. All stands were located on hillsides with slopes averaging 17.2° (standard deviation = 5.4°); oak forests are generally absent from ridgetops or valleys within this region. According to management records obtained from the Minnesota Department of Natural Resources none of the stands had undergone management within the last ~40 years, but all likely experienced some selective harvesting and grazing within the last 100 years.

Our sampling framework consisted of three transects located 25 m apart and running perpendicular to the agricultural edge. The middle transect was established at the approximate midpoint of the agricultural edge, based on Minnesota Department of Natural Resources stand assessment maps. Each transect was composed of four sampling plots centered 15, 40, 65, and 90 m from the agricultural edge. Within each plot, we measured slope and canopy cover and sampled trees, saplings, seedlings, shrubs, vegetation in the herb layer, and soils. Slope was recorded to the nearest degree at the center of each plot using a Suunto height and slope angle meter. We estimated canopy cover at four times each plot center, once in each of the cardinal directions, using a convex spherical densitometer; canopy cover readings were then averaged to form a single plot-level estimate. We recorded (*i*) tree (≥10 cm diameter at breast height (DBH)) species and DBH within a 200 m^2 circular area centered on the plot, (*ii*) large sapling (2.5 ≤ DBH < 10 cm) species and number within a 150 m^2 circular plot centered on the plot center, (*iii*) small sapling and shrub (<2.5 cm DBH and >0.5 m tall) species (except dogwoods (*Cornus* spp.) and gooseberries (*Ribes* spp.), which were recorded to genus) and number within two 5 m^2 circular plots located 5 m from each sampling plot center, and (*iv*) woody seedlings (<0.5 m tall) species and number within four 1.0-m^2 quadrats located 3 m in each of the cardinal directions from the plot center. We further scored the level of common buckthorn or Tartarian honeysuckle invasion by making qualitative visual assessments of the density of these shrubs in each 200 m^2 plot, with 0 = absent, 1 = present at low levels, 2 = moderately abundant, 3 = abundant, and 4 = infested. Also, within the tree seedling quadrats, we estimated the percent cover for all herbs, live woody plants (tree stems of any size and woody shrub cover), coarse woody debris (dead wood including stems, branches, or sheets of bark), and exposed rock. Surface soils were sampled at 3 m distance from the plot center in each of the cardinal directions using a 11.5 cm deep by 5.9 cm diameter core; this sample included the O and the top portion of the A horizon. Samples were combined into one composite sample to eliminate fine-scale variability and then double bagged, kept cool, and placed in a 4 ° C cold room within 1 week of sampling. We measured soil sample bulk density by drying the soil samples at 40 °C overnight and recording the mass of the samples to the nearest 0.1 g. Total carbon, total nitrogen, pH, and sodium, calcium, magnesium, and potassium concentrations were analyzed using procedures outlined in Brown (1998). More specifically, combustion analysis was used to determine total carbon and total nitrogen content, a 1:1 soil-to-water ratio was used to measure pH with an electronic meter, and cations were extracted with ammonium acetate and read on an inductive coupled plasma emission spectrometer (Brown 1998).

Data analysis

Oak forest composition, structure, and community relationships

We calculated relative importance values for trees ≥10 cm DBH to compare overstory communities among our sampling sites. Relative importance is considered a holistic measure of overstory community conditions, as it combines both compositional and structural information, allowing for a single composite measure to be used in our statistical analyses. We used a combination of relative dominance (based on basal area) and relative density in calculating relative importance values as outlined by Curtis (1971).

We employed nonmetric multidimensional scaling (NMS) ordination to examine compositional differences among sites, tree species, invasive shrub scores, and environmental variables. We chose NMS as an analytical tool, as it avoids assumptions of linear relationships, uses ranked distances among data, and allows for the use of distance measures best suited to specific ecological community data (McCune and Grace 2002). Our NMS analyses were performed using PC-ORD (McCune and Mefford 1999) using Bray–Curtis distance as a distance measure because it is generally regarded to be a robust measure for ecological community data (McCune and Grace 2002). We ran NMS ordination using a combination of vegetation data, including tree (relative importance values), large sapling (stems per hectare), small sapling–shrub (stems per hectare), and seedling species (stems per hectare) that represented ≥5% of the total in each category and invasive shrub scores (common buckthorn score and Tartarian honeysuckle score). Preliminary analysis re-

Table 1. Tree species relative importance values (IV): means and SDs for 17 study sites.

Species	Mean IV (%)	SD
Red oak, *Quercus rubra* L.	30.5	15.2
American elm, *Ulmus americana* L.	16.3	11.7
Bur oak, *Quercus macrocarpa* Michx.	14.8	16.7
American basswood, *Tilia americana* L.	6.3	7.0
White oak, *Quercus alba* L.	5.0	6.1
Quaking aspen, *Populus tremuloides* Michx.	4.5	7.7
Paper birch, *Betula papyrifera* Marsh.	3.7	5.4
Boxelder, *Acer negundo* L.	3.2	3.2
Hophornbeam, *Ostrya virginiana* (Mill.) K. Koch	3.1	4.6
Common hackberry, *Celtis occidentalis* L.	2.4	2.6
Sugar maple, *Acer saccharum* Marsh.	2.0	4.7
Black cherry, *Prunus serotina* Ehrh.	1.7	1.8
Black walnut, *Juglans nigra* L.	1.6	3.2
Black oak, *Quercus velutina* Lam.	0.9	2.5
White ash, *Fraxinus americana* L.	0.8	1.9
Eastern cottonwood, *Populus deltoides* Bartr. ex Marsh.	0.7	2.7
Shagbark hickory, *Carya ovata* (Mill.) K. Koch	0.5	1.3
Red pine, *Pinus resinosa* Ait.	0.4	1.2
Pin oak, *Quercus palustris* Muenchh.	0.4	1.6
Northern pin oak, *Quercus ellipsoidalis* E.J. Hill	0.4	1.0
Eastern redcedar, *Juniperus virginiana* L.	0.2	0.6
Bitternut hickory, *Carya cordiformis* (Wangenh.) K. Koch	0.2	0.6
Black locust, *Robinia pseudoacacia* L.	0.1	0.4
Black ash, *Fraxinus nigra* Marsh.	0.0	0.2
Pin cherry, *Prunus pensylvanica* L. f.	0.0	0.2
Common serviceberry, *Amelanchier arborea* (Michaux f.) Fernald	0.0	0.1
Hawthorn, *Crataegus* spp.	0.0	0.1

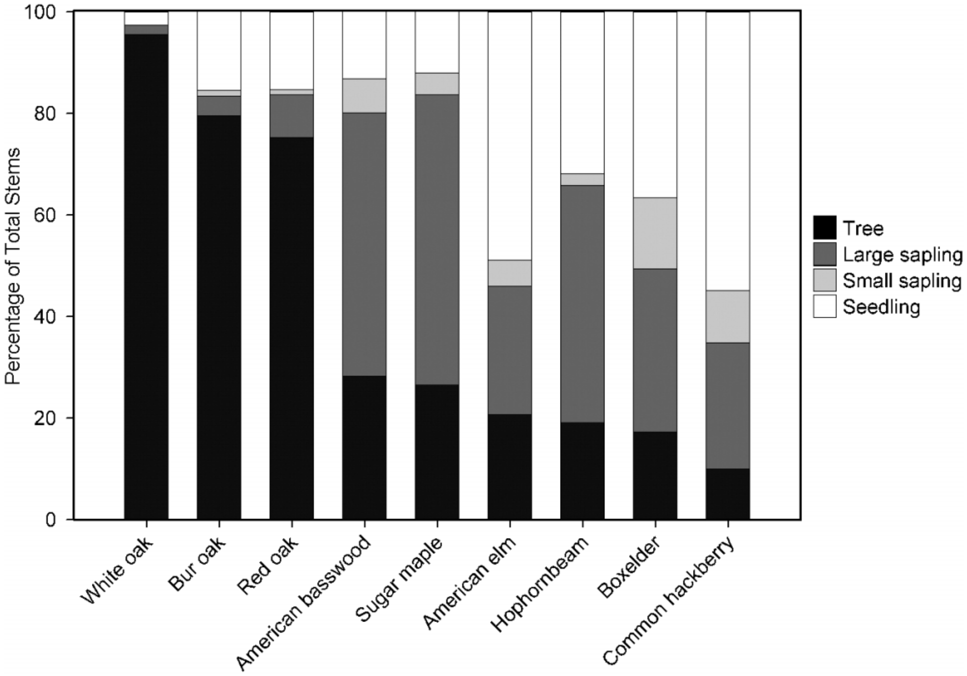


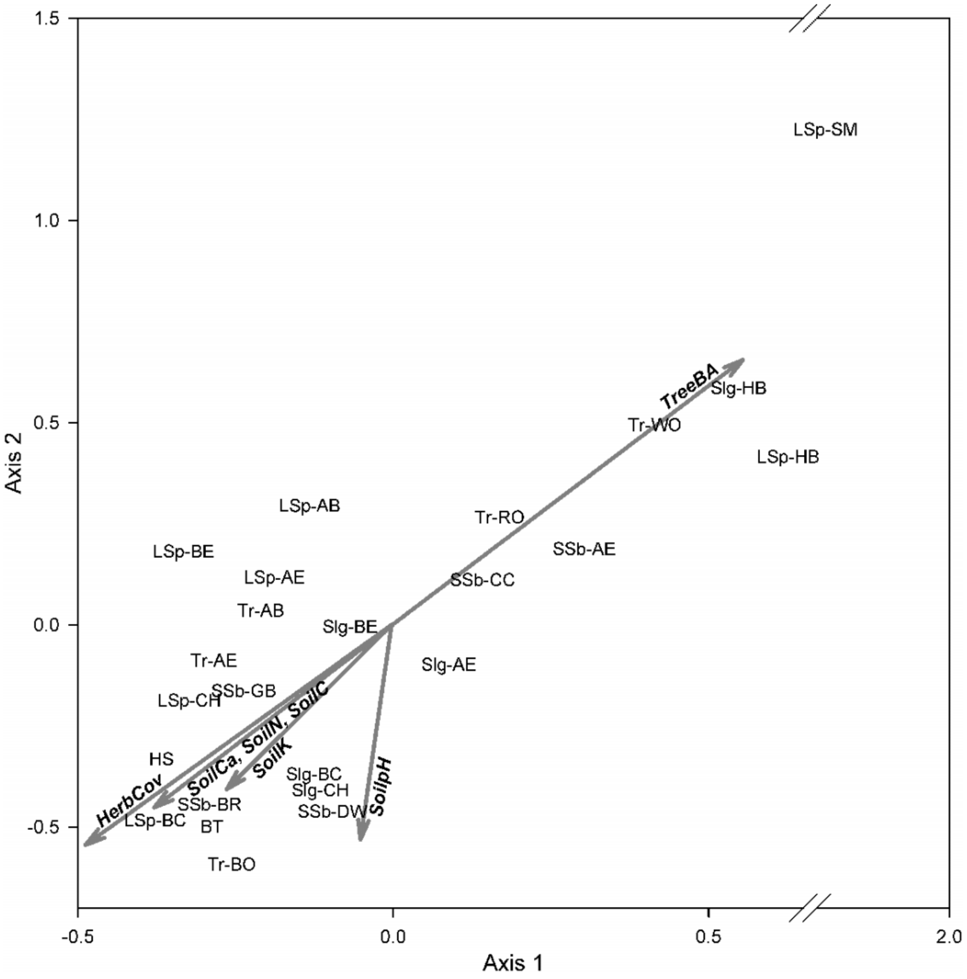
Fig. 1. Percentage of total stems within each vegetation layer for dominant tree species (see Table 1 for scientific names).

Table 2. Correlations between nonmetric multidimensional scaling ordination Axis 1 ($r^2 = 0.60$) and Axis 2 ($r^2 = 0.30$) and community and environmental variables (see Table 1 for scientific names).

Community or environmental variable	Axis 1 *r*	Axis 2 *r*
Common buckthorn score	–0.43	–0.71
Tartarian honeysuckle score	–0.44	–0.40
Trees		
American basswood	–0.28	0.05
American elm	–0.58	–0.18
Bur oak	–0.33	–0.76
Red oak	0.49	0.77
White oak	0.50	0.59
Large saplings		
American basswood	–0.18	0.40
American elm	–0.47	0.29
Black cherry	–0.57	–0.73
Boxelder	–0.51	0.28
Common hackberry	–0.46	–0.27
Hophornbeam	0.62	0.43
Sugar maple	0.77	0.57
Small saplings–shrubs		
American elm	0.48	0.29
Black raspberry	–0.36	–0.56
Chokecherry	0.29	0.27
Dogwood species	–0.14	–0.64
Gooseberry species	–0.63	–0.43
Seedlings		
American elm	0.17	–0.19
Black cherry	–0.09	–0.30
Boxelder	–0.15	–0.01
Common hackberry	–0.15	–0.52
Hophornbeam	0.26	0.25
Environmental vector		
Total tree basal area	0.63	0.63
Total canopy cover	0.28	0.44
Herbaceous cover	–0.55	–0.60
Slope	0.07	0.10
Heat load index	–0.19	–0.40
Soil total carbon	–0.46	–0.52
Soil total nitrogen	–0.52	–0.55
Soil calcium	–0.48	–0.58
Soil magnesium	–0.17	–0.50
Soil potassium	–0.38	–0.58
Soil sodium	0.10	–0.12
Soil pH	–0.22	–0.65
Soil bulk density	0.19	0.10

vealed the qualitative invasive shrub scores to be highly correlated with common buckthorn and Tartarian honeysuckle stem counts; we used the qualitative scores instead of the stem count data in this analysis because they holistically incorporated the information from multiple strata. The 5% cutoff was chosen based on natural breaks in the data and because it met our objective of incorporating dominant species. Five tree, eight large sapling, six shrub, and five seedling species met this criterion and, respectively, represented 72.9% of total tree importance, 81.3% of total large sapling stems, 76.3% of all small sapling–shrub stems, and 78.9% of all seedling stems; common buckthorn met the 5% cutoff in the case of large saplings and small saplings–shrubs but was subsequently eliminated from these categories because of high correlation with and duplication of the more holistic buckthorn score. Preliminary analyses were run with as many as six ordination axes, but substantial contributions to stress reduction were only made by the first two axes. Thus, the final NMS run included two axes, a random starting configuration, and one iteration with real data. The stress and instability of this final solution were, respectively, 11.26 and 0.00046, which are reasonable for ecological community data (McCune and Grace 2002). We then overlayed environmental data, i.e., total tree basal area, canopy cover, herba-

Fig. 2. Axis 1 and 2 results of nonmetric multidimensional scaling plant community analysis. Abbreviations for tree (Tr), large sapling (LSp), small sapling–shrub (SSb), and seedling (Slg) species are as follows: AB, American basswood; AE, American elm; BC, black cherry; BE, boxelder; BO, bur oak; BR, black raspberry; CC, chokecherry; CH, common hackberry; DW, dogwood; GB, gooseberry; HB, hophornbeam; RO, red oak; SM, sugar maple; WO, white oak; BT, common buckthorn score; HS, Tartarian honeysuckle score (see Table 1 for scientific names). Environmental vectors correlated with the ordination at $r^2 > 0.30$ are displayed including total tree basal area (TreeBA), percent herbaceous cover (HerbCov), total soil carbon (SoilC), total soil nitrogen (SoilN), soil pH (SoilpH), soil calcium concentration (SoilCa), and soil potassium concentration (SoilK).



ceous cover, slope, heat load index, total soil carbon, total soil nitrogen, soil pH, soil bulk density, and soil sodium, calcium, magnesium, and potassium concentrations, as regressed vector arrows. Total tree basal area, canopy cover, and herbaceous cover were used as proxies for forest structural conditions and light availability within different forest strata and hence treated as environmental variables.

Spatial distribution of vegetation and environmental metrics

To determine the effects of edge, we analyzed the following variables using first-order autoregression in SAS (SAS Institute Inc. 2011): (*i*) tree relative importance values and large sapling densities for the three dominant oak species (white, bur, and red oak), (*ii*) measures of the invasive shrubs common buckthorn and Tartarian honeysuckle, (*iii*) environmental metrics as potential drivers (same variables as in NMS, except heat load index, which was only recorded at a stand level), and (*iv*) other vegetation variables that were highly correlated ($r \geq 0.6$) in the NMS. One stand, the only stand where the forest edge was located at the bottom rather than the top of the slope, was eliminated from these tests, as preliminary analysis revealed it as an outlier according to some within-stand environmental measures (e.g., slope and soil variables).

Variables were included in this analysis based on our original study goals and key results from the NMS analysis. The first-order autoregression procedure that we used accounts for autocorrelation within the data by assuming that measures spatially closer to one another are more highly correlated than measures farther apart. This analysis allowed us to account for autocorrelation due to spatial proximity of our sampling points and demonstrate differences due to edge effects. We used a mixed linear model (SAS Institute Inc. 2011) in which plot and stand were, respectively, treated as fixed and random effects and transect was treated as a repeated effect. The most interior forest plot (90 m from agricultural edge) was our baseline with which measurements from each of the other three plots (15, 40, and 65 m) were statistically compared.

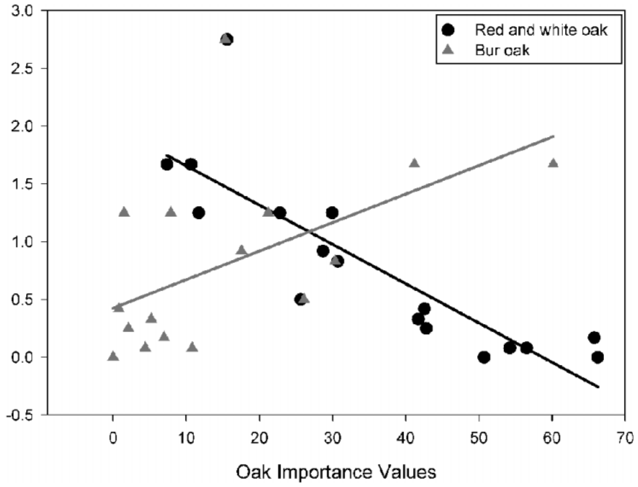
We recognize that results related to edge distance from these statistical models may be confounded with slope position, i.e., distances from the edge and slope position are not independent, since (after elimination of the one outlier stand mentioned above) edge plots were always at the top of the slope and interior plots were always downslope. However, preliminary analyses (not shown) revealed a strong potential for cofounding between only slope position and soil magnesium concentrations.

Results

Native species composition

We recorded a total of 27 trees species in the overstory of the 17 stands sampled. Only five of these species had mean relative importance values of ≥5.0% (Table 1). These included red oak (importance value = 30.5 ± 15.2, mean ± 1 SD), American elm (*Ulmus americana* L.) (16.3 ± 11.7), bur oak (14.8 ± 16.7), American basswood (*Tilia americana* L.) (6.3 ± 7.0), and white oak (5.0 ± 6.1). Red oak was present at all sites, while American elm and bur oak were each present at 16 of 17 sites. Eight species had relative importance values ranging 1.0%–4.9%, while the remaining 14 species were uncommon, with average relative importance values below 1.0% (Table 1). Thirty-eight species were recorded in the large sapling size class, but eight species comprised >81% of all stems. These included American elm (1114 ± 67 saplings per hectare, mean ± 1 SD), American basswood (68 ± 73 saplings per hectare), hophornbeam (*Ostrya virginiana* (Mill.) K. Koch) (54 ± 79 saplings per hectare), common buckthorn (44 ± 73 saplings per hectare), black cherry (38 ± 37 saplings per hectare), boxelder (*Acer negundo* L.) (34 ± 32 saplings per hectare), sugar maple (29 ± 90 saplings per hectare), and common hackberry (*Celtis occidentalis* L.) (28 ± 30 saplings per hectare). Oak species made up just over 2% of all large sapling stems. The majority of these were red oaks, which were found at a density of 10 ± 11 saplings per hectare; bur and white oak large saplings were found at respective densities of 2 ± 4 and 0 ± 1 saplings per hectare. The small sapling–shrub size class was dominated by gooseberry (6431 ± 3573 stems per hectare), which comprised 43% of all shrub stems, and lesser and highly variable amounts of common buckthorn (1642 ± 3814 stems per hectare), dogwood (907 ± 993 stems per hectare), chokecherry (*Prunus virginiana* L.) (827 ± 623 stems per hectare), American elm (818 ± 755 stems per hectare), black raspberry (*Rubus occidentalis* L.) (784 ± 936 stems per hectare), black cherry (696 ± 483 stems per hectare), and prickly ash (*Zanthoxylum americanum* P. Mill.) (642 ± 730 stems per hectare), among other species. Bur, red, and white oak comprised <0.5% of the stems recorded within this size class. Thirty different tree species were recorded as seedlings across all sites; however, this layer was largely dominated by five species, including American elm (5944 ± 4462 seedlings per hectare), common hackberry (1801 ± 2601 seedlings per hectare), black cherry (1176 ± 2289 seedlings per hectare), boxelder (1103 ± 761 seedlings per hectare), and hophornbeam (1029 ± 3121 seedlings per hectare), which comprised 78.9% of all seedlings recorded. Oak species made up only a 6.8% of the overall seedling abundance across all sites. Red oaks seedlings were the most widely distributed; they were found at 13 sites with an average abundance of 441 ± 382 seedlings per hectare. Bur oak seedlings were found at six sites and averaged 257 ± 518 seedlings per hectare. White oak seedlings were found at only one site; their average abundance was 231 ± 982 seedlings per hectare. Relative percent tree, sapling, shrub, and seedling stem counts per hectare for nine dominant canopy species show a forest converting from dominance by oak to dominance by more mesic, shade-tolerant species, including sugar maple, American basswood, American elm, and boxelder (Fig. 1).

Fig. 3. Relationship between mean common buckthorn score and mean oak relative importance values by stand. Red and white oak were grouped due to their positive association, as revealed through ordination. Linear trend lines fitted for red and white oak in combination (r^2 = 0.71) and bur oak (r^2 = 0.29).



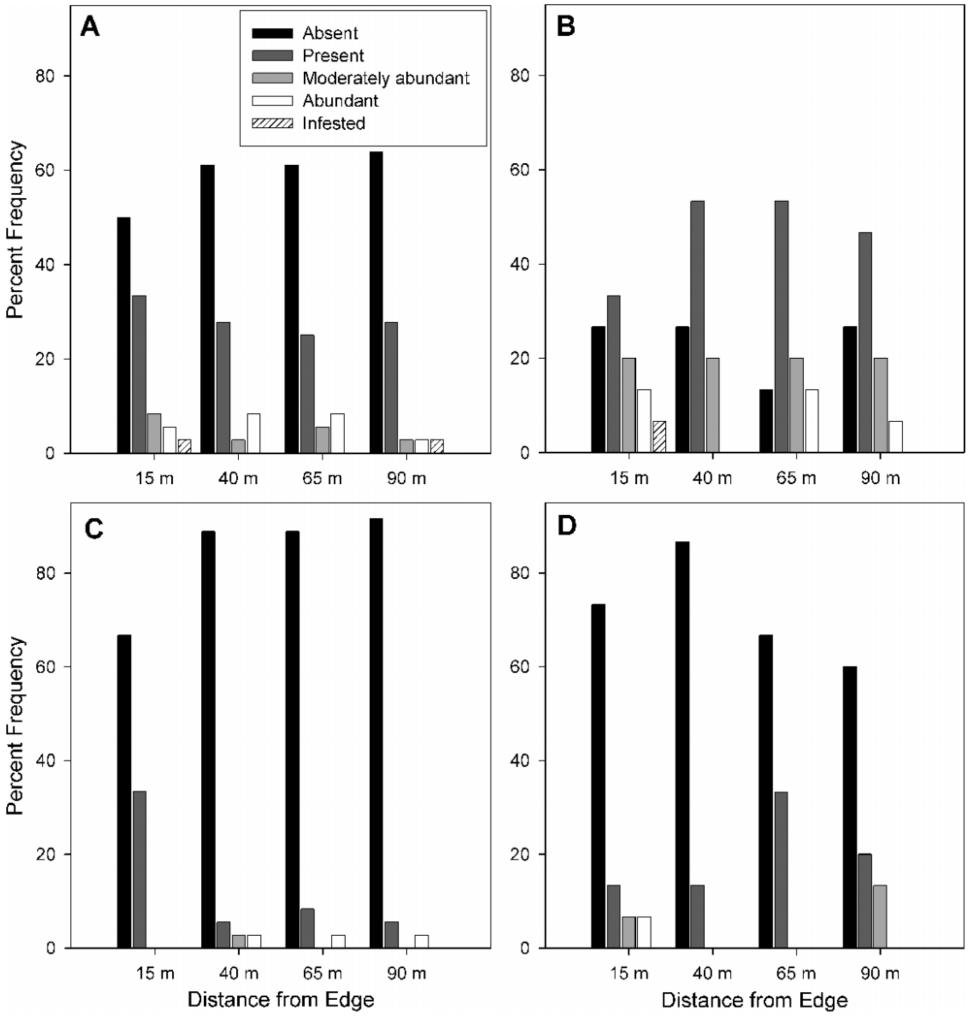
Exotic invasive species

We found common buckthorn in 15 of the 17 stands studied and, where present, it was generally abundant in all subcanopy strata. The average diameter of the largest individual within the plots where common buckthorn was present was 4.5 ± 3.0 cm. The density of large common buckthorn saplings averaged 44 ± 73 stems per hectare (mean ± 1 SD) and ranged from 0 to as high as 256 stems per hectare. In the small sapling–shrub size class, common buckthorn was the second most frequently recorded species, with a mean density of 1650 ± 3800 stems per hectare. Tartarian honeysuckle was found in the large sapling and small sapling–shrub size classes in six of 17 stands. The density of large Tartarian honeysuckle saplings and small Tartarian honeysuckle saplings–shrubs, respectively, averaged 3 ± 6 and 74 ± 169 stems per hectare. The mean qualitative invasion scores for common buckthorn and Tartarian honeysuckle were 0.79 ± 0.77 and 0.25 ± 0.30, respectively.

Community relationships

The two ordination axes from the NMS together explained almost all of the variation in the data (r^2 = 0.90), with Axis 1 explaining the majority of the variation (r^2 = 0.60) and Axis

Fig. 4. Frequency and spatial distribution of (A) common buckthorn within red and white oak stands, (B) common buckthorn within bur oak stands, (C) Tartarian honeysuckle within red and white oak stands, and (D) Tartarian honeysuckle within bur oak stands. Red and white oak were grouped due to their positive association, as revealed through ordination. Bur oak stands included five stands where the relative importance of bur oak exceeded 20%.



2 a lesser amount ($r^2 = 0.30$). Axis 1 was positively correlated with sugar maple and hophornbeam saplings and negatively correlated with the relative importance of American elm, the abundance of black cherry saplings, and gooseberry shrubs (Table 2). Axis 2 reflected positive associations among the relative importance of red and white oak, the abundance of sugar maple saplings, and total tree basal area (Table 2; Fig. 2). These community and structural (basal area) characteristics were in turn negatively associated with the occurrence of common buckthorn, the relative importance of bur oak, the abundance of black cherry saplings, dogwood and raspberry shrubs, herbaceous cover, and measures of soil quality (Table 2; Fig. 2). The relationship between common buckthorn score and the relative importance of different oak species was subsequently confirmed within our data (Figs. 3 and 4). Tartarian honeysuckle score was less strongly correlated with Axis 2 but generally showed similar relationships to community and environmental variables as common buckthorn (Fig. 2).

Spatial distribution of vegetation and environmental metrics

Distance from edge effects were found for 16 of 28 metrics tested, with significant ($p < 0.05$) responses being more consistently recorded among environmental than vegetation measures (Table 3). Canopy cover, slope, total soil carbon, total soil nitrogen, and the concentration of soil nutrients were positively correlated with distance from edge, while total tree basal area, soil bulk density, and gooseberry shrub densities were negatively correlated with distance from edge. The relative importance of the dominant oak tree species did not vary in accordance with edge; however, the density of red oak saplings was significantly higher at stand edges than at any of the more interior positions (Table 3). The densities of American basswood, hophornbeam, and sugar maple saplings were higher within more interior stand positions. Red oak sapling density ($p < 0.01$) and common buckthorn score ($p < 0.01$) were significantly higher in the 15 m plot compared with the 90 m plot (Table 3).

Table 3. Response of vegetation and environmental metrics to distance from edge (see Table 1 for scientific names).

	Plot 1 (15 m)			Plot 2 (40 m)			Plot 3 (65 m)			Plot 4 (90 m)*		Overall	
Metric	Mean	SE	*p*	Mean	SE	*p*	Mean	SE	*p*	Mean	SE	$F_{[3,173]}$	*p*
Common buckthorn score	0.88	0.15	0.02	0.54	0.09	0.89	0.69	0.12	0.34	0.56	0.11	2.55	0.06
Tartarian oneysuckle score	0.40	0.09	0.18	0.19	0.08	0.57	0.21	0.08	0.70	0.25	0.09	1.47	0.22
Trees													
Bur oak importance (%)	4.19	1.08	0.21	3.51	0.97	0.39	3.02	0.86	0.59	2.61	0.65	0.57	0.63
Red oak importance (%)	10.16	2.09	0.39	9.42	1.91	0.58	9.48	1.77	0.56	8.07	1.40	0.26	0.85
White oak importance (%)	1.48	0.64	0.56	1.35	0.73	0.45	0.94	0.37	0.20	1.94	0.59	0.56	0.64
American elm importance (%)	1.07	0.33	0.17	2.86	0.51	<0.01	1.82	0.32	0.11	0.99	0.22	4.51	<0.01
Large saplings													
Bur oak (stems/ha)	1.39	1.39	1.00	1.39	1.39	1.00	2.78	2.78	0.60	1.39	1.39	0.93	0.93
Red oak (stems/ha)	26.39	7.36	<0.01	5.56	3.34	0.60	4.17	3.08	0.67	1.39	1.39	6.81	<0.01
White oak (stems/ha)	0.00	0.00	1.00	0.00	0.00	1.00	1.40	1.39	0.16	0.00	0.00	1.01	0.39
American basswood (stems/ha)	41.69	11.17	0.03	52.81	14.31	0.11	102.77	22.80	0.42	86.08	17.07	3.79	0.01
Black cherry (stems/ha)	58.42	19.92	0.03	33.38	3.16	0.50	18.08	6.20	0.81	22.25	8.73	2.38	0.07
Boxelder (stems/ha)	54.21	14.68	0.05	27.81	8.39	0.68	37.52	14.03	0.32	20.88	8.23	1.51	0.21
Common hackberry (stems/ha)	34.75	10.50	0.99	26.44	6.80	0.54	25.06	12.81	0.48	34.73	11.05	0.29	0.83
Hophornbeam (stems/ha)	26.39	8.82	<0.01	52.78	18.1	0.10	69.44	18.6	0.48	81.94	23.09	3.80	0.01
Sugar maple (stems/ha)	4.17	3.08	<0.01	27.78	15.35	0.03	30.56	13.16	0.04	62.50	27.60	4.89	<0.01
Small saplings–shrubs													
Gooseberry species (stems/ha)	7937.5	1084.39	<0.01	7083.33	983.84	<0.01	6833.33	1028.55	<0.01	3833.33	663.33	5.10	<0.01
Environmental metric													
Total tree basal area (m^2/ha)	25.29	2.30	<0.01	23.25	2.02	<0.01	19.75	1.65	0.16	16.15	1.40	4.74	<0.01
Total canopy cover (%)	83.96	0.90	0.01	85.95	0.79	0.87	86.88	0.77	0.38	86.09	0.82	4.17	<0.01
Herb cover (%)	21.23	2.23	0.29	23.30	2.17	0.05	19.96	1.91	0.59	18.80	1.31	1.44	0.23
Slope (°)	10.72	0.63	<0.01	16.60	1.06	<0.01	19.43	1.05	<0.01	21.67	1.14	82.34	<0.01
Soil total carbon (%)	3.36	0.09	<0.01	4.34	0.22	0.08	4.47	0.23	0.12	5.00	0.36	7.36	<0.01
Soil total nitrogen (%)	0.27	0.01	<0.01	0.33	0.01	0.32	0.34	0.02	0.39	0.36	0.02	6.33	<0.01
Soil calcium (ppm)	2235.71	83.75	<0.01	2668.25	141.22	0.09	2718.00	166.48	0.14	2978.58	155.70	5.87	<0.01
Soil magnesium (ppm)	351.71	11.55	<0.01	463.50	32.08	<0.01	542.25	34.87	0.01	627.54	35.13	24.32	<0.01
Soil potassium (ppm)	131.83	5.96	<0.01	170.85	11.2	0.77	164.50	9.33	0.74	168.23	8.98	7.18	<0.01
Soil sodium (ppm)	7.90	0.63	0.07	7.89	0.48	0.06	8.51	0.56	0.42	9.08	0.74	1.62	0.19
Soil pH	6.30	0.06	0.02	6.43	0.08	0.21	6.43	0.10	0.18	6.57	0.09	1.98	0.13
Soil bulk density (g/cm^3)	3.52	0.06	<0.01	3.35	0.07	0.04	3.17	0.09	0.67	3.11	0.09	5.89	<0.01

*No *p* value is reported for Plot 4, the interiormost plot, because it is treated as a baseline with which Plots 1, 2, and 3 are compared.

While the level of common buckthorn and Tartarian honeysuckle invasion did not consistently decline with distance from edge as expected, the common buckthorn score was nearly significant ($p = 0.06$) and was significantly higher at the edge (15 m plot) in comparison with the interior (90 m plot) position ($p < 0.01$) (Table 3). Our statistical approach of combining all oak stands obfuscated more specific relationships revealed through graphical analysis (Fig. 4). Common buckthorn tended to be more abundant at the edge of red–white oak stands, whereas it was distributed throughout bur oak stands (Figs. 4A and 4B). Similarly, while the density of Tartarian honeysuckle was low overall, the spatial distribution of this species varies with tree importance: again, Tartarian honeysuckle is found mostly at the edge of red–white oak stands, whereas these shrubs are distributed throughout bur oak stands (Figs. 4C and 4D).

Discussion

Our study supports shifts in the composition and structure of oak forests observed in other regions (Pallardy et al. 1988; Shotola et al. 1992; Pierce et al. 2006), namely that smaller size classes are dominated by more shade-tolerant, nonoak species (Fig. 1). The tree layers of our stands were dominated by a combination of large white, bur, and red oak trees, which are relatively few in number (Table 1), but few individuals of these species are found in the sapling and seedling layers (Fig. 1). In contrast, several shade-tolerant species were abundant in the seedling and sapling size classes (e.g., American elm, American basswood, sugar maple, hophornbeam, boxelder, and common hackberry). American basswood and sugar maple in particular have the potential to greatly increase in dominance in the future. While American elm already comprised 16.3% of the mean relative importance, its long-term persistence and ability to substantially increase in dominance in the tree layer are limited by mortality from Dutch elm disease. Although we recorded oaks, especially red and bur, as seedlings, they do not appear to be recruiting into the sapling size class (Fig. 1). Overall, our data support the hypothesized trend toward “mesophication” of oak forests in the eastern United States, promoted by Nowacki and Abrams (2008).

The abundance of common buckthorn and Tartarian honeysuckle differed among and within oak stands. Among stands, we found a strong positive association among the exotic shrubs, bur oak, herb cover, and soil quality and a disassociation with total tree basal area, the relative importance of red and white oak, and the abundance of sugar maple saplings (Figs. 2 and 3). Positive correlations between soil nutrient concentrations and invasive plant abundance, including Tartarian honeysuckle, have been found elsewhere (Woods 1993; Howard et al. 2004; Heneghan et al. 2006).

Both species of invasive shrubs were found throughout bur oak dominated stands (Figs. 4B and 4D) but tended to occupy the edge position in red–white oak stands (Figs. 4A and 4C). Bur, red, and white oak tree relative importance values did not differ with distance from edge, indicating that large individuals of these oaks were distributed relatively evenly throughout the forest stands. In contrast, large red oak saplings were more abundant at stand edges (Table 3). This pattern may relate to higher light availability, as indicated by patterns in canopy cover (Table 3), near the high-contrast edges of red–white oak dominated forests, as red oak is relatively intolerant of shade (Johnson et al. 2002). The additional light filtering in from the edge of these stands might provide adequate light for red oak saplings, whereas the species does not appear to survive to sapling size in more interior plots. The lack of response of bur and white oak saplings to edge distance was likely related to overall sample size; we only sampled four bur oak saplings and one white oak sapling within all 17 stands studied. By comparison, we recorded 27 red oak saplings.

The higher abundance of red oak saplings along forest edges potentially puts them in competition with common buckthorn, and to some extent Tartarian honeysuckle (Figs. 4A and 4C), given that we found greater infestation of exotic species closer to forest edges (Table 3). Common buckthorn has high shade tolerance, rapid growth, and high fecundity and is known to alter soil properties to favor its own recruitment (Harrington et al. 1989; Heneghan et al. 2004; Knight et al. 2007). The ability of these species, especially common buckthorn, to successfully infest forest habitat (Gill and Marks 1991; Archibold et al. 1997; Czarapata 2005), particularly along edges as found in this study, may result in yet another threat to the sustainability of oaks in the region.

Management implications

Several implications for the management of the oak forests that we examined, and perhaps midwestern US oak forests more generally, can be drawn from this study. First, although oak forests here, as elsewhere, are converting to mesic, shade-tolerant species (Nowacki and Abrams 2008; McEwan et al. 2011), substantial opportunities to maintain the resource remain, as mature oaks still dominate the overstory (Table 1; Fig. 1). Second, different degrees of effort may be required to maintain oak within different portions of the landscape. Our research suggests that competition from common buckthorn may be most intense on high-light, high-nutrient sites that tend to be dominated by bur oak (Fig. 2). Maintaining oaks in these locations may require intensive buckthorn cutting and herbicide control, with annual to semi-annual followup treatment for an undetermined number of years. This finding could facilitate a focused approach to minimizing the impacts and spread of common buckthorn. The strong association between common buckthorn and bur oak may allow managers to use forest inventory data to identify areas potentially experiencing high levels of common buckthorn invasion. In contrast, inhibition by common buckthorn may not be as much of a concern, or require as large of an expense to control, on lower-light, low-nutrient slopes, which tend to be dominated by red and white oak forests (Fig. 2). Oak recruitment within these red and white oak stands may be facilitated by management approaches that vary depending on the spatial proximity to forest edges. While oak recruitment is hampered throughout stands, our research suggests that different constraints are likely predominant at interior versus edge microsites. The potential for competition with shade-tolerant tree species (i.e., American elm, American basswood, hopornbeam, and sugar maple) was most pronounced within stand interiors, whereas potential competition from common buckthorn was more prominent along stand edges. Standard seed tree silvicultural management or targeted thinning to remove shade-tolerant competitors from both the canopy and understory, with little to no followup treatment, is likely to be effective in maintaining oak as at least a component of future red and white oak stands, but not without additional attention to common buckthorn established along stand margins. Overall, if managers and landowners wish to maintain oak forests in this region, they need to undertake management practices that give oak species a competitive advantage over both shade-tolerant native species and invasive common buckthorn shrubs (Dey et al. 2010; Knoot et al. 2010*b*). Without significant efforts to improve conditions that facilitate their recruitment, oaks are likely to lose their historical dominance within the next several decades.

Acknowledgements

Funding for this research was provided by the US Forest Service Northern Research Station and the Agriculture Experiment Station at Iowa State University (project IOW5057). Philip Dixon, Kirk Moloney, Todd Hanson, and Todd Ontl provided statistical and technical assistance. Jaymi LeBrun and Dan Gates assisted with field data collection. Jon Cole, Larry Gates, Ann Pierce, and Dave Svien provided input on research design and accessing field locations.

References

Albert, D.A. 1995. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. U.S. For. Serv. Gen. Tech. Rep. NC-178.

Archibold, O.W., Brooks, D., and Delanoy, L. 1997. An investigation of the invasive shrub European buckthorn, *Rhamnus cathartica* L., near Saskatoon, Saskatchewan. Can. Field-Nat. **111**: 617–621.

Brothers, T.S., and Spingarn, A. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conserv. Biol. **6**(1): 91–100. doi:10.1046/j.1523-1739.1992.610091.x.

Brown, J.R., ed. 1998. Recommended chemical soil test procedures for the north central region. North Central Region Research Publication No. 221 (revised). Missouri Agricultural Experiment Station, Colombia, Mo.

Cadenasso, M.L., Traynor, M.M., and Pickett, S.T.A. 1997. Functional location of forest edges: gradients of multiple physical factors. Can. J. For. Res. **27**(5): 774–782. doi:10.1139/x97-013.

Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C., and Jones, C.G. 2003. A framework for a theory of ecological boundaries. Bioscience, **53**(8): 750–758. doi:10.1641/0006-3568(2003)053[0750:AFFATO]2.0.CO;2.

Curtis, J.T. 1971. The vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press, Madison, Wis.

Czarapata, E.J. 2005. Invasive plants of the upper Midwest. University of Wisconsin Press, Madison, Wis.

Dey, D.C., Royo, A.A., Brose, P.H., Hutchinson, T.F., Spetich, M.A., and Stoleson, S.H. 2010. An ecologically based approach to oak silviculture: a synthesis of 50 years of oak ecosystem research in North America. Rev. Colomb. For. **13**: 200–222.

Didham, R.K. 1998. Altered leaf-litter decomposition rates in tropical forest fragments. Oecologia (Berl.), **116**(3): 397–406. doi:10.1007/s004420050603.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., von Holle, B., and Webster, J.R. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. **3**(9): 479–486. doi:10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2.

Flory, S.L., and Clay, K. 2006. Invasive shrub distribution varies with distance to roads and stand age in eastern deciduous forests in Indiana, USA. Plant Ecol. **184**(1): 131–141. doi:10.1007/s11258-005-9057-4.

Fralish, J.S. 2004. The keystone role of oak and hickory in the central hardwood forest. *In* Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability. *Edited by* M.A. Spetich. U.S. For. Serv. Gen. Tech. Rep. SRS-73. pp. 78–87.

Gill, D.S., and Marks, P.L. 1991. Tree and shrub seedling colonization of old fields in central New York. Ecol. Monogr. **61**(2): 183–205. doi:10.2307/1943007.

Grubh, K.R. 2010. Historical vegetation reconstruction using spatial modeling on pre-Euro-American data to inform ecosystem restoration in the Driftless Area of the US Midwest. M.Sc. thesis, Ecology and Evolutionary Biology, Iowa State University, Ames, Iowa.

Harrington, R.A., Brown, B.J., and Reich, P.B. 1989. Ecophysiology of exotic and native shrubs in southern Wisconsin: I. Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. Oecologia (Berl.), **80**(3): 356–367. doi:10.1007/BF00379037.

Hartman, K.M., and McCarthy, B.C. 2008. Changes in forest structure and species composition following invasion by a non-indigenous shrub, Amur honeysuckle (*Lonicera maackii*). J. Torrey Bot. Soc. **135**(2): 245–259. doi:10.3159/07-RA-036.1.

Heneghan, L., Rauschenberg, C., Fatemi, F., and Workman, M. 2004. European buckthorn (*Rhamnus cathartica*) and its effects on some ecosystem properties in an urban woodland. Ecol. Res. **22**(4): 275–280. doi:10.3368/er.22.4.275.

Heneghan, L., Fatemi, F., Umek, L., Grady, K., Fagen, K., and Workman, M. 2006. The invasive shrub European buckthorn (*Rhamnus cathartica*, L.) alters soil properties in Midwestern U.S. woodlands. Appl. Soil Ecol. **32**(1): 142–148. doi:10.1016/j.apsoil.2005.03.009.

Hester, A.J., and Hobbs, R.J. 1992. Influence of fire and soil nutrients on native and non-native annuals at remnant vegetation edges in the Western Australia wheatbelt. J. Veg. Sci. **3**(1): 101–108. doi:10.2307/3236003.

Hobbs, H. 1999. Origin of the Driftless Area by subglacial drainage — a new hypothesis. *In* Glacial processes past and present. *Edited by* D.M. Mickelson and J.W. Attig. Geological Society of America Special Paper 337, Boulder, Co. pp. 93–102.

Honnay, O., Verheyen, K., and Hermy, M. 2002. Permeability of ancient forest edges for weedy plant species invasion. For. Ecol. Manage. **161**(1–3): 109–122. doi:10.1016/S0378-1127(01)00490-X.

Honu, Y.A.K., and Gibson, D.J. 2006. Microhabitat factors and the distribution of exotic species across forest edges in temperate deciduous forest of southern Illinois, USA. J. Torrey Bot. Soc. **133**(2): 255–266. doi:10.3159/1095-5674(2006)133[255:MFATDO]2.0.CO;2.

Howard, T.G., Gurevitch, J., Hyatt, L., Carreiro, M., and Lerdau, M. 2004. Forest invisibility in communities in southeastern New York. Biol. Invasions, **6**(4): 393–410. doi:10.1023/B:BINV.0000041559.67560.7e.

Johnson, P.S., Shifley, S.R., and Rogers, R. 2002. The ecology and silviculture of oaks. CABI Publishing, Oxon, U.K.

Knight, K.S., Kurylo, J.S., Endress, A.G., Stewart, J.R., and Reich, P.B. 2007. Ecology and ecosystem impacts of common buckthorn (*Rhamnus cathartica*): a review. Biol. Invasions, **9**(8): 925–937. doi:10.1007/s10530-007-9091-3.

Knoot, T.G., Schulte, L.A., Tyndall, J.C., and Palik, B.J. 2010*a*. The state of the system and steps toward resilience of disturbance-dependent oak forests. Ecol Soc. **15**: 5 [online]. Available from http://www.ecologyandsociety.org/vol15/iss4/art5/ [accessed 25 February 2011].

Knoot, T.G., Schulte, L.A., and Rickenbach, M. 2010*b*. Oak conservation and restoration on private forestlands: negotiating a social–ecological landscape. Environ. Manage. **45**: 155–164. doi:10.1007/s00267-009-9404-7.

López-Barrera, F., Manson, R.H., González-Espinosa, M., and Newton, A.C. 2006. Effects of the type of montane forest edge on oak seedling establishment along forest–edge–exterior gradients. For. Ecol. Manage. **225**(1–3): 234–244. doi:10.1016/j.foreco.2005.12.055.

Lorimer, C.G. 2003. The decline of oak forests. Bioscience, **53**(10): 915. doi:10.1641/0006-3568(2003)053[0915:TDOOF]2.0.CO;2.

Lorimer, C.G., Chapman, J.W., and Lambert, W.D. 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. J. Ecol. **82**(2): 227–237. doi:10.2307/2261291.

Lovett, G.M., Weathers, K.C., Arthur, M.A., and Schultz, J.C. 2004. Nitrogen cycling in a northern hardwood forest: do species matter? Biogeochemistry, **67**(3): 289–308. doi:10.1023/B:BIOG.0000015786.65466.f5.

Matlack, G.R. 1994. Vegetation dynamics of the forest edge — trends in space and successional time. J. Ecol. **82**(1): 113–123. doi:10.2307/2261391.

McCune, B., and Grace, J.B. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Ore.

McCune, B., and Keon, D. 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. **13**(4): 603–606. doi:10.1111/j.1654-1103.2002.tb02087.x.

McCune, B., and Mefford, M.J. 1999. PC-ORD: multivariate analysis of ecological data. Vol. 4. MjM Software Design, Gleneden Beach, Ore.

McEwan, R.W., Dyer, J.M., and Pederson, N. 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. Ecography, **34**(2): 244–256. doi:10.1111/j.1600-0587.2010.06390.x.

Meekins, J.F., and McCarthy, B.C. 1999. Competitive ability of *Alliaria petiolata* (Garlic Mustard, Brassicaceae), an invasive, nonindigenous forest herb. Int. J. Plant Sci. **160**(4): 743–752. doi:10.1086/314156.

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**(2): 247–255. doi:10.1674/0003-0031(2002)147[0247:SOAHDT]2.0.CO;2.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. **10**(2): 58–62. doi:10.1016/S0169-5347(00)88977-6.

Nowacki, G.J., and Abrams, M.D. 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience, **58**(2): 123–138. doi:10.1641/B580207.

Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. Updated edition. John Wiley & Sons, Inc., New York.

Palik, B.P., and Murphy, P.G. 1990. Disturbance versus edge effects in sugar-maple/beech forest fragments. For. Ecol. Manage. **32**(2–4): 187–202. doi:10.1016/0378-1127(90)90170-G.

Pallardy, S.G., Nigh, T.A., and Garrett, H.E. 1988. Changes in forest composition in central Missouri: 1968–1982. Am. Midl. Nat. **120** (2): 380–390. doi:10.2307/2426010.

Pierce, A.R., Parker, G., and Rabenold, K. 2006. Forest succession in an oak–hickory dominated stand during a 40-year period at the Ross Biological Reserve, Indiana. Nat. Areas J. **26**(4): 351–359. doi:10.3375/0885-8608(2006)26[351:FSIAOD]2.0.CO;2.

Rodewald, A.D., and Abrams, M.D. 2002. Floristics and avian community structure: implications for regional changes in eastern forest composition. For. Sci. **48**: 267–272.

Ross, M.A., and Harper, J.L. 1972. Occupation of biological space during seedling establishment. J. Ecol. **60**(1): 77–88. doi:10.2307/2258041.

SAS Institute Inc. 2011. SAS online doc, version 9.2 [online]. Available from http://support.sas.com/documentation/cdl_main/index.html [accessed 25 February 2011].

Shotola, S.J., Weaver, G.T., Robertson, P.A., and Ashby, W.C. 1992. Sugar maple invasion of an old-growth oak–hickory forest in southwestern Illinois. Am. Midl. Nat. **127**(1): 125–138. doi:10.2307/2426328.

Vasconcelos, H.L., and Laurance, W.F. 2005. Influence of habitat, litter type, and soil invertebrates on leaf-litter decomposition in a fragmented Amazonian landscape. Oecologia (Berl.), **144**(3): 456–462. doi:10.1007/s00442-005-0117-1.

Vasconcelos, H.L., and Luizão, F.J. 2004. Litter production and litter nutrient concentrations in a fragmented Amazonian landscape. Ecol. Appl. **14**(3): 884–892. doi:10.1890/03-5093.

Vogelmann, J.E., Howard, S.M., Yang, L.M., Larson, C.R., Wylie, B. K., and Van Driel, N. 2001. Completion of the 1990s national land cover data set for the conterminous United States from Landsat Thematic Mapper data and ancillary data sources. Photogramm. Eng. Remote Sensing, **67**: 650–652.

Ward, K., Kromroy, K., and Juzwik, J. 2007. Transformation of the oak forest spatial structure in the Minneapolis/St. Paul metropolitan area, Minnesota, USA over 7 years. Landsc. Urban Plan. **81** (1–2): 27–33. doi:10.1016/j.landurbplan.2006.10.001.

Williams, K., Westrick, L.J., and Williams, B.J. 2006. Effects of blackberry (*Rubus discolor*) invasion oak population dynamics in a California savanna. For. Ecol. Manage. **228**(1–3): 187–196. doi:10.1016/j.foreco.2006.03.002.

Woods, K.D. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. Am. Midl. Nat. **130**(1): 62–74. doi:10.2307/2426275.