

Colonization of successional grassland by *Ulmus rubra* Muhl. in relation to landscape position, habitat productivity, and proximity to seed source¹

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FOSTER, B. L. AND C. D. COLLINS (Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045). Colonization of successional grassland by *Ulmus rubra* Muhl. in relation to landscape position, habitat productivity, and proximity to seed source. *J. Torrey Bot. Soc.* 136: 392–402. 2009—Evaluating the factors that regulate woody plant invasion into grassland is important for understanding the process of succession, for predicting potential impacts of global change on grassland ecosystem structure and function and for informing the restoration and management of grasslands. In this study we investigate factors influencing seedling establishment and spatial distribution of an invading native woody plant (*Ulmus rubra* Muhl.) across a heterogeneous successional grassland landscape in eastern Kansas. Using data collected from a landscape-level seedling census of an abandoned hayfield undergoing succession, we relate *U. rubra* stem abundance to landscape gradients in topographic position, soil texture, soil fertility, plant productivity, and proximity to seed sources. We also present results from a fertilization experiment to more directly evaluate the potential effect of grassland fertility and productivity on *U. rubra* invasion, independent from other potential causal factors that covary with soil fertility and plant productivity across the natural topographic gradient. In the landscape census, *U. rubra* stem densities were greatest in low-productivity micro-sites located at higher elevations in the landscape on hill-slopes and ridges. Highly productive micro-sites at low positions in the landscape and dominated by the introduced rhizomatous hay grass, *Bromus inermis*, contained few if any *U. rubra* stems despite close proximity to a seed source. In the fertilization experiment, fertilization increased plant biomass, but reduced *U. rubra* stem densities, confirming the suppressive influence of high productivity on *U. rubra* stems in the landscape. In control plots of the fertilization experiment, *U. rubra* stem density was negatively correlated with distance from seed source, a pattern that was obliterated by fertilization, illustrating the interaction of habitat productivity and dispersal limitation in regulating current patterns of establishment and distribution of invading *U. rubra* seedlings at the site. We suggest that current patterns of woody plant invasion in this region are very different from what likely occurred historically prior to settlement, due to major anthropogenic shifts in ecological context. This altered context includes the suppression of wildfire, legacy effects of prior agricultural activity and increased availability of woody plant propagules across the region.

Key words: colonization, fertilization, productivity, successional grassland, *Ulmus rubra*, woody plant invasion.

Prior to settlement by Europeans, upland habitats at the prairie-forest ecotone of the Midwestern and Central USA primarily supported a mixture of tall-grass prairie and savanna vegetation, resulting from interactions of climate and fire (Sampson and Knopf 1994, Knapp and Seastedt 1998, Chagnon et al. 2003). Much of this region is now agricultural, highly fragmented, and characterized by large tracts of land in various stages of abandonment, resulting in a mosaic of

vegetation types (Kettle et al. 2000, Briggs et al. 2005). As a result of widespread fire suppression and the inability of fires to spread extensively due to landscape fragmentation, succession on these lands typically leads to the development of woodland, rather than reverting back to native grassland or savanna (Robinson et al. 1992, Yao et al. 1999, Ross et al. 2003), with important consequences at the ecosystem level (changes in productivity, nutrient cycling, soil development, hydrology, and habitat structure for wildlife; Briggs et al. 2005, Knapp et al. 2008). Woody plant invasion and conversion of former grassland to woodland are not unique to this region, but represent a trend observed in many regions of the world attributed to interactions among global change factors such as altered land-use, habitat fragmentation, nitrogen (N) deposition and eutrophication, elevated CO₂, and a changing climate (Archer et al. 1995, Yao et al.

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1999, Jackson et al. 2002, Briggs et al. 2005). Evaluating the factors governing woody plant invasion into grassland is important for understanding the process of succession, for predicting potential impacts of global change on ecosystem structure and function and for informing the restoration and management of grasslands.

In the absence of fire, rates and spatial patterns of woody plant invasion into grassland can be influenced by numerous factors such as seed predation, herbivory, soil disturbance, resource availability, interactions with resident vegetation, and landscape-level factors that influence dispersal and seed input (Foster and Gross 1999, McDonnell and Stiles 1983, Myster and Pickett 1993, Brigg et al. 2005). Understanding how these processes vary throughout a landscape and along environmental gradients is important for predicting future patterns of woody plant invasion and distribution in response to anthropogenic environmental change.

In this study we investigate factors influencing seedling establishment and spatial distribution of an invading, native tree (*Ulmus rubra* Muhl.) across a heterogeneous, successional grassland landscape in eastern Kansas. *Ulmus rubra* (slippery elm) is an abundant, wind-dispersed woodland species of the central and eastern USA, historically associated with fertile soils of floodplains and lower slopes along stream courses. In the absence of fire, this species is also a common invader of upland habitat, particularly on soils originating from limestone parent material such as those that occur in eastern Kansas (Scholz 1958). *Ulmus rubra* is currently abundant along forest-field edges and is the dominant tree species colonizing successional grasslands and old-fields at our study site (Yao 1999, Ross et al. 2003). *Ulmus rubra* does not have a persistent seed bank and so must establish in abandoned lands by dispersing from an external source.

Our objective was to explore factors generating spatial patterns of establishment and abundance of invading *Ulmus rubra* seedlings across a topographically heterogeneous grassland landscape within the context of understanding current constraints on woody plant invasion and distribution and secondary succession. Using data collected from a landscape-level seedling census of an abandoned hayfield undergoing succession, we examine

patterns of *U. rubra* seedling distribution to landscape gradients in topographic position, soil texture, soil fertility, plant productivity, and proximity to seed source. In addition, we present results from a fertilization experiment conducted in the same landscape to more explicitly evaluate the potential effects of grassland fertility and productivity on *U. rubra* invasion, independent from other potential causal factors that covary with soil fertility and plant productivity across the natural landscape gradient.

Materials and Methods. **STUDY SITE.** Our study was conducted at the Nelson Environmental Studies Area (NESA) which is part of the University of Kansas Field Station and Ecological Reserves. NESA is located in the prairie-forest ecotone of northeastern Kansas, USA, 12 km north of the city of Lawrence (39° 03' N, 95° 12' W). The focus of our research is a 20 ha abandoned agricultural landscape with a long history of row crop cultivation (at least 100 years). More recently, the site was used for cool-season hay production, but was abandoned from this use in the early 1980s and then maintained as open grassland by frequent mowing until 1997 when mowing was ceased. Topography across this landscape is rolling, forming the ridge-to-swale geomorphology typical for the region. Uplands are comprised of convex ridges and hill-slopes. Lowlands are gently concave, forming swales along ephemeral drainages (Kettle and Whittemore 1991). Soils are clay loam (montmorillonitic, mesic Aquic Arguidolls), but vary somewhat in texture and organic matter content depending on landscape position (Collins and Foster 2008). Vegetative productivity varies considerably across the site, ranging from 78 g m⁻² on eroded, upland hill-slopes to 866 g m⁻² in productive lowland swales (Foster et al. 2004).

At the start of this study in 2000, the landscape was dominated by non-native C₃ grasses originally sown for hay: *Bromus inermis* Leyss. and *Lolium arundinacea* Schreb. However, the study site was undergoing secondary succession and was also being colonized by the opportunistic native grass, *Andropogon virginicus* L., by native prairie plants from a nearby prairie relict, and by woody plants invading from a forested lowland located at the northwest corner of the field. As initially observed in June 2000,

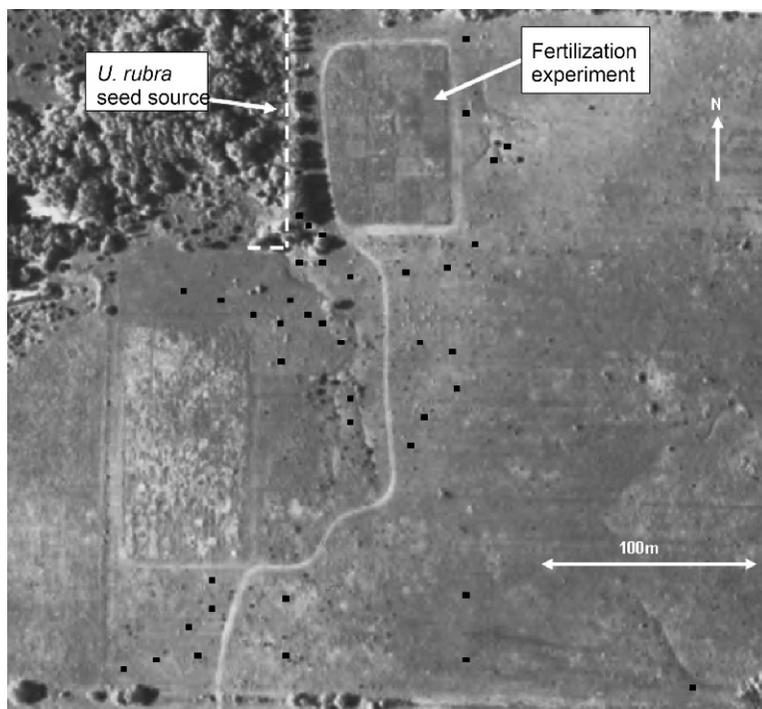


FIG. 1. Aerial photograph of the study landscape (taken in 2006) showing the approximate positions of the 40 landscape census plots (black squares) and the location of the fertilization experiment. The portion of the *Ulmus rubra*-dominated fence-line that served as a seed source is indicated by the dashed white line.

newly-established seedlings of *Ulmus rubra* were particularly abundant at our site in some locations. Other common woody invaders include: *Cornus drummondii* C.A.Mey. (native shrub), *Juniperus virginiana* L. (native tree), *Rhus typhina* L. (native shrub), and *Symphoricarpos orbiculatus* Moench. (native shrub).

LANDSCAPE CENSUS OF *ULMUS RUBRA* SEEDLINGS. In June 2000 we established forty, 3×3 m plots throughout the landscape to census *Ulmus rubra* seedlings. Plot locations were selected using a stratified random approach that assured representation of ridge, mid-slope, and swale micro-sites (12, 15, and 13 plots per micro-site type, respectively). Spatial location of each plot within the landscape and distances between them were determined using a Garmin eTrex® handheld GPS receiver (Garmin Company, Kansas City, MO, USA). Relative elevation for each plot within the landscape was determined by topographic survey using differential leveling. Using GPS-determined plot location data, we calculated the distance of a given plot to the main seed source by calculating the shortest straight-line distance of that plot to a fence-line located in a

lowland area at the northwest corner of the study site (Fig. 1). The fence line was inhabited by a stand of adult *U. rubra* trees that produced large crops of seeds between 2000 and 2003.

During June 10–12, 2000, all stems of *Ulmus rubra* were counted in each of the 40 seedling census plots. An attempt was made to determine the age of the seedlings by counting annual bud scars on each *U. rubra* stem. Although herbivore damage precluded precise aging for some of the stems, we determined that most stems were between a few months and 3 years of age. Because of their relatively young age, seedlings were generally small ranging from approximately 3–10 cm in height.

Aboveground plant biomass was sampled in each plot in mid July 2000 to provide an index of plant productivity for each plot location. Vegetation was harvested by clipping a $0.08 \text{ m} \times 1 \text{ m}$ strip of vegetation about 2 cm above the soil surface in each plot using electric shears. Each harvested sample was separated into live and litter fractions, dried at 74°C to constant mass and weighed.

In mid July 2001 we measured canopy penetration of photosynthetically active radiation (PAR penetration) in all plots using a 0.8 m Accupar® Ceptometer probe (Decagon Devices, Pullman, WA, USA). Multiple measurements below and above the plant canopy were made at two locations within each subplot between the hours of 1100 and 1400. PAR penetration was calculated as a percentage of full sun ((PAR below canopy/PAR above canopy) \times 100).

To characterize soil variability across the landscape, we collected soil samples at locations immediately adjacent to (within 0.5 m) the census plots. Using a 2.54×15 cm tube sampler we collected one core of soil per plot over the course of five days in October 2004. Each soil sample was air dried and then analyzed for particle size distribution, pH, total soil carbon (C), and total soil nitrogen (N). Particle sized distribution (% sand, silt, clay) was determined using the hydrometer method. Soil pH was measured for each soil sample by mixing 25 g soil into 30 ml distilled water and measuring pH with a pocket-size, microprocessor-based pH meter (Oakton, Van Nuys, CA, USA) that was calibrated using a buffer solution of pH 7. Total soil C and N were analyzed at the Kansas State University Soil Testing Lab using a LECO CN dry combustion analyzer.

FERTILIZATION EXPERIMENT. In 2000 we established a long-term grassland management experiment at the site to investigate effects of fertilization and haying on plant community structure and ecosystem dynamics (Billings et al. 2006). March 2000, a 4×4 grid of sixteen 10×20 m plots was established in the northern-most section of the 20-ha landscape on moderately productive upland soil (Fig. 1). Plots were separated from each other by 3 m buffer strips. We further divided each 10×20 m plot into two 10×10 m subplots, and assigned a 2×2 factorial set of fertilization and haying treatments to the 32 subplots in a randomized-block, split-plot design. Two levels of nutrient fertilization (fertilized; not fertilized) were applied to plots as the whole-plot factor and two levels of haying (hayed; not hayed) were applied to the subplots within each plot as the split-plot factor. Each north-south column of four plots in the grid formed one of four experimental blocks, each containing two replicates of each unique treat-

ment combination. Each north-south block/column of plots was situated parallel to the *Ulmus rubra*-inhabited fence-line which served as the primary seed source for colonization into the field (Fig. 1). Plot distances to the seed source were determined by measuring distances (with a measuring tape) from the western edge of plots located closest to the tree line. We then calculated distances for all other plots in the grid from those baseline measurements.

In the spring of each year we spread NPK fertilizer (29-3-4) at $14\text{--}16$ g N m² yr⁻¹, rates at the high end of what is typically applied to cool-season hayfields of this region (Moyer and Sweeney 1988, Lamond et al. 1992). From 2001 through 2003 appropriate subplots were hayed once annually in mid-June. For the purposes of this study we took advantage of the non-hayed plots only to evaluate the effects of fertilization and increased production on *Ulmus rubra* establishment. Hayed subplots were not surveyed because haying destroys woody seedlings.

In early June 2000, just after the first application of fertilizer, and again in late June 2003, all non-hayed 10×10 m subplots were surveyed for *Ulmus rubra* seedlings by exhaustive searches of the subplots. In 2003 *Ulmus* seedlings ranged in estimated age from 2–6 years. Most of these seedlings were small (between 3 and 12 cm in height) although a few were larger, exceeding 15 cm.

Total aboveground plant biomass was sampled in each subplot in mid June 2003. Vegetation was harvested by clipping two randomly located 0.08×1 m strips of vegetation about 2 cm above the soil surface in each subplot using electric shears. Each sample was separated into live and litter fractions, dried at 74 °C to constant mass and weighed.

In May 2003, prior to the biomass harvest, we measured canopy PAR penetration using the same method described above for the landscape census plots.

DATA ANALYSIS. In the landscape census, correlations among variables measured in the landscape census were evaluated by calculating a matrix of Spearman Rank Correlation Coefficients. Polynomial regressions were performed to evaluate several bivariate relationships that appeared to be unimodal upon inspection of the bi-plots.

Table 1. Inter-correlation of soil and environmental variables measured in the landscape census. Correlation analyses were performed using Spearman Rank correlation coefficients. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	Elevation	Dispersal distance	Biomass	Litter	% Light	Soil sand	Soil silt	Soil clay	Soil pH	Soil C
Elevation										
Dispersal distance	0.58***									
Biomass	-0.56***	-0.36*								
Litter	-0.44**	-0.45**	0.22							
% Light	0.34*	0.348*	-0.72**	-0.12						
Soil sand	-0.55***	-0.44**	0.39*	0.20	-0.25					
Soil silt	-0.33*	-0.17	0.25	0.06	-0.21	0.63**				
Soil clay	0.44**	0.29	-0.33*	-0.12	0.25	-0.84***	-0.95***			
Soil pH	0.30	0.41*	-0.62***	-0.08	0.63***	-0.20	-0.33*	0.30		
Soil C	-0.47**	-0.53**	0.63***	0.36*	-0.66***	0.37*	0.20	-0.29	-0.41*	
Soil N	-0.45**	-0.52**	0.64***	0.36*	-0.67***	0.36*	0.18	-0.27	-0.37*	0.98***

To evaluate the effects of fertilization on plant and litter biomass and % PAR penetration, we used one-way analysis of variance (ANOVA) on log-transformed data. In the fertilization experiment parametric methods could not be used to examine the influences of fertilization and distance to seed source on *Ulmus rubra* stem densities because data were highly irregular and were not transformable to meet the assumptions of ANOVA. Instead, at each time period (2000 and 2003) we used the non-parametric Mann-Whitney *U*-test for independent samples to evaluate effects of fertilization. We then used Spearman Rank correlation to assess correlations with distance for non-fertilized and fertilized plots separately. To evaluate changes in stem density between the two time periods we used the non-parametric Wilcoxon signed ranks test for paired samples. All statistical analyses were performed using SPSS (version 12.0). Nomenclature follows Kartesz and Meacham (2004).

Results. LANDSCAPE CENSUS. Environmental variables were strongly inter-correlated and all but soil pH were significantly correlated with elevation (Table 1). Plant biomass, litter biomass, soil sand, soil silt, soil C, and soil N were all negatively correlated with elevation. Light penetration and soil clay content were positively correlated with elevation. Also note that distance from seed source was correlated with many of the other variables including elevation, plant biomass, and soil N (Table 1).

Of the 40 plots examined, 18 contained at least one *Ulmus rubra* stem. Among these 18 plots, *U. rubra* stem density ranged from 1–9 stems per plot (0.1–1 stems m^{-2}). *Ulmus rubra*

stem density was significantly and positively correlated with elevation (Table 2, Fig. 2a) and soil clay content (Table 2). Significant negative relationships were found for *U. rubra* stem density with plant biomass (Table 2, Fig. 2b), soil sand and soil silt. Although the negative relationship of *U. rubra* stem density to plant biomass was significant at the $P < 0.05$ level, the scatter plot of the data indicates more of a unimodal envelope pattern, exhibiting highly variable stem densities at low-to-intermediate biomass and consistently low densities at biomass levels above about 240 $g\ m^{-2}$ (Fig. 2b).

Using simple correlation, we found no monotonic relationship of *Ulmus rubra* stem density to distance from seed source (Table 2). Polynomial regression did reveal a significant quadratic relationship ($r^2 = 0.18$, $P = 0.045$), but the scatter plot of the data (Fig. 2c) indicates more of a unimodal envelope with

Table 2. Correlation of *Ulmus rubra* stem density to soil and environmental variables measured in the landscape census. Correlation analyses were performed using Spearman Rank correlation coefficients. * $P < 0.05$; ** $P < 0.01$.

Independents variables	Correlation coefficient (r_s)
Elevation	0.60**
Distance	0.14
Plant biomass	-0.34*
Plant litter	-0.24
Light penetration	0.29
Soil sand content	-0.34*
Soil silt content	-0.36*
Soil clay content	0.39*
Soil pH	0.05
Soil C content	-0.24
Soil N content	-0.23

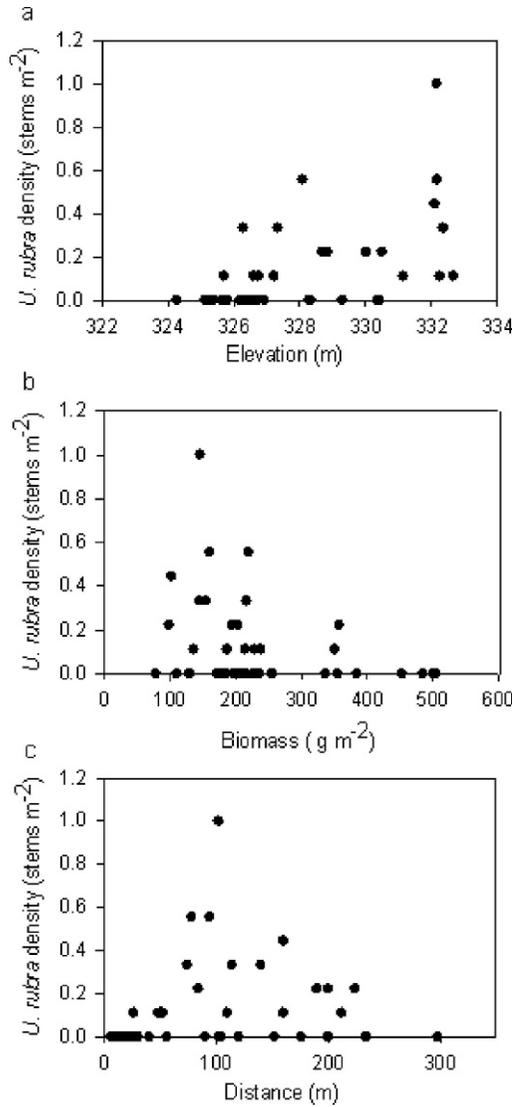


FIG. 2. Relationship of *Ulmus rubra* stem density to: a) elevation ($r_r = 0.60$; $P < 0.05$); b) plant biomass ($r_r = -0.34$; $P < 0.05$); c) distance to seed source (quadratic relationship: $r^2 = 0.18$; $P < 0.05$).

highly variable stem densities at intermediate distances, and consistently low densities at near and far distances.

FERTILIZATION EXPERIMENT. As measured in 2003, fertilization significantly increased above-ground living biomass by a factor of 2.6 and increased litter biomass by a factor of 1.96 (Fig. 3a). Fertilization also significantly reduced PAR penetration of the canopy by a factor of 2.6 (Fig. 3b).

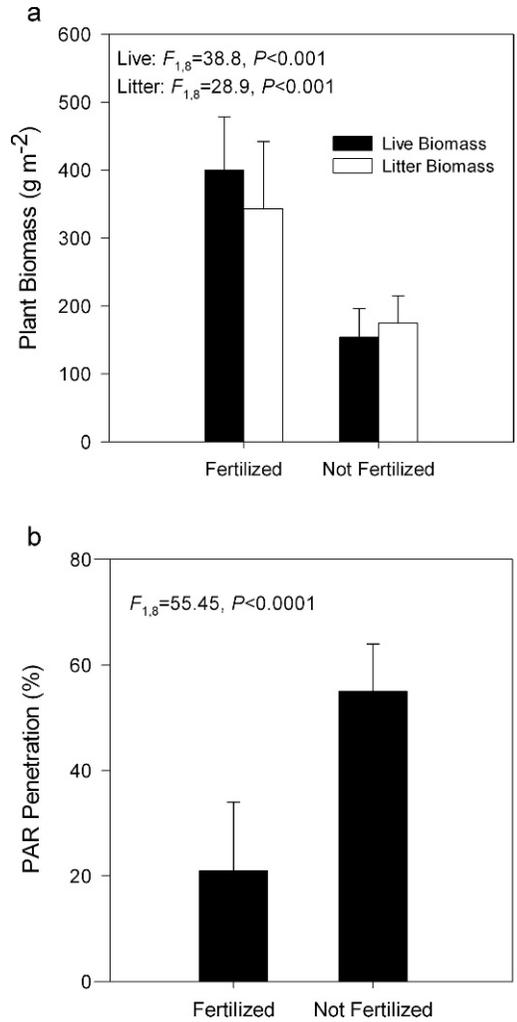


FIG. 3. Responses (mean \pm 1 SD) to fertilization of: a) live plant biomass and litter; b) penetration of photosynthetically-active radiation (% PAR penetration).

At the start of the experiment in 2000, *Ulmus rubra* seedling density ranged from 0 to 28 stems per plot (0–0.28 stems m⁻²) and did not differ significantly between fertilized and non-fertilized plots (Fig. 4a). From 2000 to 2003, *U. rubra* seedling density increased in the non-fertilized plots (Wilcoxon signed ranks test for paired samples: $Z = -2.20$, $P = 0.028$), but declined to low levels in the fertilized plots ($Z = -2.03$, $P = 0.042$). As a result, *U. rubra* seedling density was significantly greater in non-fertilized than fertilized plots in 2003 (Fig. 4b). In 2000, *U. rubra* seedling density was negatively correlated with distance from seed source in both the non-

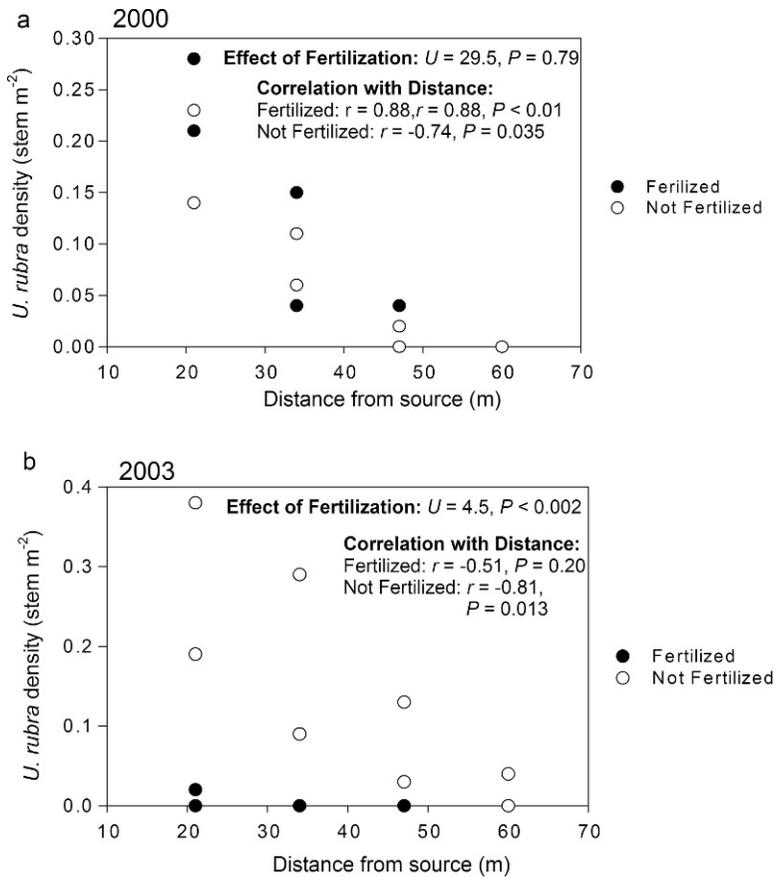


FIG. 4. Response of *Ulmus rubra* stem density to fertilization and distance from seed source in 2000 and 2003.

fertilized and non-fertilized plots (Fig. 4a). In 2003, this negative correlation was detectable only in the non-fertilized plots (Fig. 4b).

Discussion. Although our study focused on a single woody species at single research site, our findings highlight the potential influences of landscape position, soil fertility, productivity, and dispersal limitation on rates and spatial patterns of invasion by woody plants encroaching into grasslands of the central USA. In addition, our findings suggest ways that recent human activity has altered historical patterns of woody plant establishment.

Ulmus rubra stem densities in this study were relatively low, but variable throughout the landscape. Despite this variability, stem densities in the landscape census tended to be greatest in plots located at higher elevations on eroded hill-slopes and ridges. These sites have finer textured soils, lower production, reduced

litter, greater available light and greater bare ground than low elevation swales at the bottom of hills. These environmental differences undoubtedly reflect spatial variation in the natural processes of soil development, deposition and erosion along topographic gradients, but also reflect modifications of the environment resulting from a history of tillage. For example, surface soils of slopes and ridges consist primarily of exposed B horizon high in clay content: the trademark of severe erosion and top-soil loss resulting from a history of cultivation (Murphy et al. 2004).

A negative effect of soil fertility and productivity on establishment of *Ulmus rubra* was suggested by low stem densities observed in landscape census plots with high plant biomass. However, variations in biomass across the landscape were confounded by covariation with elevation and other variables. Although suggested by the landscape census,

our fertilization experiment confirmed the suppressive effect of high plant production on *U. rubra* establishment at our site, independent of other covarying factors. Fertilization increased biomass production and reduced *U. rubra* stem density measured three years after the start of the experiment. In fertilized plots, stem densities declined from a mean of 9 stems per plot at the start of the study in 2000 to a mean of 0.25 seedlings per plot in 2003, indicating that fertilization increased rates of mortality and reduced rates of establishment over that time period. In contrast, stem densities increased over time in non-fertilized plots, indicating additional establishment after 2000.

These findings parallel a negative effect of fertilization on plant diversity previously observed in this same experiment (Foster et al. in press) and a negative relationship between plant diversity and biomass that exists across the larger landscape (Foster 2001, Foster et al. 2004). Reduced colonization and diversity in response to fertilization and productivity are often interpreted in terms of competitive exclusion (Grime 1973, Tilman 1982, Huston 1994). It is possible that intense competition with dominant grasses at high productivity, particularly for light, may have influenced establishment of *Ulmus rubra* at our study site. Both in the landscape census and the fertilization experiment, light penetration tended to be lowest in plots exhibiting the greatest levels of biomass and lowest stem densities.

Factors in addition to competition may have contributed to low stem densities at high productivity. For example, plant litter in productive communities can interfere with establishment by further reducing light, by physically interfering with germination or by impeding seedling emergence (Facelli and Pickett 1991). Dense vegetation and thick litter such as that observed in this study at low elevations and in response to fertilization, may also increase risk of seedling mortality by promoting herbivory by invertebrates and activity of fungal pathogens (Facelli and Pickett 1991). *Ulmus rubra* seedlings are known to be particularly susceptible to damping off fungus (Cooley et al. 1990).

These findings indicate that the quality of the establishment micro-site, as determined by topographic position, soil texture, soil fertility, and vegetative productivity likely influence

probabilities of *Ulmus rubra* seedling establishment in this landscape. However, superimposed on these constraints of micro-site quality are factors that limit accessibility of seeds to receptive micro-sites. Like most woody plants in this region, *U. rubra* does not have a persistent seed bank. As a result, establishment in early stages of woody plant succession is dependent on dispersal by wind from external sources. Seed rain generally declines exponentially with distance from source trees (Hughes and Fahey 1988, Yao et al. 1999, Standish et al. 2007). Correspondingly, woody plant abundances often decline exponentially with distance from nearby forests in studies of old-field succession (Myster and Pickett 1993, Yao et al. 1999). Because *U. rubra* is wind-dispersed, patterns of abundance with distance should be more distinct than for woody plants dispersed by animals, given that animal behavior and movement patterns further influence seed distributions (McDonnell and Stiles 1983). In a study of old-field succession conducted near our site, Yao et al. (1999), found negative exponential patterns of stem abundance with distance from source for *U. rubra* and for an abundant bird-dispersed shrub, *Cornus drummodii*. However, the relationship was much more distinct for wind-dispersed *U. rubra*.

Ulmus rubra distribution at our site then appears to at least partially reflect the joint influence and interaction of micro-site suitability and dispersal limitation, most clearly suggested by the results of the fertilization experiment where the negative relationship of stem density to distance, evident across control plots, was obliterated by fertilization. This suggests that although dispersal limitations likely play a role in regulating colonization rates and seedling distribution, undisturbed micro-sites of high fertility and productivity may be resistant to establishment regardless of seed input. This interaction was also hinted at from the landscape census where we found a unimodal envelope relationship between stem density and distance rather than a negative monotonic relationship. This pattern may partially reflect the spatial autocorrelation of distance, topography and plant biomass observed as one moves in the landscape from productive low areas to upland ridges. A number of the most productive lowland plots were located very close to the seed source yet had very low stem

densities, consistent with the negative effect of fertilization and high productivity observed in the fertilization experiment. The low invasability of high productivity sites near the seed source may explain why we did not see a monotonic negative relationship with distance as observed in the control plots of the fertilization experiment. The greatest stem densities in the landscape census were found in plots of intermediate distance, at higher positions in the landscape, and where biomass productivity tended to be lowest. However we also note that stems densities were highly variable at these intermediate distances, reflecting the highly stochastic nature of seedling establishment at our site.

Our finding that *Ulmus rubra* establishment is largely restricted to unproductive upland locations seems surprising on first inspection given that this species was historically not common in uplands and was restricted to fertile soils at the base of hills and along stream courses (Scholz 1958). Differences between current patterns of establishment observed at our field site and historic landscape distributions of *U. rubra* undoubtedly reflects major changes in ecological context associated with recent human activity. Fire suppression and habitat fragmentation have largely eliminated fire from the system, allowing *U. rubra* and many other fire-sensitive woody plants that were historically restricted to riparian areas to invade uplands (Briggs et al. 2005). Erosional processes associated with tillage history may have also created greater opportunity for woody plant establishment on uplands by reducing productivity and herbaceous cover and by increasing the availability of bare ground microsites for establishment.

The limited capacity of *Ulmus rubra* to invade productive lowland sites in this abandoned hayfield may partially reflect the agricultural legacy of planting non-native grasses for hay. In particular, the non-native and rhizomatous hay grass, *Bromus inermis*, currently dominates fertile lowland sites, forming near monocultures that are resistant to invasion. The invasion resistance of productive *B. inermis* swards is further implicated by a previous study at our site where 32 grassland species sown into lowland plots were unable to invade unless litter was experimentally removed and the *B. inermis* canopy was clipped (Foster et al. 2004). Suppression of *U. rubra* by a productive *B. inermis* sward was

also illustrated at our site in a competition experiment where *B. inermis* biomass removal from around focal *U. rubra* seedlings stimulated seedling growth and reduced seedling mortality (Ross et al. 2003). The competitive effects of productive *B. inermis* swards on *U. rubra* germination and initial seedling establishment may be particularly strong because *B. inermis* is a C₃ grass that begins its growth early in the spring at the same time that *U. rubra* seedlings start to emerge (Scholz 1958).

We cannot rule out the possibility that intact native prairie vegetation in lowland areas was not also resistant to invasion by *Ulmus rubra* and other species historically. The successful establishment of *U. rubra* in productive lowland areas may require periodic disturbances that provide open micro-sites for germination and which reduce competition during the early establishment stages of the life history. Historically it may have been that infrequent fire in lowlands or periodic flooding disturbances adjacent to streams provided the occasional window of opportunity for establishment of *U. rubra* cohorts in otherwise resistant lowland habitat while frequent fire consistently prevented establishment in uplands.

Finally, it is likely that the human-induced expansion of woody plant distribution observed regionally over the last century has increased the overall availability of woody plant propagules within and among landscapes, relaxing dispersal limitation and fueling further spread of this species onto uplands (Briggs et al. 2005).

To conclude, our results indicate that conditions for establishment of *Ulmus rubra* in this landscape are currently most favorable in upland locations. Productive lowland portions of the landscape appear to be highly resistant to invasion due to competitive interference imposed by the dominant introduced grasses that currently thrive in fertile areas. This conclusion was supported from field survey data showing limited establishment of *U. rubra* in productive locations within the landscape and from a controlled experiment showing that N fertilization inhibited establishment of this woody species. Results from the fertilization experiment also suggest that anthropogenic eutrophication of grasslands could have significant consequences for patterns of woody plant establishment and distribution in the future. We suggest that

current patterns of establishment by woody plants in eastern Kansas, and likely other grasslands and abandoned old-fields throughout the central and eastern USA, are influenced by multiple anthropogenic changes in ecological context that have occurred since settlement by Europeans.

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