

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

---

Great Plains Research: A Journal of Natural and  
Social Sciences

Great Plains Studies, Center for

---

Fall 2002

## Community Dynamics of an Ecotonal Forest-Prairie Interface in Northeastern Kansas

Elizabeth Hane  
*Brown University*

Steven Hamburg  
*Brown University*

Follow this and additional works at: <https://digitalcommons.unl.edu/greatplainsresearch>



Part of the [Other International and Area Studies Commons](#)

---

Hane, Elizabeth and Hamburg, Steven, "Community Dynamics of an Ecotonal Forest-Prairie Interface in Northeastern Kansas" (2002). *Great Plains Research: A Journal of Natural and Social Sciences*. 617.  
<https://digitalcommons.unl.edu/greatplainsresearch/617>

This Article is brought to you for free and open access by the Great Plains Studies, Center for at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Great Plains Research: A Journal of Natural and Social Sciences by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

## **COMMUNITY DYNAMICS OF AN ECOTONAL FOREST-PRAIRIE INTERFACE IN NORTHEASTERN KANSAS**

**Elizabeth N. Hane<sup>1</sup>**

*Brown University  
Department of Ecology and Evolutionary Biology  
Providence, RI 02912  
ehane@netspace.org*

and

**Steven P. Hamburg**

*Brown University  
Center for Environmental Studies  
Providence, RI 02912*

**ABSTRACT**—Climate change models predict that ecotones, which are boundaries between two biomes, are likely to be the first place we see the effects of climate change. However, very little baseline data exist for these areas and their current community structure. In order to better understand the community dynamics of an ecotonal forest, a 2.2 ha 60-year-old upland forest in northeastern Kansas was monitored for 10 years. This oak-hickory forest at the ecotone with the tallgrass prairie biome is growing more slowly than other forests of similar species composition farther east, possibly due to lower levels of available soil moisture or nutrient-depleted soil. The aboveground biomass (122 Mg/ha) was 15%-25% less than more eastern forests of similar composition and age. The study area contained three slightly different landscape units, typical of the regional matrix of land-use histories, edaphic characteristics, and forest compositions. A portion of the study area with a history of greater disturbance had the greatest number of small trees and a higher biomass and density of early successional species. Over the 10-year study period, differences among landscape units became less pronounced, with tree biomass and species composition becoming more uniform. We expect that in the next 50 years, the forest will become more homogenous across the study area with respect to aboveground biomass and species composition. This suggests that land-use history plays a minor role in determining community composition in this ecotonal forest, and that biological and environmental factors play a larger role.

<sup>1</sup> Current Address: Proctor Maple Research Center, University of Vermont, P.O. Box 233, Underhill Center, VT 05490

**KEY WORDS:** ecotonal forest, forest-prairie interface, land-use history

### **Introduction**

Plant-community dynamics of both prairie and forest are shaped by biotic and environmental factors as well as land-use history. The role of biotic and environmental factors (such as competition, herbivory, seed dispersal, water availability, soil nutrient content, topography) in shaping forest composition has been widely studied, while land use has only recently begun to be documented as a factor in forest development (Hamburg and Sanford 1986; Glitzenstein et al. 1990; Motzkin et al. 1996, Boren et al. 1997). Northeastern Kansas currently represents the dynamic interface, or ecotone, between the eastern deciduous forest and tallgrass prairie biomes of North America. Little is known about the relationship between intensity of past land use and current forest dynamics in the Great Plains. Indeed, very few studies have been published on forests in the Plains (Braun 1950; Borland et al. 1989).

These midcontinental forests have been heavily impacted by past land use. Early survey records suggest that prior to European settlement, northeastern Kansas was approximately 95% prairie and 5% forest, with forests primarily on rocky side slopes and riparian areas that were less susceptible to fire (K. Kindesher, pers. comm.). After 1850 increasing cultivation and other farming activities affected the native communities in most of the region (Whitney 1994). In the absence of fire, those portions of the landscape no longer used for agricultural purposes such as cultivation or pasture have experienced a steady increase in woody plant encroachment (Kucera 1960; Bragg and Hulbert 1976; Borland et al. 1989). Following World War II, many farms in northeastern Kansas were abandoned, leading to the development of old-field ecotonal forests.

Although fire plays a role in maintaining the forest-prairie boundary on a local scale (Bock and Bock 1984; Abrams 1986; Briggs and Gibson 1992), it is hypothesized that the landscape-level boundary is maintained by water availability (Davis 1983; Harrison et al. 1995; Williams et al. 2000). Water stress is therefore likely to play a large role in the future of these forests, as global climate-change models predict rising temperatures and broad shifts in precipitation patterns (Watson et al. 1996). This suggests that ecotonal vegetation is likely to be the first to experience the effects of climate change (Nielson 1993; Risser 1993; Allen and Brashears 1998). Because of the encroachment of these forests into former prairie, understanding their dynamics is paramount to guiding management decisions

about protection of the natural areas in the Great Plains in a changing climate (Halpin 1997).

Variable precipitation, frequent droughts, and a low precipitation-to-evapotranspiration index cause trees in midcontinental ecotonal forests to be more water stressed than those in more eastern forests (Thorntwaite 1948). Evapotranspiration potential in the Midwest is higher than in the eastern United States, and average monthly precipitation in the Midwest is more variable. In addition, erosion of fine-textured soils and oxidation of organic matter resulting from over 100 years of agricultural activity have decreased water-holding capacity for much of the region, making the vegetation even more susceptible to water stress and reducing the amount of nutrients available in the soil (Davidson and Ackerman 1993; Compton et al. 1998). These combined stresses influence forest growth rates, as well as community structure and succession.

In this study we used 10 years of vegetation composition data from a 2.2 ha permanent plot to identify community characteristics of a midcontinental ecotonal forest responding to varied land use. The characteristics include density, basal area, aboveground biomass, size structure of populations, and species shifts. We asked: (1) Do the forests of northeastern Kansas have similar community characteristics to eastern forests? and, (2) Does the varied land-use history within the ecotonal forest play a role in determining community characteristics?

### Study Area

The study was conducted within the Kansas Ecological Reserve, a 500 ha reserve in Douglas County, Kansas, (39°03'N, 95°12'W). Rolling topography typifies the site, which has an average elevation of 300 m (Fitch and Hall 1978). Mean monthly temperature ranges from 26°C in July to -2°C in January. Mean annual precipitation is 900 mm, of which an average of 70% falls during the growing season (April through September). During the 10 years of the study (1988-1998), total growing season precipitation varied from 430 to 1190 mm. Soils in this area are mollisols, with well-drained stony soils on the slope (Dickey et al. 1977).

The study plot was located in a larger forest-prairie matrix composed primarily of oaks (*Quercus* spp.), shagbark hickory (*Carya ovata*), and hackberry (*Celtis occidentalis*) with a relatively open understory. The site varied both with regard to topography and land-use history (Fitch and Hall 1978). Presettlement use of the site likely included burning by Native Americans to maintain a tallgrass prairie ecosystem (Pyne 1983; Whitney

1994). All farming in the study area stopped by the 1940s, when the land was purchased by the University of Kansas and incorporated into the Fitch Natural History Reservation. The land has not been actively managed since that time.

### Methods

We determined land-use history using aerial photographs obtained from the US Department of Agriculture for the years 1937, 1941, and 1954 as well as ownership records and existing landmarks. The history and topography of the study area are typical of the larger region. Areas that have been plowed in the past have a distinct layer of homogenous soil (Ap layer). Presence and absence of an Ap layer provided additional information about land-use boundaries. We aged 20 large trees (>20 cm diameter at breast height, or dbh) to determine time of abandonment. The oldest trees dated from 1930 to 1940.

The western 1.4 ha of the 2.2 ha study area was flat and the remaining 0.8 ha was steeply sloped to the east. The co-occurrence of land-use patterns and topography, such as sloped or rocky areas, led to our division of the study area into three landscape units (Fig. 1): (1) edge unit, the formerly plowed agricultural area abandoned in the 1930s, (2) flat unit, cleared and used as pasture until 1940, and (3) sloped unit, un-plowed rockier pasture abandoned in 1940. This 2.2 ha study area was divided into 220 10 x 10 m contiguous permanently marked plots in 1988 (Fig. 1).

In 1988, 1993, and 1998 the diameter at breast height of all trees (dbh >5.0) within the permanent plots was recorded. In order to determine if there was a relationship between rainfall patterns and growth rates, we installed dendrometer bands on four mature individuals of each of four species (*Quercus rubra*, *Ulmus rubra*, *Carya ovata*, and *Juglans nigra*). Dendrometer bands measure fine-scale changes in trunk diameter, allowing correlation of growth with rainfall and other variables. Changes in diameter were measured every three to five weeks during the growing season from 1988 to 1994. Rainfall was measured daily 500 m north-northeast of the study area.

Relative importance values were calculated using the equation

$$\text{RIV} = (\text{rf} + \text{rba} + \text{rd})/3,$$

where RIV = relative importance value, rf = relative frequency, rba = relative basal area, and rd = relative density. Aboveground biomass was estimated using allometric equations (Tritton and Hornbeck 1982).

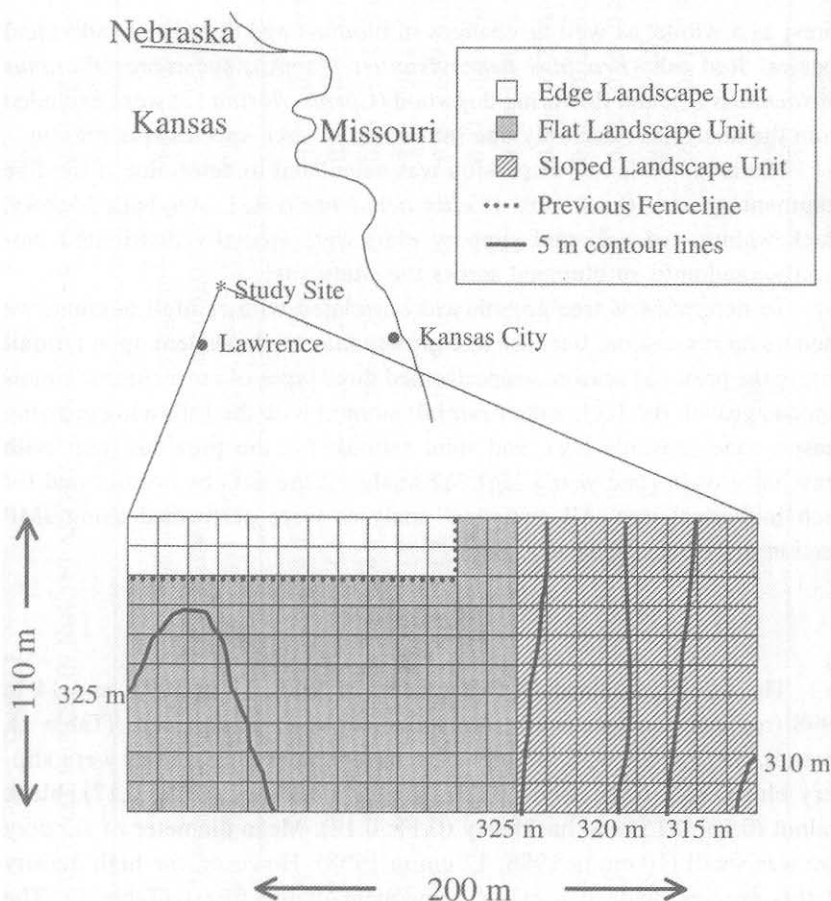


Figure 1. The study area in northeastern Kansas, near the junction of Douglas, Jefferson, and Leavenworth Counties. The 2.2 ha area was divided into three areas based on topography and land-use history. The edge unit (0.2 ha) was plowed until the late 1930s. The flat unit (1.2 ha) was used for pasture during the same time period. The sloped unit (0.8 ha) is steep and rocky, and was not plowed nor was it likely to have been used heavily for pasture.

### Statistical Analysis

We were interested in both the growth rate (change in biomass during the 10 years) and in the final density and biomass in 1998. We were also interested in knowing if these characteristics varied by landscape unit. To compare growth rates and final density and biomass among landscape units, we used nested multiple regression analysis. We examined changes in the

forest as a whole, as well as changes in biomass and density of individual species. Red ash (*Fraxinus pennsylvanica* Marsh.), sycamore (*Platanus occidentalis* L.), and flowering dogwood (*Cornus florida* L.) were excluded from the analysis, since only one individual of each species was present.

Morisita's index of dispersion was calculated to determine if the five dominant species (hackberry [*Celtis occidentalis* L.], shagbark hickory, black walnut, red oak, and slippery elm) were spatially distributed uniformly, randomly, or clumped across the study site.

To determine if tree growth was correlated with rainfall amount, we used linear regression. Because tree growth may be dependent upon rainfall during the previous season, we performed three types of correlations: simultaneous growth (no lag), winter rainfall amount with the following growing season (one season's lag), and total rainfall for the previous year with seasonal growth (one year's lag). We analyzed the data by species and for each individual tree. All statistical analyses were performed using JMP version 3.1 (SAS 1995).

## Results

The forest contained 14 tree species in 1988, 13 in 1993, and 14 in 1998 (red ash was lost, while flowering dogwood was gained) (Table 1). Overall, the species with the highest relative importance values were slippery elm (1988: 0.25; 1998: 0.26), shagbark hickory (0.19; 0.17), black walnut (0.13; 0.15) and hackberry (0.11; 0.12). Mean diameter of slippery elm was small (10 cm in 1988; 12 cm in 1998). However, the high density of this species made it a major component of the forest (Table 1). The relative importance value of the other key species was influenced more by fewer, larger individuals than by a high density of small individuals.

Between 1988 and 1998 the forest as a whole increased in basal area (21 m<sup>2</sup>/ha to 23 m<sup>2</sup>/ha) and in aboveground biomass (108 Mg/ha to 121 Mg/ha). However, it decreased in density (981 stems/ha to 795 stems/ha) (Table 1). The rate of decrease in density was similar among all of the common species, with the two exceptions of shagbark hickory, which showed a larger decline (28%), and hackberry, which had a smaller decline (3%) than average (Table 1). Black walnut, shagbark hickory, and slippery elm comprised over 60% of the biomass in both 1988 and 1998 (Table 1).

Comparisons between units of different land-use history and topography show that significant differences exist among the units with regard to density, species composition, and aboveground biomass (Appendix). Trees in the edge unit were the youngest and most dense. The edge unit also had

TABLE 1  
SELECTED CHARACTERISTICS OF AN ECOTONAL FOREST IN NORTHEASTERN KANSAS IN 1988, 1993, AND 1998

Species	Common name	Density (#/ha)			Basal area (m <sup>2</sup> /ha)			Aboveground biomass (Mg/ha)			Relative importance value		
		1988	1993	1998	1988	1993	1998	1988	1993	1998	1988	1993	1998
<i>Ulmus rubra</i> Muhl	Slippery elm	356	324	286	3.9	4.0	4.0	21	22	21	0.25	0.28	0.26
<i>Carya ovata</i> Miller (K. Koch)	Shagbark hickory	199	157	142	4.4	4.4	4.5	21	23	24	0.19	0.17	0.17
<i>Juglans nigra</i> L.	Black walnut	65	59	55	5.0	4.8	5.1	28	27	29	0.13	0.14	0.15
<i>Celtis occidentalis</i> L.	Hackberry	115	108	111	1.5	1.8	2.0	6	7	8	0.11	0.12	0.12
<i>Quercus muehlenbergii</i> Engelm.	Chinquapin oak	79	74	69	1.7	1.7	1.8	10	10	11	0.09	0.08	0.08
<i>Tilia americana</i> L.	Basswood	35	34	35	0.8	0.9	1.0	3	3	4	0.07	0.07	0.07
<i>Quercus rubra</i> L.	Northern red oak	27	25	24	1.3	1.5	1.6	9	10	12	0.05	0.05	0.06
<i>Cercis canadensis</i> L.	Redbud	32	21	23	0.3	0.2	0.2	1	1	1	0.03	0.02	0.02
<i>Gymnocladus dioica</i> L.(K. Koch)	Coffeetree	15	14	13	0.6	0.6	0.7	2	3	3	0.02	0.02	0.02
<i>Gleditsia triacanthos</i> L.	Honey locust	9	6	6	0.9	0.8	0.9	5	5	5	0.02	0.02	0.02
<i>Morus rubra</i> L.	Mulberry	39	30	23	0.6	0.6	0.6	1	1	1	0.02	0.02	0.02
Other <sup>1</sup>		11	8	7	0.3	0.3	0.3	1	1	1	0.01	0.01	0.01
	TOTAL	981	860	795	21.2	21.5	22.6	108	114	120			

<sup>1</sup>Includes the following infrequent species: osage orange (*Maclura pomifera* Raf.), sycamore (*Platanus occidentalis* L.), red ash (*Fraxinus pennsylvanica* Marsh.), and dogwood (*Cornus florida* L.)



the highest biomass, largely caused by a few very large honey locust trees (50+ cm dbh, 24% of total biomass) growing along a former fenceline. This unit was dominated by large numbers (430/ha) of small slippery elms (<15 cm dbh), both large and small black walnuts, and many small hackberry. In contrast, the flat unit was of intermediate density consisting predominantly of small slippery elms, large black walnuts, and intermediate-sized shagbark hickories. We found no evidence of regeneration of black walnut in this unit, unlike the edge unit (Fig. 2). The sloped unit had both the lowest density and the largest trees and was dominated by shagbark hickory, which is declining in the small size classes and increasing in the large size classes (Appendix). Slippery elm and black walnut also had high importance values in the sloped unit, though slippery elm is again only small individuals.

Morisita's index of dispersion showed that red oak and shagbark hickory were clumped in the less disturbed parts of the forest ( $X^2 = 20.4$  and  $18.2$ , respectively;  $X^2_{crit} = 12.34$ ,  $P < 0.01$ ). Black walnut, hackberry, and slippery elm were uniformly distributed throughout the study area. Net aboveground productivity rates also varied among units, with the edge growing the fastest ( $1.9 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ) and the sloped unit ( $1.2 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ) growing at a rate similar to the flat unit ( $1.1 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ).

We found no significant difference in growth, evaluated as change in aboveground biomass, among species or among landscape units for the forest as a whole ( $F = 0.81$ ,  $P < 0.63$  for species;  $F = 0.58$ ,  $P < 0.95$  for species among landscape units). For the response variable of aboveground biomass in 1998, both species ( $F = 14.53$ ,  $P < 0.0001$ ) and species among landscape units ( $F = 2.90$ ,  $P < 0.0001$ ) are good predictors, showing that there are large differences among species in total aboveground biomass in 1998, and species response depended on the landscape unit in which the species is located. The same was true for density in 1998 (species:  $F = 110.14$ ,  $P < 0.0001$ ; unit by species:  $F = 8.96$ ,  $P < 0.0001$ ).

Populations varied in their size structure both overall and between units. Slippery elm had the greatest density in the smallest age classes, probably due to Dutch elm disease having killed the larger size classes (Thompson et al. 1964). Red oak, which has experienced limited regeneration over most of its range because of deer herbivory and other factors (Heinen and Sharik 1990; Lorimer 1993), declined in the smallest size classes, but the population was not large enough to determine if this trend was significant. Black walnut was not regenerating in the flat or sloped units, but there was a cohort of small trees in the edge unit (Fig. 2). However, the number of small trees declined over time, showing little new recruitment into the smallest age class (Fig. 2).

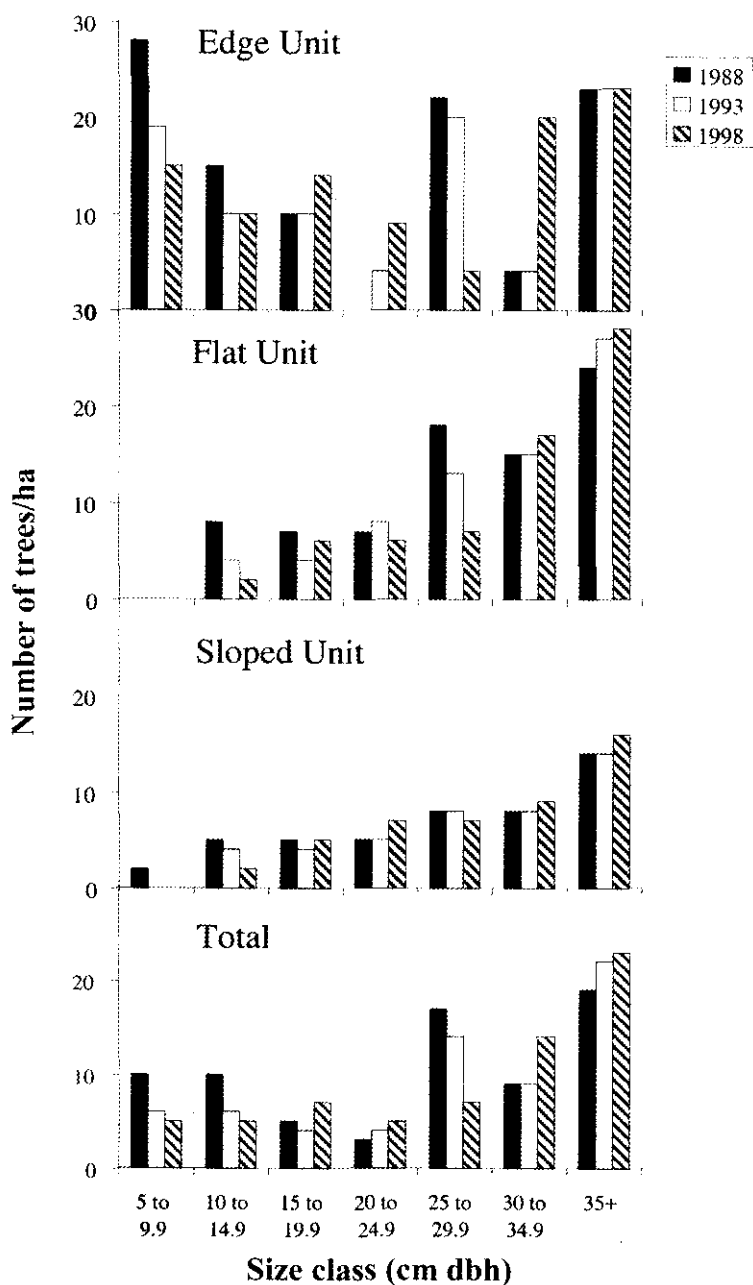


Figure 2. Size class distributions for black walnut (*Juglans nigra*) in the three landscape units and the study area as a whole.

The results from the dendrometer-band study showed no significant correlation between rainfall amounts and tree growth, either individually or grouped by species. The amount of variation in tree growth, expressed by  $R^2$  values, that could be explained by rainfall amount varied from 0.2% to 55%, with most values falling below 20%. Annual rainfall amounts during the study period varied greatly, from a drought in 1988 and severe flooding in 1993. These severe fluctuations in rainfall amounts led to the expectation that tree growth would reflect rainfall amount between 1988 and 1995.

## Discussion

### Ecotonal versus Eastern Forests

The forest in this study was approximately 60 years old in 1998 and was dominated by slippery elm, shagbark hickory, black walnut, and hackberry. The early successional species such as coffeetree (*Gymnocladus dioica*), honey locust (*Gleditsia triacanthos*), and osage orange (*Maclura pomifera*) were present as adults, but we found no evidence of regeneration anywhere in the study area. Over the next 30 years, as the adults of these early successional species die, the species are likely to disappear from the area, giving way to later successional species such as red oak and shagbark hickory. Though red oak does not yet make up a dominant part of the forest, the species showed a 25% increase in biomass over the 10-year study period, and density in the smaller size classes held steady over the 10-year period. There is little information about how long it takes for an oak-hickory overstory to grow in the forest-prairie transition area, but clearly after 60 years the forest is still changing in composition.

In many ways this ecotonal forest followed successional trends similar to eastern deciduous forests. Old-field succession in the oak-hickory region of eastern deciduous forests generally starts with herbs, and after 15 years the herbs are replaced by an understory of hardwoods, including oak and hickory (Weaver and Clements 1929; Oosting 1948; Braun 1950). By 200 years after abandonment, the forest is an oak-hickory "climax forest," with few or no pines or early successional species remaining.

Forest invasion of the prairie in the "forest-prairie transition" area of northeast Kansas and southeast Nebraska starts with red cedar (*Juniperus virginiana*) and other early successional species such as flowering dogwood (*Cornus florida*) and redbud (*Cercis canadensis*). Unlike the eastern forests, ecotonal forests in the prairie transition area do not have a stage of succes-

sion that is dominated by pine. Early successional species are instead replaced with red oak (*Quercus rubra*), basswood (*Tilia americana*), hickory (*Carya* spp.), and sugar maple (*Acer saccharum*) (Braun 1950).

The forest we studied had a lower basal area and aboveground biomass than eastern forests (Table 2). Also, the forest thinned out over the 10-year study period, since density decreased by 19% and aboveground biomass increased by 10% ( $1.2 \text{ Mg ha}^{-1} \text{ y}^{-1}$ ). These changes indicate that the forest is increasingly composed of fewer, larger individuals. The rate of the forest's self-thinning was consistent with those reported in other forests, which means that the proportional decline of density and rise of biomass is similar to that of other forests (Yoda 1963; White 1980). Our forest had a lower basal area and biomass than other oak-hickory forests of similar age, with the exception of a disturbed forest in New York (Glitzenstein et al. 1990), which had a similar value for basal area (Table 2); however, the density of the New York forest was only two-thirds of that of our Kansas site, indicating that the forest in New York was made up of fewer, larger trees and had considerably more living aboveground biomass. The forest in New York was also an old-field forest dating to the late 1930s.

Climate parameters such as highly variable rainfall patterns and high evapotranspiration have been cited frequently as the mechanisms that maintain the ecotonal boundary between forest and prairie (Davis 1983; Williams et al. 2000). These factors may contribute to the low biomass observed for this forest. The lack of correlation in our results between rainfall amounts and individual tree growth rates suggests that precipitation may not be a good indicator of water availability for trees (Fralish 1994). Severe stress in the form of drought, such as the one in 1988, can also impose long-term limitations on cambial growth of trees, even in years when conditions might be favorable for growth otherwise (Jenkins and Pallardy 1995). Past soil erosion also may have exacerbated the lower water-holding capacity of the fine-textured soils of the site, decreasing overall growth rates (Glitzenstein et al. 1990; Foster 1992). Thus, we conclude that, for our study site, the key factor controlling the low biomass of the forest is likely related to recent climatic variability and land-use history of the site, rather than actual rainfall amounts.

### Future of the Forest

Black walnut, slippery elm, and shagbark hickory are key to understanding the future of this forest. Projections of the future slippery elm

TABLE 2

COMPARISON OF ABOVEGROUND BIOMASS AND BASAL AREA ESTIMATES FOR THE ECOTONAL FOREST STUDIED AND OTHER OAK FORESTS IN THE UNITED STATES

Forest type	Location	Age (yr)	Aboveground biomass	
			(Mg/ha)	Reference
Temperate oak	(Maximum)	Un	432	Ovington et al. (1963)
Oak-hickory	Smoky Mountains	Un	420	Whittaker (1966)
Temperate oak	(Average)	Un	166	Ovington et al. (1963)
Mixed oak	Minnesota	60	163	Ovington et al. (1963)
Oak-hickory	Georgia Piedmont	Un	145	Monk et al. (1970)
Oak-hickory	North Carolina	50	140	Day and Monk (1974)
Oak-hickory	Oak Ridge, TN	Un	136	Sollins (1972)
Oak-hickory	Nebraska Kansas	60	122	<b>Present study</b>
			Basal area (m <sup>2</sup> /ha)	
Oak-hickory	Tennessee	Un	43	Held and Winstead (1975)
Oak (river floodplain)	Central Kansas	>60	39	Bellah and Hulbert (1974)
Oak-hickory	Barren County, KY	Un	30	Held and Winstead (1975)
Oak-hickory	Illinois (undisturbed)	Un	30	Fralish (1994)
Oak-hickory	Anderson County, KY	Un	26	Held and Winstead (1975)
Oak-hickory	North Carolina	50	26	Day and Monk (1974)
Oak-hickory	Illinois (disturbed)	Un	23	Fralish (1994)
Oak-hickory	Nebraska Kansas	60	22	<b>Present study</b>
Oak-Hickory	New York (disturbed)	70	20	Glitzenstein et al. (1990)
Oak (river floodplain)	Central Kansas	<10	20	Bellah and Hulbert (1974)

Note: "Un" = unreported.

population are complicated by the presence of Dutch elm disease, which generally affects trees with a diameter  $>20$  cm (Thompson et al. 1964). Slippery elm makes up almost a third of the forest by density, but  $<20\%$  of the biomass. If the fungus continues to be virulent in most of the population, it is likely that slippery elm will decline as individuals of other species mature.

Shagbark hickory is likely to increase in importance over the next 50 years since it can grow quickly and exploit openings in the canopy better than other species (Burns and Honkala 1990). The high mortality rate in the smallest size class of shagbark hickory was likely a short-term phenomenon related to the high initial density. Reproductive capacity of this species will increase dramatically as the trees mature. Currently, only a few of the hickory at the study site are older than 60 years, yet the optimum seed-bearing age is between 60 and 200 years (Burns and Honkala 1990). We expect the study forest to be dominated by shagbark hickory and black walnut over the next several decades, with some adult red oak and with slippery elm primarily in the understory.

Other studies of the impacts of land-use history suggest that the disturbance of the soil and altered nutrient content in the plowed soil will lead to differences in species composition relative to areas that were not plowed (Glitzenstein et al. 1990; Foster 1992; Bratton et al. 1994). The edge unit, which was previously plowed, could mature into a slightly different forest in terms of tree community composition, since the future of shagbark hickory in the edge unit is uncertain. There was a small but steady recruitment into the smallest size class, but densities were very low when compared to the flat and sloped units. There were no large adults in the edge unit, possibly indicating the limited availability of seeds. Alternatively, shagbark hickory may not compete well in disturbed soil. Shagbark hickory dominated the sloped unit, which is the oldest part of the study area, so if shagbark hickories were recruitment-limited in the edge unit, we may find that the future forest in this unit will be dominated by black walnut or hackberry.

It is quite clear that topography and time since abandonment have resulted in variation in tree community composition, but how much these differences will diminish with time is less clear. The co-occurrence of land-use patterns and natural topographical boundaries such as steep slopes or rocky areas made it difficult to determine any causal relationship between environment and vegetation patterns (Glitzenstein et al. 1990). The oldest trees on the slope were older than any of the trees in the flat unit, suggesting that the two units were of different ages, even though they had both been

pastured but not plowed. Whether the differences among units was due to successional, stochastic, or soil nutrient factors is unclear.

Despite the current differences in species composition and biomass, the changes observed over the 10-year study period suggest that biomass will converge and species composition may become more uniform. In contrast, many forests in the east show longer lasting effects of land-use history (Motzkin et al. 1996; Compton et al. 1998; Foster et al. 1998). The current differences in productivity rates, aboveground biomass, and species composition indicate that the units may respond differently to climate change, and that if ecotonal forests are used as an indicator community, care should be taken to understand the land-use history of the area.

### Acknowledgments

We would like to thank the Kansas Ecological Reserves, Dean Kettle, and Galen Pittman for access to the study site and for use of precipitation data. Special thanks to Chris Payne, Anna Busby, Andrew Hane, and Amy Hester who carried out much of the field work, and to Carl and Nancy Hane who helped with the collection of the tree cores. This study was supported by grants from the Environmental Protection Agency and the Andrew W. Mellon Foundation to the second author and by funds from Experimental and Applied Ecology Program at the University of Kansas.

### References

- Abrams, M.D. 1986. Historical development of gallery forests in northeast Kansas. *Vegetatio* 65:29-37.
- Allen, C.D., and D.D. Brashears. 1998. Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Science* 95:14839-42.
- Bellah, G.R., and L.C. Hulbert. 1974. Forest succession on the Republican River floodplain in Clay County, Kansas. *Southwest Naturalist* 19:155-66.
- Bock, J.H., and C.E. Bock. 1984. The effect of fires on woody vegetation in the pine-grassland ecotone of the Southern Black Hills. *American Midland Naturalist* 112:35-42.
- Boren, J.C., D.M. Engle, M.S. Gregory, R.E. Masters, T.G. Bidwell, and V.A. Mast. 1997. Landscape structure and change in a hardwood forest-tallgrass prairie ecotone. *Journal of Range Management* 50:244-49.

- Borland, D.E., T.B. Bragg, and D.M. Sutherland. 1989. Woody-plant succession in an eastern Nebraska (USA) bluff forest. *Transactions of the Nebraska Academy of Sciences* 17:61-64.
- Bragg, T.B., and L.C. Hulbert. 1976. Woody plant invasion of an unburned Kansas bluestem prairie. *Journal of Range Management* 29:19-24.
- Bratton, S.P., J.R. Hapeman, and A.R. Mast. 1994. The lower Susquehanna River gorge and floodplain (U.S.A.) as a riparian refugium for vernal, forest-floor herbs. *Conservation Biology* 8:1069-77.
- Braun, E.L. 1950. *Deciduous Forests of Eastern North America*. Philadelphia: Blackiston Co.
- Briggs, J.M., and D.J. Gibson. 1992. Effect of fire on tree spatial patterns in a tallgrass prairie landscape. *Bulletin of the Torrey Botanical Club* 119:300-7.
- Burns, R.M., and B.H. Honkala. 1990. *Silvics of Forest Trees of the United States*, vol. 2. Agricultural Handbook No. 654. Washington, DC: US Forest Service, Dept. of Agriculture.
- Compton, J.E., R.D. Boone, G. Motzkin, and D.R. Foster. 1998. Soil carbon and nitrogen in a pine-oak sand plain in central Massachusetts: Role of vegetation and land-use history. *Oecologia* 116:536-42.
- Davidson, E.A., and I.L. Ackerman. 1993. Changes in soil carbon inventories following cultivation of previously untilled soils. *Biogeochemistry* 20:161-93.
- Davis, M.B. 1983. Quaternary history of deciduous forests of eastern North America and Europe. *Annals of the Missouri Botanical Gardens* 70:550-63.
- Day, F.P., and C.D. Monk. 1974. Vegetation patterns on a southern Appalachian watershed. *Ecology* 55:1064-74.
- Dickey, H.P., J.L. Zimmerman, R.O. Plinsky, and R.D. Davis. 1977. *Soil Survey of Douglas County, Kansas*. Washington, DC: US Soil Conservation Service.
- Fitch, H.S., and E.R. Hall. 1978. A 20-year record of succession on reseeded fields of tallgrass prairie on the Rockefeller experimental tract. University of Kansas, Museum of Natural History Publication 4. Lawrence: University of Kansas.
- Foster, D. 1992. Land use history (1730-1990) and vegetation dynamics in central New England, USA. *Journal of Ecology* 80:753-71.
- Foster, D., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. *Ecosystems* 1:96-119.



- Fralish, J.S. 1994. The effect of site environment on forest productivity in the Illinois Shawnee Hills. *Ecological Applications* 4:134-43.
- Glitzenstein, J.S., C.D. Canham, M.J. McDonnell, and D.R. Streng. 1990. Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York. *Bulletin of the Torrey Botanical Club* 117:106-22.
- Halpin, P.N. 1997. Global climate change and natural-area protection: Management responses and research directions. *Ecological Applications* 7:828-43.
- Hamburg, S.P., and R.L. Sanford. 1986. Disturbance, *Homo sapiens* and ecology. *Bulletin of the Ecological Society of America* 67:169-71.
- Harrison, S.P., J.E. Kutzback, I.C. Prentice, P.J. Behling, and M.T. Sykes. 1995. The response of northern hemisphere extratropical climate and vegetation to orbitally induced changes in insolation during the last interglaciation. *Quaternary Research* 43:174-84.
- Heinen, J.T., and T.L. Sharik. 1990. The influence of mammalian browsing on tree growth and mortality in the Pigeon River State Forest, Michigan. *American Midland Naturalist* 123:202-6.
- Held, M.E., and J.E. Winstead. 1975. Basal area and climax status in mesic forest systems. *Annals of Botany* 39:1147-48.
- Jenkins, M.A., and S.G. Pallardy. 1995. The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. *Canadian Journal of Forest Research* 25:1119-27.
- Kucera, C.L. 1960. Forest encroachment on native prairie. *Iowa State Journal of Science* 34:635-40.
- Lorimer, C.G. 1993. Causes of the oak regeneration problem. In *Oak Regeneration: Serious Problems, Practical Recommendations*, ed. D. Loftis and C.E. McGee. Washington, DC: US Forest Service General Technical Report SE-84.
- Monk, C.D., G.I. Child, and S.A. Nicholson. 1970. Biomass, litter and leaf surface area estimates of an oak-hickory forest. *Oikos* 21:138-41.
- Motzkin, G., D. Foster, A. Arthur, J. Harrod, and R. Boone. 1996. Controlling site to evaluate history: Vegetation patterns of a New England salt plain. *Ecological Monographs* 66:345-65.
- Nielson, R.P. 1993. Transient ecotone response to climatic change: Some conceptual and modeling approaches. *Ecological Applications* 3:385-95.
- Oosting, H.J. 1948. *The Study of Plant Communities*. San Francisco: W. H. Freeman.

- Ovington, J.P., D. Hertcamp, and D.B. Lawrence. 1963. Plant biomass and productivity of prairie, savanna, oakwood and maize field ecosystems in central Minnesota. *Ecology* 44:52-63.
- Pyne, S.J. 1983. Indian fires. *Natural History* 2:6-11.
- Risser, P.G. 1993. Ecotones. *Ecological Applications* 3:367-68.
- SAS Institute. 1995. JMP version 3.1. Cary, NC: SAS Institute.
- Sollins, P. 1972. Organic matter budget and model for a southern Appalachian *Liriodendron* forest. Ph.D. diss., University of Tennessee, Knoxville.
- Thompson, H.E., C.L. Kramer, and R.A. Keen. 1964. Dutch elm disease and its control in Kansas. *Kansas Agriculture Experiment Station Bulletin* 860:1-12.
- Thornwaite, C.W. 1948. An approach toward a rational classification of climate. *Geography Review* 38:55-94.
- Tritton, L.M., and J.W. Hornbeck. 1982. Biomass equations for major tree species of the northeast. Washington, DC: US Forest Service General Technical Report NE-69.
- Watson, R.T., M.C. Zinyowera, and R.H. Moss, eds. 1996. *Climate Change 1995: Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.
- Weaver, J.E., and F.E. Clements. 1929. *Plant Ecology*. New York: McGraw-Hill.
- White, J. 1980. Demographic factors in populations of plants. In *Demography and Evolution in Plant Populations*, ed. O.T. Solbring. Oxford, UK: Blackwell Scientific.
- Whitney, G.G. 1994. *From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America*. Cambridge, UK: Cambridge University Press.
- Whittaker, R.H. 1966. Forest dimensions and production in the Great Smoky Mountains. *Ecology* 47:103-21.
- Williams, J.W., T. Webb III, P.J. Richard, and P. Newby. 2000. Late Quaternary biomes of Canada and the Eastern United States. *Journal of Biogeography* 27:585-607.
- Yoda, K., T. Kira, H. Ogawa, and K. Hozumi. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University* 14:107-29.

## APPENDIX

SELECTED CHARACTERISTICS BY LANDSCAPE UNIT OF AN ECOTONAL FOREST  
IN NORTHEASTERN KANSAS IN 1988, 1993 AND 1998

A. Edge Unit		Density (#/ha)			Basal area (m <sup>2</sup> /ha)			Aboveground biomass (Mg/ha)			Relative importance value		
Species	Common name	1988	1993	1998	1988	1993	1998	1988	1993	1998	1988	1993	1998
<i>Ulmus rubra</i>	Slippery elm	515	460	430	4.8	4.9	5.3	20	22	25	0.34	0.34	0.34
<i>Juglans nigra</i>	Black walnut	110	100	95	5.2	5.3	5.7	27	29	31	0.16	0.17	0.17
<i>Celtis occidentalis</i>	Hackberry	170	140	130	2.1	1.8	2.0	8	7	8	0.12	0.11	0.11
<i>Gleditsia tracanthos</i>	Honey locust	45	30	30	5.2	4.4	4.8	29	26	29	0.12	0.11	0.11
<i>Quercus rubra</i>	Northern red oak	50	55	45	1.2	1.7	1.9	7	11	12	0.05	0.06	0.06
<i>Gymnocladus dioica</i>	Coffeetree	30	30	30	1.2	1.3	1.5	5	5	6	0.04	0.05	0.05
<i>Carya ovata</i>	Shagbark hickory	40	40	40	0.9	1.0	1.2	4	5	6	0.04	0.04	0.05
<i>Tilia americana</i>	Basswood	40	40	40	0.9	0.9	1.0	3	3	4	0.04	0.04	0.04
<i>Morus rubra</i>	Mulberry	40	40	25	0.7	0.7	0.7	2	2	3	0.03	0.03	0.03
<i>Cercis canadensis</i>	Redbud	25	20	20	0.2	0.2	0.2	0.6	0.6	0.6	0.02	0.02	0.01
<i>Quercus muehlenburgii</i>	Chinquapin oak	30	20	20	0.2	0.1	0.1	0.9	0.4	0.6	0.02	0.01	0.01
Other <sup>1</sup>		20	10	10	0.5	0.3	0.3	1.8	1.4	1.5	0.02	0.02	0.02
	Total	1115	985	915	22.9	22.8	24.7	108	113	127			

<sup>1</sup>Includes the following infrequent species: osage orange (*Maclura pomifera* Raf.), sycamore (*Platanus occidentalis* L.), red ash (*Fraxinus pennsylvanica* Marsh.), and dogwood (*Cornus florida* L.)

## APPENDIX CONTINUED

## B. Flat Landscape Unit

Species	Common name	Density (#/ha)			Basal area (m <sup>2</sup> /ha)			Aboveground biomass (Mg/ha)			Relative importance value		
		1988	1993	1998	1988	1993	1998	1988	1993	1998	1988	1993	1998
<i>Ulmus rubra</i>	Slippery elm	427	395	343	4.4	4.5	4.4	24	25	22	0.31	0.32	0.30
<i>Juglans nigra</i>	Black walnut	74	66	61	5.8	5.7	5.9	32	32	34	0.17	0.17	0.16
<i>Carya ovata</i>	Shagbark hickory	166	140	130	2.9	3.1	3.3	13	15	17	0.15	0.15	0.15
<i>Celtis occidentalis</i>	Hackberry	112	101	99	1.4	1.6	1.8	5	6	7	0.09	0.09	0.10
<i>Quercus muehlenburgii</i>	Chinquapin oak	80	81	76	1.6	1.8	1.9	9	10	11	0.08	0.08	0.09
<i>Tilia americana</i>	Basswood	45	43	5	1.2	1.2	1.4	4	4	5	0.05	0.05	0.06
<i>Morus rubra</i>	Mulberry	42	33	30	0.9	0.9	1.0	3	3	4	0.04	0.04	0.04
<i>Quercus rubra</i>	Northern red oak	20	16	15	1.0	1.0	1.1	6	7	7	0.03	0.03	0.03
<i>Gymnocladus dioica</i>	Coffeetree	13	12	11	0.6	0.7	0.7	3	3	3	0.02	0.02	0.02
<i>Gledisia triacanthos</i>	Honey locust	8	6	6	0.8	0.8	0.9	4	4	5	0.02	0.02	0.02
<i>Cercis canadensis</i>	Redbud	41	25	22	0.3	0.2	0.2	0.8	0.5	0.6	0.02	0.02	0.02
Other <sup>1</sup>		15	10	9	0.5	0.4	0.5	1.8	1.7	1.9	0.02	0.01	0.01
	Total	1044	928	847	21.4	21.9	23	107	112	117			

<sup>1</sup>Includes the following infrequent species: osage orange (*Maclura pomifera* Raf.), sycamore (*Platanus occidentalis* L.), red ash (*Fraxinus pennsylvanica* Marsh.), and dogwood (*Cornus florida* L.)

## APPENDIX CONTINUED

## C. Sloped Landscape Unit

Species	Common name	Density (#/ha)			Basal area (m <sup>2</sup> /ha)			Aboveground biomass (Mg/ha)			Relative importance value		
		1988	1993	1998	1988	1993	1998	1988	1993	1998	1988	1993	1998
<i>Carya ovata</i>	Shagbark hickory	280	209	182	7.0	6.7	6.7	36	36	37	0.32	0.29	0.28
<i>Ulmus rubra</i>	Slippery elm	240	208	188	3.0	3.2	3.2	16	19	19	0.20	0.21	0.20
<i>Juglans nigra</i>	Black walnut	47	42	41	3.9	3.6	3.9	23	21	23	0.11	0.11	0.12
<i>Celtis occidentalis</i>	Hackberry	110	111	124	1.6	1.9	2.2	6	8	9	0.10	0.12	0.13
<i>Quercus muehlenburgii</i>	Chinquapin oak	91	80	73	2.2	2.0	2.1	13	12	13	0.10	0.10	0.10
<i>Quercus rubra</i>	Northern red oak	31	31	31	1.7	2.0	2.1	12	15	17	0.06	0.07	0.07
<i>Tilia americana</i>	Basswood	68	68	64	0.4	0.4	0.5	1	1	2	0.05	0.05	0.06
<i>Morus rubra</i>	Mulberry	35	24	15	0.3	0.2	0.2	1	1	0	0.03	0.02	0.01
<i>Cercis canadensis</i>	Redbud	24	17	26	0.2	0.2	0.2	1	0	1	0.02	0.01	0.02
<i>Gymnocladus dioica</i>	Coffeetree	14	13	11	0.4	0.4	0.5	1	2	2	0.01	0.01	0.01
<i>Gledisia triacanthos</i>	Honey locust	1	0	0	0	0	0	0	0	0	0	0	0
Other <sup>1</sup>		3	6	3	0	0	0	0	0	0	0	0	0
	Total	943	803	757	20.6	20.8	21.6	110	116	123			

<sup>1</sup>Includes the following infrequent species: osage orange (*Maclura pomifera* Raf.), sycamore (*Platanus occidentalis* L.), red ash (*Fraxinus pennsylvanica* Marsh.), and dogwood (*Cornus florida* L.)