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Tree seedling survivorship, growth, and allocation in the Cross Timbers ecotone of Oklahoma, USA

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Abstract In order to better understand tree dynamics and maintenance of the ecotone between eastern deciduous forest and tallgrass prairie, I planted seedlings of five different species into a Cross Timbers area in North West Oklahoma for one-year. The seedlings were planted in four different patch-types under two different herbivore treatments. I found that (1) out of the original 200 seedlings, 58 survived after one-year with lacebark elm (*Ulmus parrifolia*), osage orange (*Maclura pomifera*), and eastern redbud (*Cercis canadensis*) surviving the most and protection from herbivores increasing survivorship by more than an order of magnitude, (2) elm (*Ulmus parrifolia*) showed the slowest stem growth but protection from herbivory increased stem growth rate by approximately 50%, leaf area ratio was largest for elm (*Ulmus parrifolia*) but seedlings growing in sumac (*Rhus copallina*) patches had the smallest values, specific leaf area was the largest for orange (*Maclura pomifera*) seedlings with tree seedlings growing in grass patches showing greater values than those grown in other patches, and (3) leaf mass ratio was largest for elm (*Ulmus parrifolia*) with seedlings grown in sumac (*Rhus copallina*) patches showing the smallest values and rough-leaf dogwood (*Cornus drummondii*) had the most root biomass relative to shoot biomass compared to all other species. Results suggest tree invasion and establishment across this ecotone is influenced both by species identity and by the variation in resources associated with the distribution and patch dynamics of vegetation from both eastern deciduous forest and tallgrass prairie.

Keywords Tallgrass prairie · Eastern deciduous forest

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Introduction

Terrestrial vegetation can be organized into large-scale biomes (Walter 1973) which meet in dynamic border regions called ecotones (Gosz 1993). Ecotones are defined by their mix of plant species and are very sensitive to changes in environmental conditions often associated with natural (e.g. lightning fires) and human-induced (e.g. agriculture: Myster (1993, 2007)) disturbances. Of particular importance for the human future, alterations in ecotone borders can be a early indicator of climate change (Emanuel et al. 1985; Kupfer and Cairns 1996).

Whereas many ecotones involve transitions between woody and non-woody vegetation (Hoffmann et al. 2004; Malanson et al. 2001; Schwartz et al. 1996; Studer-Ehrensberger et al. 1993), in the

United States a large and important ecotone connects the eastern deciduous forest and the tallgrass prairie of the southern Great Plains (Johnson and Riser 1975). Referred to as the Cross Timbers (Kroh and Nisbet 1983; Collins and Klahr 1991; Engle et al. 1991), this ecotone may have once covered nearly 8,000,000 ha (Duck and Flecher 1945; Kuchler 1964). The Cross Timbers is defined as a patchwork of plant species found on both sides of the ecotone including oak-dominated forests, the exotic tree red cedar whose invasion may have long-ranging ecological consequences (Briggs et al. 2002), asexual shrubs that may facilitating tree invasion (as seen in old fields of the eastern US: Myster 1993), and various tall grasses.

Here, I continue a past field experiment of this ecotone—that found shumard oak seedlings survived and grew twice as much when protected from below-ground competition from grasses and leaf chlorophyll content increased two-fold when, in addition, water as added or the seedling was planted under a shrub (Myster in press)—by including in this new study several more common tree species, a herbivory treatment, and new patch-types to better reflect the natural ecotone dynamics. The design of this new study has also been motivated by other past forest/grassland ecotone study that has shown that the survival, growth, and allocation of its tree seedlings are influenced by species, patch-type, herbivory, and competition for water (Davis et al. 1999; Petranka and McPherson 1979; Hoffmann et al. 2004). Consequently I performed field experiments on the seedlings of five common trees in the Oklahoma Cross Timbers and tested the main effects of species, patch-type, and herbivory—and all their interactive effects—on their survivorship, growth, and allocation after one-year in the field.

Study site and methods

The study site was a Cross Timbers ecotone area near Lake Carl Blackwell, located approximately 15 km west of Stillwater Oklahoma USA (36′ 47″ N, 96′ 25″ W: Petranka and McPherson 1979). Lake Carl Blackwell is in the Central Redbed Plains composed mainly of red sandstones and shales (Johnson et al. 1972). Across this ecotone, temperature has a yearly range between 38°C and −18°C, precipitation is approximately 82 cm a year (Myers 1976; Hoagland et al. 1999), and soils have low fertility (Therrell and Stahle 1998). Oaks dominate forested areas, especially blackjack oak (*Quercus marilandica*) and post oak (*Q. stellata*), but Shumard oak (*Q. shumardii*), bur oak (*Q. macrocarpa*), and chinquapin oak (*Q. muhlenbergii*) are also common (Petranka and McPherson 1979; Hoagland et al. 1999). Sumac (*Rhus copallina*) clumps form between forest and tallgrass prairie as well as red cedar (*Juniperius virginiana*) patches and grasses such as indiangrass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*) and big bluestem (*Andropogon gerardii*: Hoagland et al. 1999).

In June 2004, five replicates of four common patch-types dominating the ecotone landscape—grass, red cedar, oak forest, sumac shrub—were selected in the study area. In July 2004, 40 rough-leaf dogwood (*Cornus drummondii*), 40 lacebark elm (*Ulmus parrifolia*), 40 Osage orange (*Maclura pomifera*), 40 eastern redbud (*Cercis canadensis*), and 40 shumard oak (*Q. shumardii*), seedlings were planted in these patches 1 m apart in a grid with half of them covered by a plastic cage (Forestry suppliers inc., Jackson, Mississippi) to prevent herbivory and half of them left uncovered as a control (same design as in Myster and McCarthy 1989), for a total of 200 seedlings (i.e., five replicates × five species × four patch-types × two herbivory treatments). Each of these tree species is found naturally in these areas (D. Engle, pers. comm.) and were purchased from the State of Oklahoma, Department of Agriculture, food & Forestry, Forestry Services Division. Red Cedar, Blackjack oak, and Post oak seedlings were not used either because Oklahoma state law prohibits their use or because they were unavailable. All seedlings were approximately 20 cm tall at planting.

After one-year in the field, surviving seedlings were measured for final height and then gently harvested. In the laboratory, each seedling was first measured for total leaf area using a LI-3100C leaf area meter (LI-COR, Inc. Lincoln NE). Second, seedlings were dried at room temperature for a month in paper bags before being weighted for total leaf biomass, total stem biomass, and total root biomass. Third, using these measurements relative growth rate (RGR = (ln[final height] − ln[initial height of 20 cm])/1 year), leaf area ratio (LAR = total leaf area/total biomass which is a better predictor of relative growth rate than A_{max}:

Poorter et al. 1990; Kitajima 1994), specific leaf mass (SLM = total leaf biomass/total leaf area), leaf mass ratio (LMR = total leaf biomass/total biomass), and root-to-shoot ratio (ROOT/SHOOT = root biomass/(stem biomass + leaf biomass)) were computed. And fourth, a 3-way analysis of variance (ANOVA: SAS 1985) was performed on (1) percent survivorship, (2) the growth parameters of RGR, LAR, and SLM, and (3) the allocation parameters of LMR and ROOT/SHOOT using the main effects of species, patch-type, and herbivory, with all their interactive effects. Before performing the analysis, data were graphed and found to be normally distributed.

Results

Out of the original 200 seedlings planted, 58 survived after one-year in the field. Species differed significantly in their survival, and it also made a significant difference if seedlings were protected from herbivores (Table 1). In addition, there was a significant species–patch-type interaction (Table 1). Species that survived the best were lacebark elm, osage orange, and eastern redbud (Fig. 1a) and protection from herbivores increased survivorship by more than an order of magnitude (Fig. 1b). The species–patch-type interaction showed that the best survival patches differed by species where elm did best in oak patches, orange did best in cedar patches, and redbud did best in sumac patches (Fig. 1c).

Relative growth rate (RGR) of those seedlings that survived was also significantly different by species

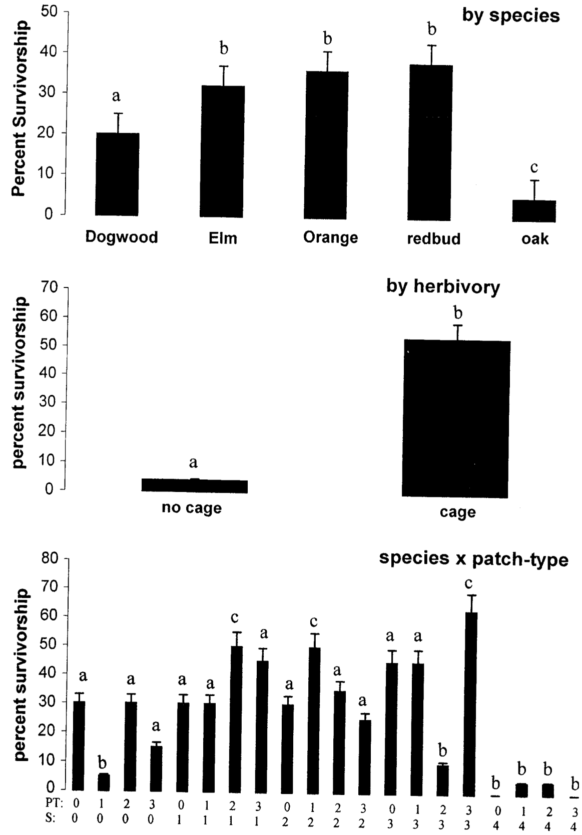

Fig. 1 Percent survivorship of seedlings after one-year in the field by species, by herbivory, and with a species–patch-type interaction where labeling preserves the species order—(0) rough-leaf dogwood, (1) lacebark elm, (2) osage orange, (3) eastern redbud, (4) shumard oak—and the patch-type order (0) grass, (1) red cedar, (2) oak, and (3) sumac. Means testing results are shown by the small letters above the standard error bars. Different letters means that those groups were significantly different

Table 1 ANOVA results summarized as F values

	Survivorship	RGR	LAR	LMR	SLM	Root/Shoot
Species(S)	5.45**	6.21**	9.83***	2.63*	926.12***	10.3**
Patch-type (P)	1.21	1.61	5.06**	4.47**	3.86*	0.05
Herbivory (H)	25.75***	5.11*	0.21	0.24	1.50	0.06
S × P	17.35**	1.68	2.70*	2.59*	1.64	1.19
P × H	0.86	2.13	1.55	1.15	0.16	0.26
S × H	-	-	-	-	-	-
S × P × H	-	-	-	-	-	-

Replication was insufficient for the investigation of some interaction effects

RGR Relative growth rate; *LAR* Leaf area ratio; *LMR* Leaf mass ratio; *SLM* Specific leaf mass; *ROOT/SHOOT* Root to shoot ratio

Where * means 0.05 > p > 0.01, ** means 0.01 > p > 0.001, and *** means 0.001 > p and by herbivory (Table 1). The species that showed the slowest growth was elm and protection from herbivory increased growth rate by about 50% (Fig. 2). Leaf area ratio (LAR) was significantly affected by species and by patch-type, with a significant species × patch-type interaction effect (Table 1). The largest value for LAR was seen for elm (Fig. 3a), but seedlings growing under sumac showed the smallest values (Fig. 3b). Interactive effects showed individualistic responses where different species had their smallest LAR under specific patches: dogwood in grass, elm in cedar, osage orange had high LAR everywhere, redbud in oak, and oak in grass and sumac (Fig. 3c). As with LAR, leaf mass ratio (LMR) was significant also among species, among patch-types and showed a significant species × patch-type interaction (Table 1). In particular, elm had the largest LMR, seedlings grown under sumac had the smallest LMR, and interactive effects again showed very individualistic responses so that different species had their smallest LMR under in these specific patches: dogwood in cedar, elm in cedar, orange had no clear trend, redbud in oak, and oak in grass and sumac (Fig. 4a, b, c). Finally, specific leaf area (SLM) was significantly different among species and among patch-type (Table 1). Osage orange had the most SLM and seedlings growing under grass were

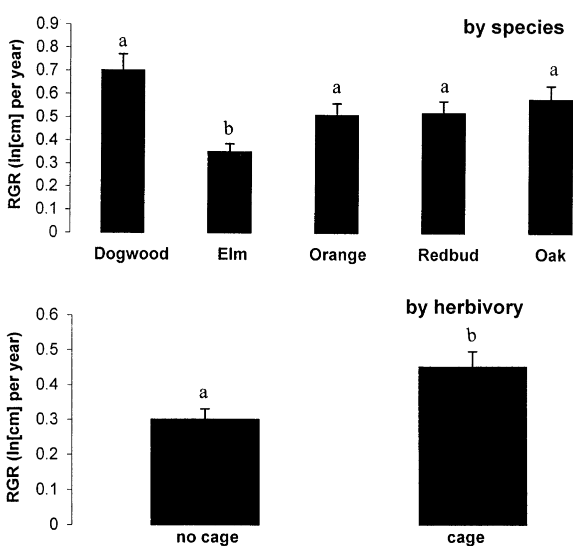

Fig. 2 Relative growth rate of surviving seedlings over a one-year period in the field by species, and by herbivory. Means testing results are shown by the small letters above the standard error bars. Different letters means that those groups were significantly different

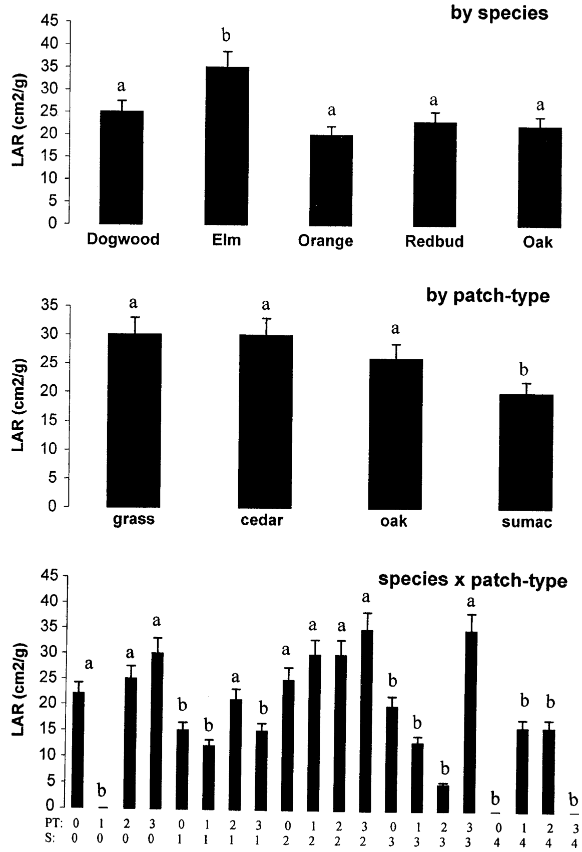

Fig. 3 Leaf area ratio of surviving seedlings after one-year in the field by species, by patch-type, and with a species–patch-type interaction where labeling is as in Fig. 1. Means testing results are shown by the small letters above the standard error bars. Different letters means that those groups were significantly different

greater than those grown in other patches (Fig. 5a, b). Root- to-shoot ratio (ROOT/SHOOT) was significant only among species (Table 1) where dogwood had the most root relative to shoot (Fig. 5c).

Discussion

There were individualistic survivorship responses among species and for the patches in which they grew most. Herbivores claimed most seedlings but without any clear tree species preferences. Herbivory at this site may have been by deer and rabbits, which claimed over 90% of *Carya tomentosa* seedlings in a similar study (Myster and McCarthy 1989). Those species that survived best were different from those with the greatest RGR. However, elm and orange

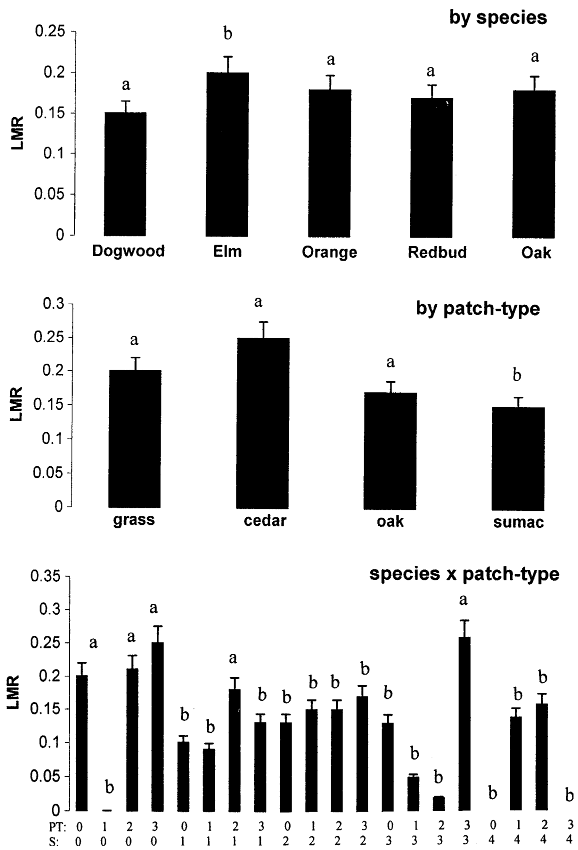

Fig. 4 Leaf mass ratio of surviving seedlings after one-year in the field by species, by patch-type, and with a species–patch-type interaction where labeling is as in Fig. 1. Means testing results are shown by the small letters above the standard error bars. Different letters means that those groups were significantly different

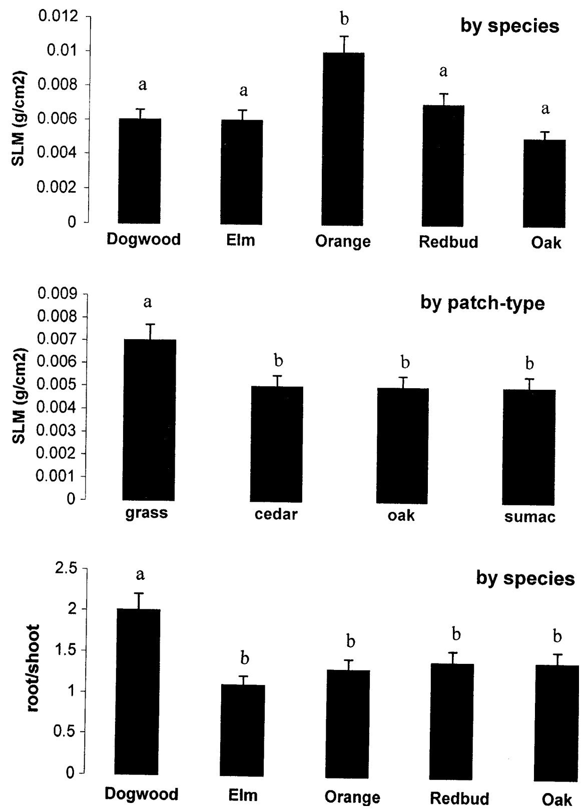

Fig. 5 Specific leaf mass of surviving seedlings after one-year in the field by species, and by patch-type. Root-to-shoot ratio of surviving seedlings after one-year in the field by species. Means testing results are shown by the small letters above the standard error bars. Different letters means that those groups were significantly different

grew the most as estimated by LAR and SLM. Sumac patches reduced tree growth most, but interaction effects were again very individualistic to species.

The large number of significant species effects suggests a species focus is warranted in this ecotone. Dogwood results were consistent in showing high survivorship in grass patches which did not inhibit spread of *Cornus racemosa* in another study (Boeken and Canham 1995) and in oak patches where *Cornus sericea* was common under low light environments elsewhere (Russell et al. 2003). For elm, results showing the highest LAR and LMR levels for any species agree with studies reviewed in Bazzaz (1979) showing *Ulmus alata* seedlings having greater photosynthesis levels than other tree species including oaks in successional environments. Oak results showed its highest survivorship in the shade of oak and red cedar and other studies have shown more oak growth in shade conditions compared to other species (McCarthy and Dawson 1990; Davis et al. 1999). In a past study at this same site, I found that shumard oak (1) seedlings in pots survived twice as much as those without pots and seedlings in unburned areas survived up to four times as much as those in burned areas, (2) seedlings in pots grew twice as fast as those planted in the soil without a pot, and (3) whereas adding water, planting in a pot, and planting under shrubs all increased leaf chlorophyll content, it was when the watered or under a shrub seedling was also in a pot that chlorophyll increases were two-fold (Myster, in press).

Results also mesh well with these more specific mechanism studies. For below-ground competition effects, as seen in the significant grass patch effects, it has been shown that grass removal can double oak establishment (Adams et al. 1992) perhaps because grasses pre-empt rainfall before it can reach the deeper tree roots. Grasses can also resist drought better than trees (Axelrod 1985) due to their higher water use efficiencies and may create negative feedbacks on soil moisture by manipulating microbe activity (Wilson 1998). Shrubs such as sumac can facilitate tree invasion (Wilson 1998) by reducing herbaceous cover and vigor (Petranka and McPherson 1979) where the exact mechanisms may include shading and increasing soil moisture, soil nutrients such as nitrogen, and relative humidity but also lowering both air and soil temperatures (Lett and Knapp 2003). In addition, some shrubs like sumac may have toxin chemicals in their leaves, rhizomes and fruit which could inhibit germination and seedling growth (Petranka and McPherson 1979) as well as reduce arbuscular mycorrhizae availability to grasses (Benjamin et al. 1989). Effects of *Rhus* spp. facilitating tree establishment has been shown in old fields elsewhere, where the exact mechanisms may include reducing herb competition and increasing bird seed dispersal (see Myster 1993 for a discussion).

In conclusion, results show recurrent significant species differences with no universal patch-type where the seedlings of all species grew well. There may have been a trade-off between survival and relative growth rate but two species—elm and osage orange—grew the most as measured by the other growth parameters. Such complexity of results suggests a tree dynamic in these ecotone areas influenced by the small-scale variation in resources found among the patches across this landscape connecting forest and prairie.

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