

## PHYSIOLOGICAL AND MORPHOLOGICAL TRAITS OF EXOTIC, INVASIVE EXOTIC, AND NATIVE PLANT SPECIES IN TALLGRASS PRAIRIE

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We compared 13 traits of invasive exotic, noninvasive exotic, and ecologically similar native species to determine if there are generalizable differences among these groups that relate to persistence and spread of exotic species in tallgrass prairie plant communities. When species were grouped as invasive (two species), noninvasive (five species), and native (six species), no differences were found for the suite of traits examined, likely because of the high variability within and between groups. However, when exotic species, regardless of invasiveness, were compared with the native species, specific leaf area was ca. 40% higher for the exotic species, a result that is consistent with that of other studies. This pattern was also observed for five of seven pairwise comparisons of exotic and native species with similar life history traits. In contrast, total end-of-season biomass was as much as three times higher for the native species in five of seven of the native-exotic species pairs. For other traits, differences between exotic and native species were species-specific and were generally more numerous for noninvasive than for invasive exotic species pair-wise comparisons. Thus, contrary to predictions, exotic species capable of successfully invading tallgrass prairie did not differ considerably from native species in most traits related to resource utilization and carbon gain. Moreover, invasive exotic species, those capable of displacing native species and dominating a community, were not distinct for the observed traits from their native counterparts. These results indicate that other traits, such as the ability to respond to resource pulses or herbivory, may explain more effectively why certain invasive species are able to invade these communities aggressively.

**Keywords:** biomass allocation, grassland, invasive plants, photosynthesis, specific leaf area.

### Introduction

Invasions by exotic plant species are occurring at unprecedented rates as a result of human activities that have increased the number of introductions and the rate of spread of many species (Lodge 1993; Chapin et al. 2000). These invasions have serious consequences for native biodiversity (Heywood 1989), disturbance regimes (D'Antonio and Vitousek 1992), and ecosystem structure and functioning (Vitousek et al. 1997a, 1997b; Chapin et al. 2000), and therefore, these invasions are considered a significant component of global change (Vitousek et al. 1997a, 1997b). Thus, identifying the factors that influence invasions by exotic plant species is of critical importance.

Plant invasions are limited primarily by dispersal of propagules or by the number of propagules entering a community (Lonsdale 1999). In the absence of dispersal limitations, the ability of exotic species to successfully invade, that is, to persist and spread in a community (Hobbs 1989), may be influenced in part by the susceptibility of a community to invasion (i.e., invasibility; Lonsdale 1999). Several hypotheses have been proposed to explain why some plant communities are more prone to invasion (Levine and D'Antonio 1999; Lonsdale 1999; Davis et al. 2000). For example, Davis and coworkers (2000) proposed that certain plant communities might be more susceptible to invasion because there is an increase in unused

resources. Other studies indicate that disturbance may be a prerequisite for invasion (Crawley 1987; Hobbs and Huenneke 1992; Burke and Grime 1996) or that other characteristics of communities, such as dominance, productivity, or diversity, may influence susceptibility to invasion (Huston 1994; Robinson et al. 1995; Burke and Grime 1996; Lonsdale 1999; Smith and Knapp 1999; Stohlgren et al. 1999). Generalizations regarding community characteristics that influence invasion have been unsuccessful, however, because invasion success depends not only on invasibility of plant community but also on the traits of the invading species (Lonsdale 1999; Davis et al. 2000).

Investigators have sought to identify traits that allow for successful invasion by comparing suites of traits between exotic and native species. Comparisons ranging from those of entire floras (e.g., Noble 1989; Thompson et al. 1995; Crawley et al. 1996; Rejmanek 1996, 1999; Williamson and Fitter 1996a) to those within or between genera (e.g., Caldwell et al. 1981; Schierenbeck et al. 1994; Williams and Black 1994; Rejmanek and Richardson 1996; Baruch and Bilbao 1999; Radford and Cousens 2000) indicate that no single trait or group of traits can completely explain the success of exotic species in new environments. Instead, differences in traits such as reproductive and dispersal capabilities, seedling establishment and survivorship, genome size, phenotypic plasticity, growth-related characteristics, plant height, susceptibility to herbivory and pathogens, phenology, mutualistic interactions, allelopathy, and plant-soil relationships may all contribute to the success

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of exotic species (Pattison et al. 1998; Rejmanek 2000; Ridenour and Callaway 2001). Moreover, these differences often are species-specific or dependent on factors other than the species themselves (e.g., habitat characteristics; Thompson et al. 1995; Rejmanek 1996; Radford and Cousens 2000), thereby making generalizations difficult. Most of these comparative studies have focused only on invasive exotic species, those that are spreading rapidly and capable of displacing native species and dominating a plant community (Davis and Thompson 2000). Yet there are numerous exotic species capable of establishing and persisting while not outcompeting native species (Rejmanek 2000). Indeed, the majority (ca. 90%) of successful exotic species are noninvasive (Williamson and Brown 1986; Williamson and Fitter 1996b). Although comparisons between invasive exotic and native species have obvious value, contrasting suites of traits among sympatric noninvasive exotic, invasive exotic, and congeneric or ecologically similar (i.e., similar growth form and life history) native plant species may provide additional insight into those traits that not only allow for successful invasion but that also enable some exotic species to spread rapidly and dominate a community (Newsome and Noble 1986; Mack 1996; Radford and Cousens 2000). Identification of these traits could provide needed predictive capabilities as new species are introduced to communities as well as allow for better management of invasive species once they are established.

The objectives of this study were to identify traits of successful exotic plant species by comparing them to native species with similar growth form and life history strategies and to determine if these traits differ consistently between invasive and noninvasive species. Although many different traits may determine the success of exotic species, we examined a subset of leaf-level and whole-plant traits related to growth and car-

bon gain, including morphological traits related to biomass allocation and growth, maximum photosynthetic rates, and dark respiration (Pattison et al. 1998). Differences in these traits appear to be related to success of invasive plant species found in forest and grassland communities (e.g., Harrington et al. 1989a, 1989b; Baruch 1996; Pattison et al. 1998; Baruch and Goldstein 1999). Specifically, we compared 13 morphological and physiological traits of invasive and noninvasive plant species to those of ecologically similar or congeneric native species found in a mesic tallgrass prairie community. Invasive exotic species are predicted to have traits that favor efficient use of resources, when, for example, life history traits or susceptibility to herbivory are similar between the native and invasive species (Vitousek 1986). Thus, we expected that traits, such as biomass allocation to leaves, specific leaf area, and maximum photosynthetic rates, which are indicative of efficient use of resources (Pattison et al. 1998), would be greater for invasive when compared to native species. In contrast, we expected that growth-related traits of noninvasive exotic species would be similar to those of the native species because these species are capable of persisting in tallgrass prairie but are not capable of outcompeting native species (Goldberg 1987).

## Material and Methods

### Study Site

This study was conducted on the Konza Prairie Biological Station, a 3487-ha tallgrass prairie preserve located in the Flint Hills region of eastern Kansas. This region is characterized by steep topographic gradients, a fact that has prevented conversion of this region to agricultural land. Konza Prairie expe-

**Table 1**  
**Mean ( $\pm 1$  SE) of Morphological and Physiological Traits of 13 Native Tallgrass Species, Noninvasive Exotic Species, and Invasive Species at the Konza Prairie Biological Station (Kansas)**

Plant traits	Native species ( <i>n</i> = 6)	Exotic species	
		Noninvasive ( <i>n</i> = 5)	Invasive ( <i>n</i> = 2)
Morphological:			
Total biomass (g)	7.46 (2.92)	4.11 (3.20)	3.35 (5.07)
Biomass allocation (g g <sup>-1</sup> ):			
Leaf	0.35 (0.06)	0.31 (0.06)	0.35 (0.09)
Stem	0.50 (0.06)	0.54 (0.06)	0.64 (0.10)
Reproductive tissue	0.15 (0.02)	0.14 (0.02)	...
TLN (per plant)	91.3 (45.2)	53.2 (20.2)	149.3 (144.0)
TLA (cm <sup>2</sup> )	313.1 (148.1)	209.6 (162.3)	68.6 (256.6)
SLA (cm <sup>2</sup> g <sup>-1</sup> )	115.1 (27.0)	195.1 (29.6)	181.5 (46.8)
LAR (cm <sup>2</sup> g <sup>-1</sup> )	37.1 (8.9)	49.8 (9.8)	47.2 (15.5)
Physiological:			
<i>A</i> <sub>max</sub> (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	21.3 (4.0)	22.4 (4.4)	19.0 (6.9)
LSPT (μmol m <sup>-2</sup> s <sup>-1</sup> )	970.2 (114.6)	1049.2 (125.6)	906.8 (198.5)
AQY (mol CO <sub>2</sub> mol photons <sup>-1</sup> )	0.047 (0.003)	0.048 (0.004)	0.045 (0.006)
LCPT (μmol m <sup>-2</sup> s <sup>-1</sup> )	27.8 (3.46)	25.0 (3.79)	18.4 (6.00)
<i>R</i> <sub>d</sub> (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	-1.89 (0.22)	-1.78 (0.24)	-1.47 (0.38)

Note. TLN = total number of leaves, TLA = total leaf area, SLA = specific leaf area, LAR = leaf area ratio, *A*<sub>max</sub> = maximum photosynthetic rates, LSPT = light saturation points, AQY = apparent quantum yield, LCPT = light compensation points, and *R*<sub>d</sub> = dark respiration.

**Table 2**  
**Morphological Traits of Native (N) and Exotic (E) Species Pairs Comprising Four Functional Groups in Tallgrass Prairie (Kansas)**

Functional group/ species pair	Total biomass	Leaf	Stem	Reproduction	TLN	TLA	LAR
<b>C<sub>3</sub> biennial forbs:</b>							
<i>Lactuca ludoviciana</i> (N)	26.85 (4.07)*	0.35 (0.01)	0.54 (0.01)	0.11 (0.01)	44.0 (6.1)	1278.8 (204.9)*	49.0 (3.7)
<i>Lactuca serriola</i> (E)	7.59 (2.00)	0.29 (0.03)	0.64 (0.03)*	0.07 (0.02)	86.6 (2.0)	485.2 (83.8)	79.0 (13.3)
<i>Lactuca ludoviciana</i> (N)	26.85 (4.07)*	0.35 (0.01)	0.54 (0.01)	0.11 (0.01)	44.0 (6.1)	1278.8 (204.9)*	49.0 (3.7)
<i>Tragopogon dubius</i> (E)	7.67 (1.12)	0.30 (0.03)	0.53 (0.02)	0.17 (0.03)	58.3 (8.0)	367.3 (52.0)	48.3 (2.7)
<b>Legumes:</b>							
<i>Psoralea tenuiflora</i> (N)	5.19 (0.71)*	0.43 (0.01)*	0.46 (0.01)	0.11 (0.01)	142.3 (18.1)	249.3 (47.0)*	45.7 (3.0)
<i>Melilotus officinalis</i> (E)	2.78 (1.25)	0.24 (0.02)	0.56 (0.02)*	0.20 (0.02)*	106.2 (14.2)	117.4 (15.5)	45.4 (3.4)
<i>Lespedeza capitata</i> (N)	2.90 (0.42)	0.35 (0.02)	0.46 (0.01)	0.19 (0.02)	50.4 (6.7)	104.0 (15.4)	36.7 (4.3)
<i>Lespedeza cuneata</i> (E)	4.71 (3.74)	0.45 (0.04)*	0.55 (0.04)	...	293.3 (56.7)*	110.6 (14.7)	80.1 (37.1)
<b>C<sub>3</sub> grasses:</b>							
<i>Koeleria pyramidata</i> (N)	2.07 (0.75)*	0.56 (0.07)	0.25 (0.04)	0.19 (0.03)	54.3 (24.7)	129.1 (54.2)	55.5 (5.9)
<i>Poa pratensis</i> (E)	0.40 (0.04)	0.53 (0.05)	0.34 (0.03)	0.13 (0.02)	10.4 (1.5)	19.7 (3.6)	47.8 (4.5)
<i>Elymus canadensis</i> (N)	1.68 (0.24)	0.18 (0.02)	0.61 (0.02)	0.21 (0.01)*	4.9 (0.2)*	35.1 (4.9)	21.4 (1.4)
<i>Bromus inermis</i> (E)	2.11 (0.23)	0.21 (0.01)	0.64 (0.01)	0.15 (0.01)	4.3 (0.2)	58.3 (4.6)*	28.5 (1.0)*
<b>C<sub>4</sub> grasses:</b>							
<i>Andropogon gerardii</i> (N)	6.08 (0.52)*	0.21 (0.02)	0.69 (0.01)	0.10 (0.01)*	9.2 (0.6)*	82.2 (12.6)*	14.6 (2.4)
<i>Andropogon bladhii</i> (E)	1.99 (0.25)	0.24 (0.01)	0.73 (0.01)	0.03 (0.003)	5.3 (0.5)	26.5 (2.8)	14.3 (1.9)

Note. Values in the leaf, stem, and reproduction columns are biomass allocation ratios. TLN = total leaf number, TLA = total leaf area, and LAR = leaf area ratio. Refer to table 1 for units and a description of the morphological traits measured. Each value represents the mean ( $\pm 1$  SE) of nine to 11 plants (for *L. cuneata*, leaf and reproductive biomass were not separated;  $n = 3$  for TLN, TLA, and LAR). Asterisks indicate statistically significant differences ( $P < 0.05$ ) between native and exotic species for a particular species pair. Nomenclature follows Great Plains Flora Association (1986).

riences a midcontinental climate. Average annual precipitation is 835 mm, with 75% of precipitation falling during the growing season (April–September), and average monthly rainfall ranges from a minimum of 20 mm in January to 136 mm in June. Monthly average temperatures range from a January low of  $-3^{\circ}\text{C}$  to a July high of  $27^{\circ}\text{C}$ , with a yearly mean temperature of  $13^{\circ}\text{C}$ .

Grassland communities at Konza Prairie are representative of the tallgrass prairie biome and consist of >250 species of vascular plants (70% perennial; Freeman 1998). These sites are dominated by several warm-season (C<sub>4</sub>) grass species, including *Andropogon gerardii* Vitman and *Sorghastrum nutans* (L.) Nash and, to a lesser extent, *Panicum virgatum* L. and *Andropogon scoparius* Michx. Interspersed within the matrix of warm-season grasses are a number of subdominant warm- and cool-season (C<sub>3</sub>) grass, forb, and woody species (Freeman and Hulbert 1985). Exotic species comprise ca. 9% of the total flora of grassland sites on Konza Prairie (Smith and Knapp 1999). Native and exotic species included in this study were collected from several upland grassland sites, which had the same soil types (clayey-skeletal, montmorillonitic, mesic, and Udic Argiustolls).

### Study Species

A total of 13 sympatric, congeneric, or ecologically similar (i.e., similar growth form and life history strategies) native ( $n = 6$ ) and exotic ( $n = 7$ ) plant species representing three plant families (Asteraceae, Fabaceae, and Poaceae) and four functional groups (C<sub>3</sub> biennial forbs, legumes, C<sub>3</sub> grasses, and C<sub>4</sub> grasses) were selected for this study. Five of the seven exotic species, all native to Europe or Eurasia, were considered non-

invasive (*Lactuca serriola* L., *Tragopogon dubius* Scop., *Melilotus officinalis* L., *Poa pratensis* L., and *Bromus inermis* Leyss) because there has been no net increase in cover of these species over a 16-yr period (1983–1998) (Smith and Knapp 1999) or because their range was limited to a few scattered populations on Konza Prairie (M. D. Smith, personal observations). The other two exotic species, *Lespedeza cuneata* (Dumont) G. Don and *Andropogon bladhii* Retz., were considered invasive because, although not yet abundant on Konza Prairie, they are aggressively invading similar tallgrass prairie sites nearby. Native to Asia and Australia, *A. bladhii* was introduced from Russia in 1919 as an alternative forage crop to the southern and central Great Plains (Oklahoma, Kansas, and Texas). Because this aggressive C<sub>4</sub> grass is resistant to drought and grazing, is a prolific seed producer, and is less palatable than its native counterpart *A. gerardii* (Christiansen and Svejcar 1987; Svejcar and Christiansen 1987; M. Raskake, J. Henning, and D. Stipes, unpublished data), it is considered a serious threat to mesic grasslands in the Great Plains. Also native to Asia, *L. cuneata* was introduced in the 1930s to the Great Plains for erosion control, wildlife cover and food, and forage and hay (Great Plains Flora Association 1986). This C<sub>4</sub> perennial legume is resistant to drought, tolerant of low soil fertility, and produces residues containing phenolic compounds, which may have allelopathic properties (Langdale and Giddens 1967; Kalburtji and Mosjidis 1992). *Lespedeza cuneata* can dramatically reduce native diversity in tallgrass prairie (Eddy and Moore 1998) and is listed as a noxious weed in Kansas (Kansas Noxious Weed Law of 1998).

Exotic species were paired with six native species for a total of five noninvasive pairs (*L. serriola* and *Lactuca ludoviciana*

*L. dubius* and *L. ludoviciana*, *M. officinalis* and *Psoralea tenuiflora* Pursh., *P. pratensis* and *Koeleria pyramidata* [Lam.] Beauv., and *B. inermis* and *Elymus canadensis* L.) and two invasive pairs (*A. bladhii* and *A. gerardii*, *L. cuneata* and *Lespedeza capitata* Michx.). When congeneric native species were unavailable for comparison, ecologically similar native species were selected that had similar phenology, photosynthetic pathway, and growth form and habit. For example, *B. inermis* and *E. canadensis* are both  $C_3$  perennial, rhizomatous grasses that flower and set seed in late June. Note that *L. ludoviciana* comprised the native counterpart for two noninvasive species pairs because this species was most ecologically similar (i.e., both biennial,  $C_3$  forbs) to *T. dubius*.

### Morphological and Physiological Traits

For each species pair, individuals were randomly selected from adjacent populations from the same watershed that was burned annually ( $C_4$  grasses, *Lespedeza* spp.), burned every 4 yr ( $C_3$  grasses), or unburned ( $C_3$  biennial forbs, *Psoralea* and *Melilotus*). This ensured that both native and exotic species were sampled under similar management, soil type, and microclimatic conditions. Nine to 11 randomly selected individuals of each species were collected at peak flowering in 1999 (early to late June for *L. serriola*, *T. dubius*, and *L. ludoviciana*, *M. officinalis*, *P. tenuiflora*, *P. pratensis*, *K. pyramidata*, *B. inermis*, and *E. canadensis*; late July for *A. bladhii*; early to late September for *L. cuneata*, *L. capitata*, and *A. gerardii*). For *A. gerardii* and *A. bladhii*, a single individual was defined as a flowering stalk since growth habits differed considerably between the two species (*A. gerardii* is rhizomatous, whereas *A. bladhii* is caespitose). Plants were divided into stems, leaves or leaves plus petioles, and inflorescences (for *L. cuneata*, inflorescences were not separated from stems). Total leaf number (TLN) was counted, and the total leaf area (TLA) was estimated by measuring the area of all leaves or of a randomly selected sample of leaves (four to 60 per plant) with a Li-Cor LI-3100 leaf area meter (Li-Cor, Lincoln, Nebr.). All mass values (to the nearest 0.1 mg) were determined after drying at 70°C for 48 h. Leaf area ratio (LAR: total leaf area divided by total plant mass,  $\text{cm}^2 \text{g}^{-1}$ ) and biomass allocation (%) to stems, leaves, and reproductive tissues were determined as well. Finally, specific leaf area (SLA) of individual leaves (leaf area divided by leaf mass,  $\text{cm}^2 \text{g}^{-1}$ ) was determined for 15–50 representative leaves from randomly selected plants.

Photosynthetic traits were determined using a Li-Cor LI-6400 open-flow gas exchange system equipped with a light source (6400-02B, Li-Cor). Measurements were made on one representative leaf on five to six randomly selected individuals of each species in a pair over consecutive days in June 1999. After initial measurement at maximum PPFD (2000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ), PPFD was decreased in a stepwise fashion to 0  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ . At each successive PPFD level, responses to the new light level were measured at similar leaf temperature (28°C) and relative humidity (45%–55%) and only after photosynthesis stabilized (2–10 min). For each replicate of each species, the apparent quantum yield (AQY; i.e., slope) and the light compensation point (LCPT; i.e., X-axis intercept) were calculated from a linear regression equation using the initial points (0–200  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) of the response curve.

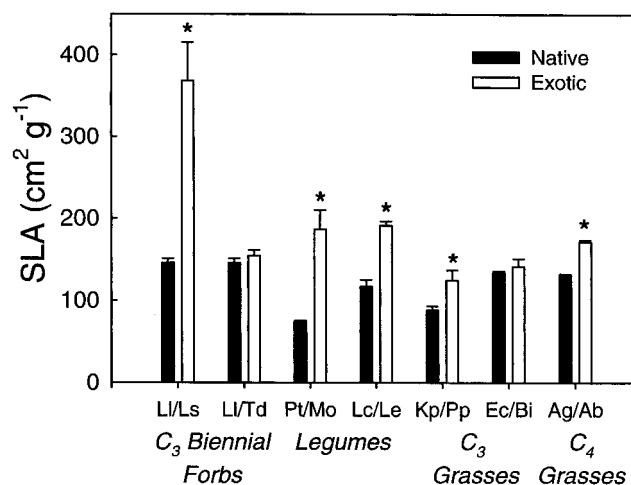
Entire light response curves were fitted (SPSS 2000) using an exponential equation (Horton and Neufield 1998):  $y = a + b(1 - e^{-k \times \text{PPFD}})$ , where  $y$  = observed photosynthetic rate,  $a$  = dark respiration ( $R_d$ ),  $b$  = maximum photosynthetic rate ( $A_{\text{max}}$ ), and  $k$  = AQY. Light saturation points (LSPT) were defined as the PPFD at which 90% of  $A_{\text{max}}$  was achieved.

### Statistical Analyses

Morphological (i.e., total biomass, biomass allocation, TLN, TLA, SLA, and LAR) and physiological (i.e.,  $A_{\text{max}}$ , LSPT, AQY, LCPT, and  $R_d$ ) traits were compared among native and invasive exotic or noninvasive exotic species groups using one-way analysis of variance, and differences in traits between native and both exotic species groups were determined using LSMEANS tests as a result of unequal sample sizes (Proc GLM; SAS Institute 1997). To determine whether exotic and native species as a group differed in these traits, average trait values for each species ( $n = 6$  native,  $n = 7$  exotic) were calculated and analyzed using a nonparametric Wilcoxon rank-sum test because of small and unequal sample sizes (Ott 1993). In addition, morphological and physiological traits were compared between pairs of exotic and native species using Student  $t$ -tests or Cochran's  $t$ -test for unequal variances. Significance levels for all tests were set at  $P < 0.05$ .

### Results

When grouped as invasive exotic, noninvasive exotic, and native species, the 13 herbaceous plant species included in this study did not differ in the suite of morphological and physiological traits examined (table 1). However, when the two



**Fig. 1** Specific leaf area (SLA) of 13 native and exotic species pairs representing four functional groups found at the Konza Prairie Biological Station (Kansas). Data are means of six plants per species per pair. Error bars indicate  $\pm 1$  SE of the mean. Native tallgrass prairie species (solid bars): LI = *Lactuca ludoviciana*, Pt = *Psoralea tenuiflora*, Lc = *Lespedeza capitata*, Kp = *Koeleria pyramidata*, Ec = *Elymus canadensis*, Ag = *Andropogon gerardii*. Exotic species (open bars): Ls = *Lactuca serriola*, Td = *Tragopogon dubius*, Mo = *Melilotus officinalis*, Le = *Lespedeza cuneata*, Pp = *Poa pratensis*, Bi = *Bromus inermis*, Ab = *Andropogon bladhii*.

Table 3

Physiological Traits of Native (N) and Exotic (E) Species Pairs Comprising Four Functional Groups in Tallgrass Prairie (Kansas)

Functional group/ species pair	$A_{\max}$	LSPT	AQY	LCPT	$R_d$
<b>C<sub>3</sub> biennial forbs:</b>					
<i>Lactuca ludoviciana</i> (N)	16.5 (0.9)	866.2 (215.4)	0.046 (0.004)	35.5 (3.3)*	-2.32 (0.16)
<i>Lactuca serriola</i> (E)	24.3 (1.1)*	1246.5 (39.4)	0.053 (0.002)*	30.2 (3.5)	-2.16 (0.19)
<i>Lactuca ludoviciana</i> (N)	16.5 (0.9)	866.2 (215.4)	0.046 (0.002)	35.5 (3.3)*	-2.32 (0.16)*
<i>Tragopogon dubius</i> (E)	25.7 (1.2)*	1086.9 (34.7)	0.053 (0.002)*	22.7 (3.9)	-1.67 (0.21)
<b>Legumes:</b>					
<i>Psoralea tenuiflora</i> (N)	42.6 (3.5)	1465.1 (20.0)	0.061 (0.004)	40.4 (4.35)	-2.97 (0.18)
<i>Melilotus officinalis</i> (E)	34.1 (2.1)	1397.0 (29.7)	0.054 (0.001)	33.1 (3.23)	-2.30 (0.16)
<i>Lespedeza capitata</i> (N)	16.7 (2.3)	980.8 (74.9)	0.041 (0.003)	33.2 (5.3)*	-1.82 (0.21)
<i>Lespedeza cuneata</i> (E)	15.8 (2.3)	943.3 (104.1)	0.039 (0.0003)	17.3 (0.8)	-1.26 (0.08)
<b>C<sub>3</sub> grasses:</b>					
<i>Koeleria pyramidata</i> (N)	12.0 (1.4)	598.5 (68.0)	0.038 (0.002)	21.6 (1.9)	-1.42 (0.07)
<i>Poa pratensis</i> (E)	9.3 (0.6)	601.2 (53.0)	0.031 (0.002)	23.8 (1.4)	-1.22 (0.07)
<i>Elymus canadensis</i> (N)	20.3 (1.1)	1028.7 (61.2)	0.049 (0.002)	13.5 (2.9)	-1.33 (0.19)
<i>Bromus inermis</i> (E)	18.5 (1.3)	914.2 (112.1)	0.050 (0.002)	14.9 (2.4)	-1.54 (0.16)
<b>C<sub>4</sub> grasses:</b>					
<i>Andropogon gerardii</i> (N)	19.9 (1.3)	881.6 (60.7)	0.046 (0.005)	22.7 (2.3)	-1.50 (0.19)
<i>Andropogon bladhii</i> (E)	22.4 (1.6)	870.4 (95.4)	0.051 (0.002)	19.5 (1.6)	-1.68 (0.11)

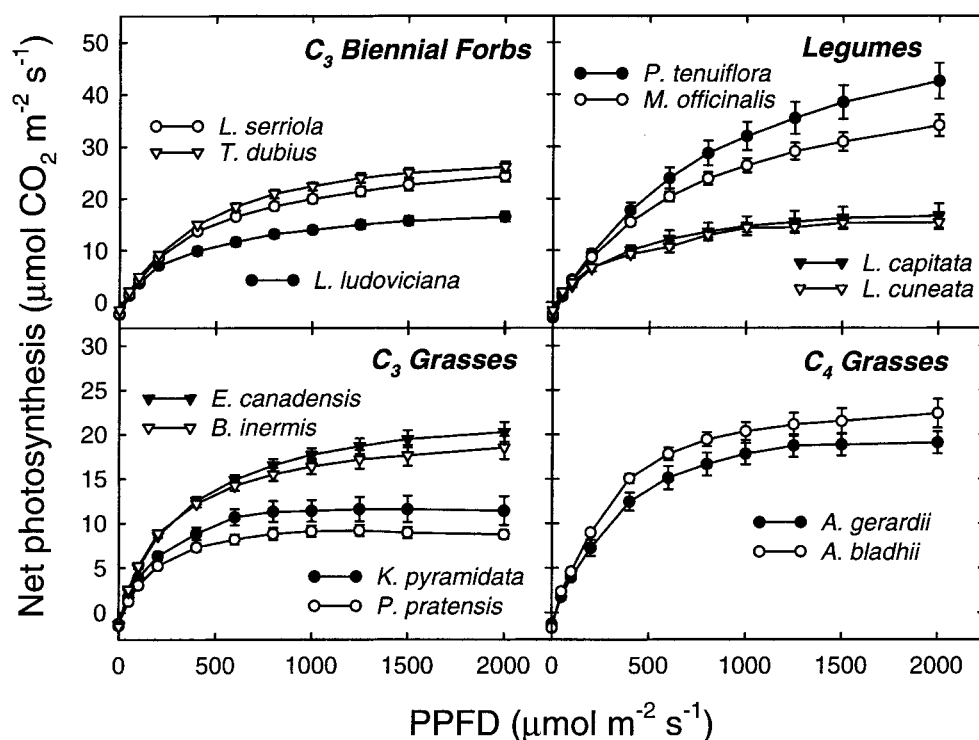
Note. Refer to table 1 for units and a description of the physiological traits measured. Each value represents the mean ( $\pm 1$  SE) of four to six plants. Asterisks indicate statistically significant differences ( $P < 0.05$ ) between native and exotic species for a particular species pair. Nomenclature follows Great Plains Flora Association (1986).

exotic species groups were combined, regardless of invasiveness, exotic species had on average SLA that was 30% higher than that of the native tallgrass species (Wilcoxon rank-sum test,  $P = 0.02$ ; table 1). The high variability among species within each group and the relatively small sample sizes (table 1) likely rendered detection of statistical differences between groups difficult. Thus, we evaluated ecologically equivalent species pairs (i.e., species with similar life forms that share the same habitats) for differences in the 13 traits. Overall, for five of the seven species pairs, total biomass was as much as three times higher for the native tallgrass species when compared to their exotic counterparts (table 2). A similar pattern, but in the opposite direction, was observed for SLA. This trait was 30%–150% higher for exotics in five of seven of the species pairs (fig. 1). Consistent differences across species pairs were not observed for the remaining physiological and morphological traits. Instead, if species pairs differed in a particular trait, these differences were variable with regard to exotic versus native species status (tables 2, 3). Although the number of differences in morphological traits between grass species pairs and forb species pairs was similar (nine vs. 11 significant differences), all significant differences in physiological traits were restricted to the two forb groups.

There were also no clear patterns of differences in morphological and physiological traits for the four functional groups of ecologically equivalent species pairs (table 2). For C<sub>3</sub> biennial forbs, four of eight morphological traits were significantly different between exotic and native species. Total biomass and TLA were greater for the native *Lactuca ludoviciana* when compared to either exotic C<sub>3</sub> biennial forb (table 2). Although biomass was lower, allocation of biomass to stems was 20% higher (table 2) and SLA was 60% higher (fig. 1) for the exotic *Lactuca serriola* than for *L. ludoviciana*. In contrast to the C<sub>3</sub> biennial forbs, exotic and native legume species

differed considerably in morphological traits, but again, these differences were variable and species-specific. Total biomass, biomass allocation to leaves, and TLA were greater for the native legume species *Psoralea tenuiflora*, whereas SLA and biomass allocation to stems and reproduction were higher for the exotic *Melilotus officinalis*. Biomass allocation to leaves was also greater for the exotic legume species *Lespedeza cuneata* when compared to its native congener, *Lespedeza capitata* Michx.; however, TLN rather than TLA was higher for this exotic legume. For the C<sub>3</sub> grass species pairs, total biomass was five times lower and SLA was 30% higher for the exotic *Poa pratensis* compared to the native *Koeleria pyramidata*. Differences in these traits were not detected for the other C<sub>3</sub> grass species pair. Instead, TLA and LAR were higher and TLN and biomass allocation to reproductive tissues were lower for the exotic *Bromus inermis* compared to its native counterpart. The C<sub>4</sub> grass species pair had the most consistent differences of all the species pairs examined. Although SLA was higher for the invasive exotic *Andropogon bladhii*, the native *Andropogon gerardii* had greater total biomass, allocation to reproduction, TLN, and TLA per individual.

In general, all species displayed typical responses to variations in PPFD, with net photosynthesis increasing with increasing PPFD until light saturation (fig. 2). Of the seven species pairs, only light responses of the exotic C<sub>3</sub> biennial forb species *L. serriola* and *Tragopogon dubius* diverged considerably from the ecologically equivalent native species *L. ludoviciana* (fig. 2). Specifically, average  $A_{\max}$  and AQY were 15%–60% higher and LCPTs and  $R_d$  were as much as 50% lower for the exotic biennial forb species (table 3). For the remainder of the species pairs, light response curves were similar between native and exotic species (fig. 2), and thus, eco-physiological traits were not significantly different, with exception of the invasive legume species, *L. cuneata*, which had



**Fig. 2** Photosynthetic response to light (photon flux density; *PPFD*) for six native tallgrass prairie species (filled symbols) and seven exotic species (open symbols) representing four functional groups found at the Konza Prairie Biological Station (Kansas). Different symbols indicate native and exotic species pairs. Note that the  $C_3$  biennial forb *Lactuca ludoviciana* comprises the native counterpart of two species pairs. Data are means ( $\pm 1$  SE) of four to six individuals.

on average 50% lower LCPTs than its native congener (table 3).

### Discussion

We found few consistent differences in the 13 growth-related traits among the exotic, invasive exotic, and native tallgrass prairie species. When the seven exotic species were examined as a group, regardless of invasiveness, SLA was consistently higher for the exotic species, as observed in other studies (Jones and McLeod 1990; Baruch and Goldstein 1999; but see Kraaij and Kramer 1999). SLA is important in the regulation and control of plant functions such as carbon assimilation and allocation and is related to higher relative growth rates (Lambers and Poorter 1992; Reich et al. 1997). Therefore, this trait may be important in determining success of these exotic species in different tallgrass prairie environments. However, given that peak biomass was higher for most of the native species, which is indicative of greater competitive ability (Gaudet and Keddy 1988), and given that physiological traits related to carbon gain did not differ between exotic and native species as a group, it is unlikely that higher SLA alone explains why these exotic species are able to compete effectively against native tallgrass prairie species.

Invasive exotic species were predicted to differ in traits related to more efficient use of resources (Pattison et al. 1998). However, invasive species as a group did not differ from native species in most of the growth-related traits examined. When

invasive-native species pairs were examined, invasive species had on average higher biomass allocation to leaves and higher total leaf number and species leaf area, whereas native species had higher peak biomass, but physiological differences were inconsistent. Thus, strong evidence for invasive species differing considerably from natives in resource-use efficiency and carbon gain was lacking. Moreover, when trait differences were detected, these were less numerous than for noninvasive species pairs, which indicates that invasive species were more like native species than they were like noninvasive species. These results contrast with those of other studies that have found considerably higher biomass production, growth rates, leaf characteristics (LAR, SLA), and photosynthesis in exotic species invading different savanna and forest habitats (Baruch et al. 1985; Jones and McLeod 1990; Williams and Black 1994; Pattison et al. 1998; Baruch and Bilbao 1999; Baruch and Goldstein 1999).

In this study, generalizable differences between invasive, non-invasive, and native species may not have been detected because of the high variability between species within each group. Therefore, it is not surprising that differences in traits related to resource use and carbon gain were observed only when ecologically equivalent native and exotic species were compared individually. For example, greater biomass allocation to stems and SLA and higher  $A_{\max}$  and AQY for the exotic  $C_3$  biennial forbs, *Tragopogon dubius* and *Lactuca serriola*, as well as lower LCPTs and  $R_d$  for *T. dubius*, may allow these exotic species to compete more effectively for limiting resources in light-limited

unburned prairie (Knapp et al. 1998). In contrast, greater biomass allocation to leaves, TLN, and SLA may in part allow the invasive species *Lespedeza cuneata* to aggressively invade annually burned prairie, which is not light limited (Knapp et al. 1998). Results from these species-pair comparisons confirm the species-specific and context-dependent nature of differences in traits between exotic and native species (Thompson et al. 1995). They also emphasize the need to examine exotic species individually within the context of different environmental conditions in order to predict which traits may be related to a species' ability to persist or spread rapidly in a community.

In summary, the lack of generalizable differences in the morphological and physiological traits examined indicates that other traits, such as seedling establishment (Radford and Cousens 2000), phenotypic plasticity (Harrington et al. 1989a, 1989b; Schierenbeck et al. 1994), or the ability to respond to herbivory (Baruch and Bilbao 1999; Smith and Knapp 1999) or to resource pulses (Davis et al. 2000) may be more important in determining success of exotic species in tallgrass prairie. For example, the invasive  $C_4$  grass, *Andropogon bladhii*, may be successful not because of its ability to capture resources more efficiently but because it responds more favorably to herbivory or drought (Christiansen and Svejcar 1987; Svejcar and Christiansen 1987), as has been observed for African grasses invading Neotropical savannas (Baruch 1996; Baruch and Bilbao 1999) or for *Agropyron cristatum* invading Great

Basin Desert communities of North America (Caldwell et al. 1981). Moreover, traits such as allelopathic properties of litter (Langdale and Giddens 1967; Kalburtji and Mosjidis 1992) or key life history traits (seed germination or seedling establishment), rather than higher biomass allocation to leaves or SLA, may enable *L. cuneata* to aggressively invade tallgrass prairie. Such traits have been shown to contribute to the success of *Centaurea maculosa* invading Palouse prairie of the Pacific Northwest (Ridenour and Callaway 2001) and to the success of an exotic *Senecio* species invading coastal pastures in Australia (Radford and Cousens 2000). Thus, including a broader range of traits than those related to carbon gain or growth may be necessary to predict which exotic plant species can successfully invade and ultimately displace native plant communities.

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