

Morphological and physiological traits in the success of the invasive plant *Lespedeza cuneata*

Brady W. Allred · Samuel D. Fuhlendorf ·
Thomas A. Monaco · Rodney E. Will

Received: 12 September 2008 / Accepted: 30 April 2009 / Published online: 17 May 2009
© Springer Science+Business Media B.V. 2009

Abstract To better understand the strategies and mechanisms of invading plants in tallgrass prairie, physiological and morphological characteristics of the invasive *Lespedeza cuneata* were compared to the dominant and abundant natives *Ambrosia psilostachya* and *Andropogon gerardii*. Gas exchange, chlorophyll fluorescence, plant water status, and total and specific leaf area were quantified in the field for each species both throughout daily sampling periods and across the growing season. Total and specific leaf area ($\text{cm}^2 \text{g}^{-1}$ of leaves) exceeded that of native species and may allow *L. cuneata* to successfully establish and dominate in tallgrass prairie, aiding in both resource acquisition and competitive exclusion. Gas exchange traits (e.g. net photosynthesis, stomatal conductance, and water use efficiency) of *L. cuneata* did not exceed other species, but remained constant throughout the daily sampling periods. The daily consistency of net photosynthesis and other gas exchange traits for *L. cuneata* reveal characteristics of stress tolerance. The combination of these characteristics and strategies may assist in the invasion of

L. cuneata and also provide insight into general mechanisms responsible for successful invasions into tallgrass prairie.

Keywords Competition · Tolerance ·
Sericea lespedeza · Leaf area · Photosynthesis ·
Invasion · Tallgrass prairie

Introduction

Invasive plants are a threat to most ecosystems. Invasions can alter disturbance regimes, biodiversity, ecosystem structure and functions, and agricultural production (D'Antonio and Vitousek 1992; Heywood 1989; Mack et al. 2000; Vitousek et al. 1997). Because of the deleterious effects and ecosystem disruption caused by invasive species, many scientific studies have addressed the mechanisms by which invasive plants succeed. Various characteristics that influence the success of invaders have been identified, but these are often generalizations (Mack 1996). Studies on specific species and communities are required to understand the mechanisms and strategies of invasive plants (Lodge 1993).

Success of an invasive species may be dependent on life history traits, response to disturbance, nutrient requirements, or, collectively, the strategy of the invader as compared to those native to the ecosystem (Davis et al. 2000; Garten et al. 2008; Schutzenhofer

B. W. Allred (✉) · S. D. Fuhlendorf · R. E. Will
Natural Resource Ecology & Management, Oklahoma
State University, 008C Ag. Hall, Stillwater,
OK 74078, USA
e-mail: brady.allred@okstate.edu

T. A. Monaco
USDA-ARS Forage & Range Research Laboratory,
Logan, UT 84322, USA

and Knight 2007). Competitive and tolerance strategies may be particularly important to the successful establishment and persistence of perennial invasive plants (D'Antonio and Vitousek 1992; Vilà and Weiner 2004). The ability to compete with native species for resources (limited or not) may greatly improve the probability of establishment and the overall fitness of the invasive plant. Along with competitive ability, higher or equal tolerance to stressful conditions, e.g. through resource conservation, compared to native species also may assist in invasive plant persistence and dominance.

The mechanisms of both competition and tolerance strategies may differ among invasive and native plants. Physiological traits related to carbon gain can directly affect fitness and differences in traits between exotic and native plants may indicate a strategy for competition and invasion (McAlpine et al. 2008). For example, competitive success may be increased by maximizing photosynthesis (Durand and Goldstein 2001; Feng et al. 2007; McDowell 2002). Higher rates of photosynthesis can lead to increased growth rates, biomass accumulation and overall production. Higher carbon gain and growth may enable invasive species to easily out compete slower growing species by facilitating colonization or resource acquisition (Lambers and Poorter 1992).

Differences in morphology may also enhance success of invasive plants (Baruch and Goldstein 1999; Pattison et al. 1998). Total leaf area can increase the ability to capture and utilize light energy. Such a process is an important factor in plant growth and overall fitness, and may be the primary process influencing successful invasions (D'Antonio et al. 2001). Greater specific leaf area (leaf area per unit leaf mass) may increase carbon assimilation due to more leaf area produced for a given investment in biomass (Lambers and Poorter 1992). Contrasting this, greater total and/or specific leaf area requires greater amounts of resources for maintenance, indicating a tradeoff between costs and benefits (Aerts 1995; Reich et al. 1997). Differences in physiological or morphological characteristics, however, may not always be present or contribute to the success of invasive species (Harrington et al. 1989; Smith and Knapp 2001) or may be required in combination to be successful (Owens 1996).

In addition in aiding in competition, physiological and morphological traits may also contribute to stress

tolerance. Tolerance may also help in successful establishment or dominance of invasive species. The ability to tolerate conditions that normally restrict native plant growth (e.g. reduced water, light, or nutrient availability) would be advantageous to an exotic species. Invasive legumes, for example, may have a greater advantage over native species in areas with nutrient limitations, due to N fixing capabilities (Brandon et al. 2004; Ritchie and Tilman 1995). Invasive species that require less water, or that have a higher water use efficiency, may perform better in areas where water is limiting (Hill et al. 2006). Constant (less variable) rates of photosynthesis throughout the day or season and small but numerous amounts of leaves are examples of such characteristics that may allow for tolerance to adverse conditions.

The objective of this study was to examine possible strategies of competition and tolerance, which may be responsible for or aid in the successful invasion of *Lespedeza cuneata* (Dum.-Cours.) G. Don. *L. cuneata* is an introduced herbaceous perennial legume that is expanding throughout the southern Great Plains (Brandon et al. 2004; Cummings et al. 2007). Introduced from Asia in the late 1800s, *L. cuneata* has primarily been planted for forage production, erosion control, and land reclamation. Invasion of *L. cuneata* into disturbed habitat (Brandon et al. 2004) and quality rangeland (Cummings et al. 2007) is rapid, displacing native species and forming dense monocultures. Possible mechanisms of invasion may include shading other vegetation (Brandon et al. 2004), allelopathy (Kalburtji et al. 2001), interactive effects of insect herbivory, propagule supply and resource availability (Sanders et al. 2007), and decreased herbivore pressure or resistance to herbivory (Donnelly 1954; Schutzenhofer and Knight 2007). Specifically, we examined possible physiological and morphological mechanisms relevant to competition and tolerance strategies, and determined if there were differences between *L. cuneata* and the native species *Ambrosia psilostachya* DC and *Andropogon gerardii* Vitman. These species were chosen for comparison due to their abundance and dominance throughout tallgrass prairie vegetation. *A. psilostachya* is a C₃ forb that is commonly widespread, but not dominating relative to grasses, while *A. gerardii* is one of the dominant C₄ grasses. Both species are frequently displaced by *L. cuneata* as it invades tallgrass prairie (Cummings et al. 2007).

Methods

Study site

This study was conducted in north central Oklahoma, on the Oklahoma State University Range Research Station, ~21 km southwest of Stillwater, OK, USA. The vegetation can be classified as tallgrass prairie, with patches of cross timbers. Average annual precipitation is 870 mm, with 60% of precipitation falling May through October. Average monthly rainfall ranges from 27 mm in February to 135 mm in June. Average monthly temperatures range from a low of -2°C in January and a high of 34°C in August. Dominant grasses include *A. gerardii*, *Schizachyrium scoparium* (Michx.) Nash, *Panicum virgatum* L., and *Sorghastrum nutans* (L.) Nash. Dominant forbs are *A. psilostachya* and *Gutierrezia dracunculoides* (DC.) S.F. Blake. Cross timbers vegetation areas are dominated by *Quercus stellata* Wang., *Quercus marilandica* Münchh., and *Celtis* spp. Species in this study were sampled from an upland site with clay loam soils where *L. cuneata* cover is increasing. An Oklahoma Mesonet (Brock et al. 1995) weather station is located 350 m east of the study area, recording various climate measurements (e.g. air temperature, relative humidity, rainfall) every 5 min.

Gas exchange and chlorophyll fluorescence

Leaf gas exchange and chlorophyll fluorescence characteristics were determined using an LI-6400 portable photosynthesis system (LI-COR Corp., Lincoln, NE, USA) equipped with an integrated fluorescence chamber head (LI-6400-40, LI-COR Corp., Lincoln, NE, USA). Net photosynthetic rate (A_{net}), stomatal conductance to water vapor (g_s), and leaf transpiration (E) were based on the equations of von Caemmerer and Farquhar (1981). Water use efficiency (WUE) was calculated as the ratio between A_{net} and E . Chlorophyll fluorescence characteristics were measured simultaneously with gas exchange. The efficiency of photosystem II (PSII) was calculated as $(F'_m - F'_o)/F'_m = F'_v/F'_m$ during illumination. Measurements were taken monthly, June–September 2007 at 12:00 and 15:00 h local time. Sampling at earlier hours was not possible due to excessive leaf-surface moisture. On each sampling date, 12 plant

individuals of each species were selected and one fully developed, unshaded representative leaf was measured. The same plant individual, but not leaf, was measured at both 12:00 and 15:00 h. During measurements, photosynthetic photon flux density (PPFD), CO_2 concentration, and airflow within the leaf chamber were maintained at 2000, 380, and $500 \mu\text{mol s}^{-1}$, respectively. Leaf chamber temperature and relative humidity were set similar to ambient conditions but held constant for each sampling period (12:00 and 15:00 h) on each day.

On separate sampling dates, photosynthetic response to light was measured on six to eight plant individuals of each species. PPFD was supplied at 2000, 1500, 1000, 750, 500, 250, 175, 100, 50, and $0 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ decreasing in a stepwise fashion. During light response measurements, leaf chamber temperature and relative humidity were held constant at ambient conditions. CO_2 concentration and airflow within the leaf chamber were again maintained at 380, and $500 \mu\text{mol s}^{-1}$, respectively. Dark respiration (R_d) and apparent quantum yield (AQY) were derived from linear regression of the first five points ($0\text{--}250 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) of each replicate curve.

Plant water status

Plant water status was determined for each species by measuring the predawn (Ψ_{pd}) and midday (Ψ_{md}) xylem water potentials. Water potentials were recorded the day after gas exchange measurements. With the exception of June, no rainfall occurred between the time of gas exchange and water potential measurement. Additionally, weather was similar between consecutive days used within sampling rounds. Fifteen samples of each species were harvested and water potentials were measured with a Soil Moisture 3000 (Soil Moisture Corp., Goleta, CA, USA) Scholander-type pressure chamber. Soil volumetric water content was measured the same day as water potentials, at 0–15 and 0–30 cm below ground level using a Soil Moisture MiniTrase (6050X3K1, Soil Moisture Corp., Goleta, CA, USA).

Morphological characteristics

For each species, aboveground plant material of 10–15 plant individuals was harvested monthly

June–September 2007. Plant height was measured, total leaf number counted, and total leaf area estimated by measuring all leaves or a randomly selected sample with a LI-3000 leaf area meter (LI-COR Corp., Lincoln, NE, USA). When leaf area of *L. cuneata* became too large to directly measure (July, August, and September), all branches of each individual were cut and their length measured. Ten branches were then randomly selected and their total leaf number counted. Branch leaf counts and length measurements were pooled for the particular month of sampling and total leaf number for each plant individual was estimated based on linear relationships of sampled branch leaf number and length ($P < 0.01$, $r^2 = 0.93$; $P < 0.01$, $r^2 = 0.83$; $P < 0.01$, $r^2 = 0.70$ for July, August, and September, respectively) plus leaves counted on the main stem. To obtain total leaf area for each plant individual, a mean of 30 randomly selected leaves was calculated and multiplied by total leaf number. Similar alternatives using linear relationships to measure leaf area have been previously used (e.g. Knapp et al. 1999; Turner and Knapp 1996). For all species, specific leaf area was calculated for five leaves from each individual plant after drying to a constant mass. Total aboveground dry biomass was also measured for each harvested plant after drying to a constant mass. Additionally, leaf N content was determined for ten individual plants of each species using a dry combustion analyzer (LECO Corp., St. Joseph, MI, USA) at the Oklahoma State University Soil, Water, and Forage Analytical Laboratory (Stillwater, OK).

Statistical analysis

Analysis of variance was used to evaluate species differences in physiological and morphological traits. Rather than examining differences across months, comparisons were only made within months to examine the separate and interactive effects of species and time of day. Tukey post hoc comparison tests were used to investigate any significant differences. All analyses were computed using Proc Mixed in SAS 9.1 (SAS Institute Inc., Cary, NC, USA). Repeated measures of gas exchange characteristics (during a daily sampling period) were accounted for within the analysis, with each plant individual as the subject of repeated measure. Significant differences were determined at $\alpha = 0.05$.

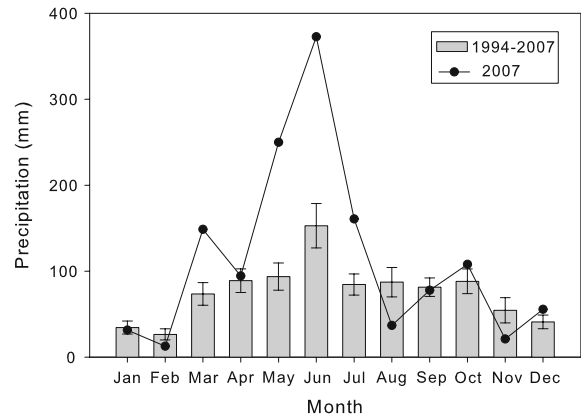


Fig. 1 Mean (\pm SE) monthly precipitation (1994–2007; bars) and monthly precipitation for 2007 (circles) at the Oklahoma State University Range Research Station

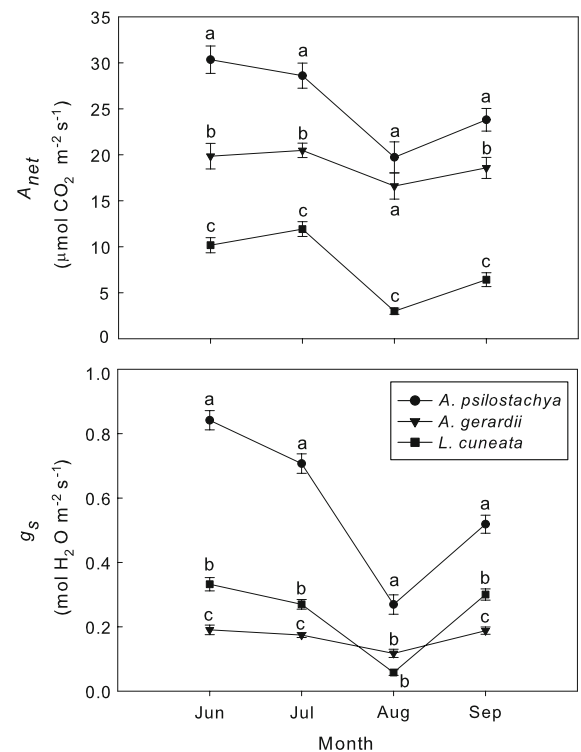


Fig. 2 Mean values (\pm SE) of monthly photosynthetic (A_{net}) and stomatal conductance (g_s) rates for *A. psilostachya*, *A. gerardii*, and *L. cuneata* June–September 2007. Values are means of measurements taken at 12:00 and 15:00 h. Differing letters indicate significant differences within month ($P < 0.05$) using Tukey's HSD

Results

Precipitation for the 2007 growing season (May–September) was 179% of the available average for

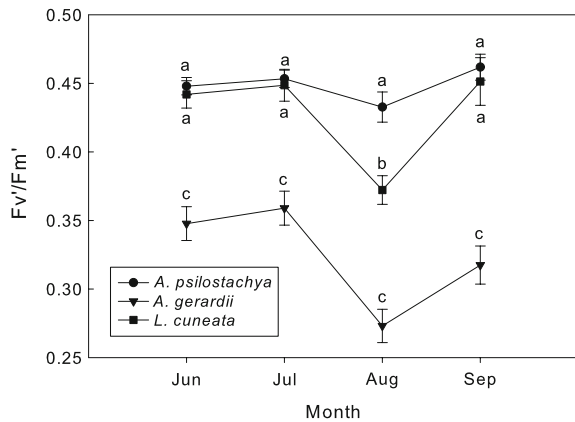


Fig. 3 Mean values (\pm SE) of monthly PSII efficiency (F_v/F_m') for *A. psilostachya*, *A. gerardii*, and *L. cuneata* June–September 2007. Values are means of measurements taken at 12:00 and 15:00 h. Differing letters indicate significant differences within month ($P < 0.05$) using Tukey's HSD

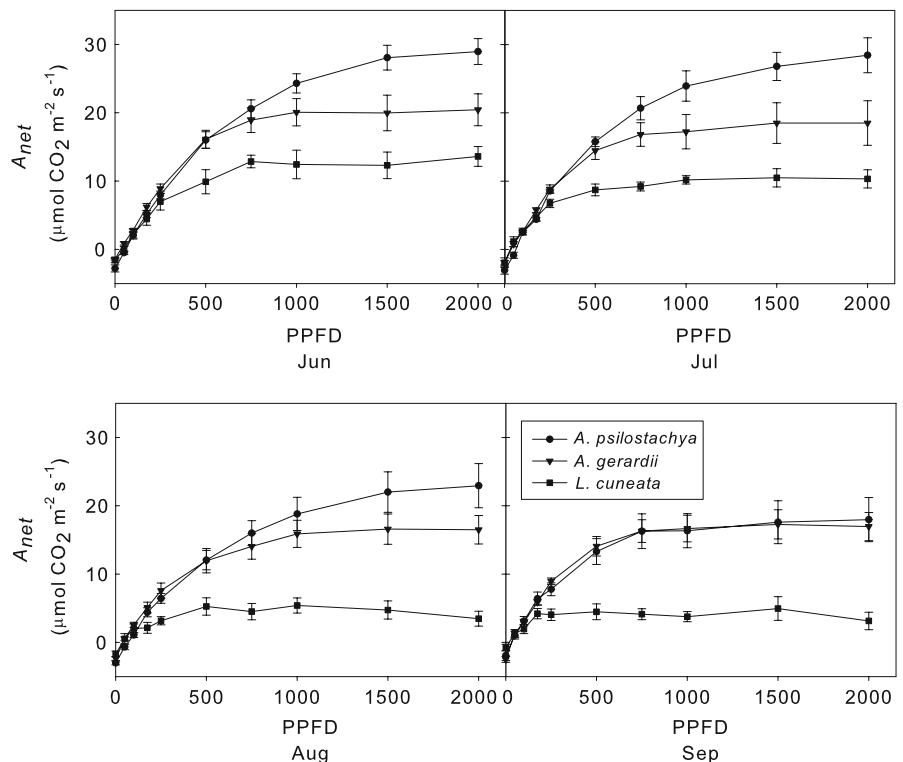
the study site (1994–2007). Precipitation in May, June, and July was over twice the monthly average (Fig. 1). Total precipitation for 2007 was above the annual average.

Comparisons of gas exchange characteristics revealed differences between species for each month of the

season. A_{net} was greatest for *A. psilostachya* in all months while lowest for *L. cuneata* (Fig. 2). At its highest (July), *L. cuneata* A_{net} was 41 and 58% of *A. psilostachya* and *A. gerardii*, respectively. Differences of A_{net} (within species) between times of day (12:00 and 15:00 h) appeared only in August ($P < 0.05$), as rates decreased $\sim 30\%$ for both *A. psilostachya* and *A. gerardii* later in the day, but remained similar in *L. cuneata* (data not shown).

Stomatal conductance rates also varied between species for all months, being greatest in *A. psilostachya* (Fig. 2). Compared to A_{net} , where *L. cuneata* had the lowest rate, g_s of *L. cuneata* was intermediate and significantly greater than *A. gerardii* on three of four sampling dates. Differences of g_s (within species) between times of day were found in all species in June, and in *A. psilostachya* in August and September ($P < 0.05$), with rates decreasing in the later hours of the day (data not shown). WUE was greatest in *A. gerardii* in all months examined (data not shown). With the exception of July, WUE was lower in *L. cuneata* than *A. psilostachya* (data not shown). Time of day differences of water use efficiency occurred in all three species in July and August, and

Fig. 4 Monthly mean values (\pm SE) of net photosynthesis in response to photosynthetic photon flux density (PPFD) for *A. psilostachya*, *A. gerardii*, and *L. cuneata* June–September 2007



additionally in September for *A. psilostachya* ($P < 0.05$). Efficiency decreased later in the day (data not shown).

Chlorophyll fluorescence measurements also varied between species throughout the season. Maximum efficiency of PSII (F_v'/F_m') was greatest in forb species *A. psilostachya* followed by *L. cuneata* (Fig. 3). In September, F_v'/F_m' was 67 and 68% of *A. psilostachya* and *L. cuneata*, respectively. Differences of PSII efficiency due to time of day were found in all species in June and August, and additionally for *A. psilostachya* and *A. gerardii* ($P < 0.05$) in September. PSII efficiency was reduced at the later hours of the day (data not shown).

In general, species responded typically to variable PPFD, with photosynthesis increasing until saturation (Fig. 4). R_d varied throughout the season, with *L. cuneata* lower (less negative A_{net}) than *A. psilostachya* in August and September (Fig. 5). AQY of *L. cuneata* also was consistently lower than that of *A. psilostachya* and *A. gerardii* (Fig. 5) for all months except June. By September, *L. cuneata* AQY was 43 and 39% of *A. psilostachya* and *A. gerardii*, respectively.

Due to excessive rain in June, Ψ_{pd} were close to zero or positive in some instances. In addition, due to rainfall after gas exchange, Ψ_{md} was not measured during the same month. Ψ_{pd} differed between species in July and September, with *A. gerardii* and *L. cuneata* being least (less negative), respectively (Fig. 6). Differences between species for Ψ_{md} varied throughout the season (Fig. 6). Similar to Ψ_{pd} in July, *A. gerardii* had higher Ψ_{md} values than the two forbs. In contrast, Ψ_{md} was greatest (more negative) for *A. gerardii* and *A. psilostachya* in August and September, respectively. Volumetric water content, measured at 0–15 and 0–30 cm belowground level, differed by small amounts in June and August (Fig. 6).

Total leaf area of *L. cuneata* exceeded other species throughout the season (Fig. 7). At its highest (July), total leaf area of *L. cuneata* was 425 and 447% greater than *A. psilostachya* and *A. gerardii*, respectively. Specific leaf area was more variable, with leaves of *L. cuneata* greater than *A. psilostachya* in August, and greater than the other species in September (Fig. 7). Total aboveground biomass was greatest in *L. cuneata* through the season (Table 1). By the end of the season, *L. cuneata* aboveground biomass was 226 and 130% greater than *A. psilostachya* and *A. gerardii*,

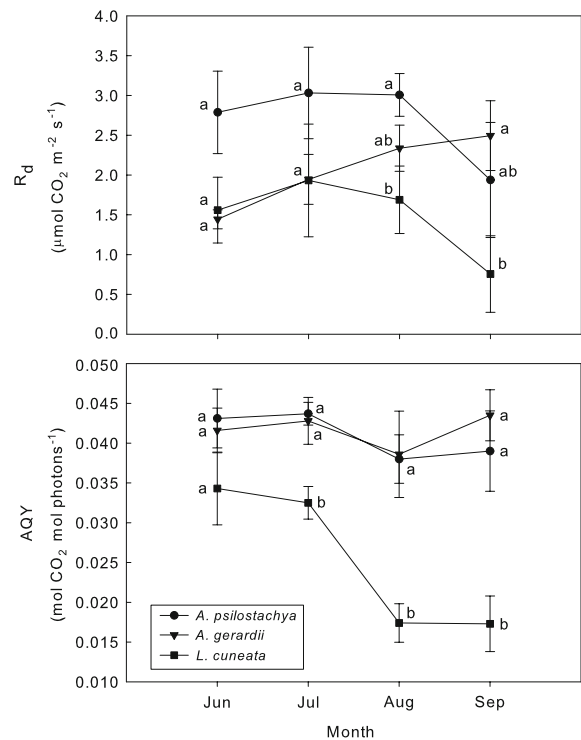


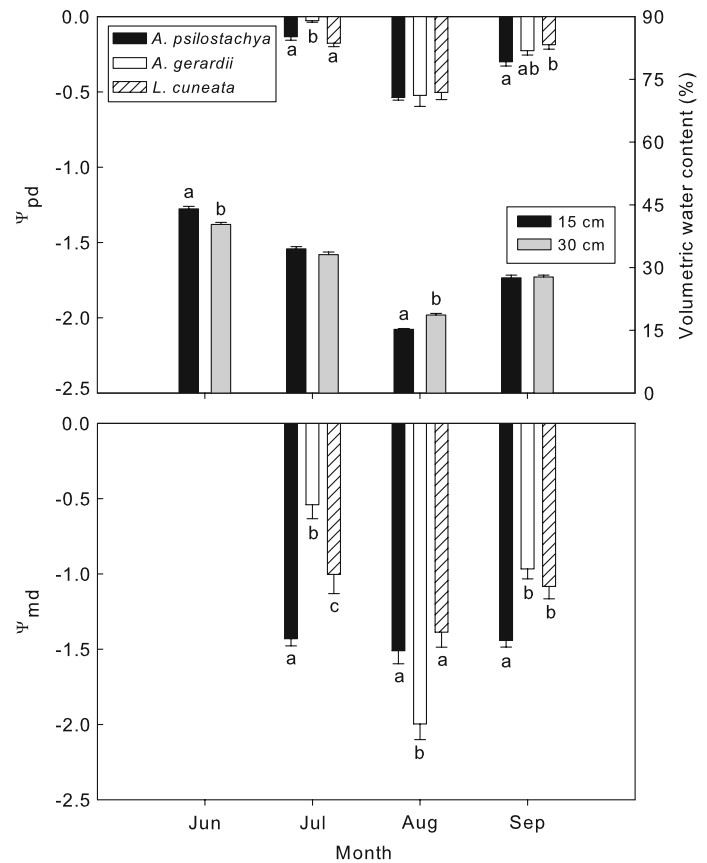
Fig. 5 Monthly mean values (\pm SE) of dark respiration rate (R_d) and apparent quantum yield (AQY), determined from light response curves for *A. psilostachya*, *A. gerardii*, and *L. cuneata* June–September 2007. Differing letters indicate significant differences within month ($P < 0.05$) using Tukey's HSD

respectively. Leaf nitrogen concentration was consistently lowest in *A. gerardii* during the season (Table 1). With the exception of June, *L. cuneata* had lower leaf nitrogen than *A. psilostachya* (Table 1).

Discussion

The success of an invasive plant may be improved by the capability to employ multiple ecological strategies to establish and persist in non native ecosystems. The ability to compete for resources and to also tolerate stressful conditions may give invasive species an advantage over native plants. *Lespedeza cuneata* has been documented to establish, spread, and alter the systems in which it invades (Brandon et al. 2004; Cummings et al. 2007). We found physiological and morphological characteristics that would be favorable for and improve strategies of both competition and tolerance. These combinations of

Fig. 6 Monthly mean values (\pm SE) of predawn (Ψ_{pd}) and midday (Ψ_{md}) xylem water potentials for *A. psilostachya*, *A. gerardii*, and *L. cuneata* (left axis) and volumetric soil water content (right axis) June–September 2007. Differing letters indicate significant differences within month ($P < 0.05$) using Tukey's HSD



characteristics and strategies may be responsible for or aid in the successful invasions of *L. cuneata* in tallgrass prairie.

While invasive species are often predicted to differ and have an advantage in traits related to leaf-level physiology (Baruch et al. 2000; Funk et al. 2008; Nagel and Griffin 2004), few of the physiological traits examined in *L. cuneata* appeared to enhance its ability to compete with other species. Unexpectedly, and in a year wetter than average, A_{net} values of *L. cuneata* were $<50\%$ of the established native species *A. psilostachya* and *A. gerardii*. Comparisons of A_{net} on a leaf mass or nitrogen basis (converted from specific leaf area and leaf nitrogen measurements) were similar as when expressed per unit leaf area (data not shown). Furthermore, the lower photosynthetic response of *L. cuneata* to variable light indicated the absence of a competitive advantage to increased light. However, the PSII efficiencies measured during illumination (F'_v/F'_m) of *A. psilostachya* and *L. cuneata* were both greater than the native C_4 grass *A. gerardii*, indicating that potential

for photochemical utilization and efficiency of light harvesting may be greater in these species. Due to increased PSII fluorescence and measurement limitations, however, C_4 plants may have lower measured values of PSII efficiency compared to C_3 plants (Pfundel 1998) and care must be taken when comparing values.

While *L. cuneata* did not exhibit greater rates of leaf-level photosynthesis, morphological characteristics may play more of an important role in carbon gain and in the strategy of competition. As invasion and increasing dominance of this species is found in unburned, light-limited tallgrass prairie (Cummings et al. 2007), greater total leaf area increases interception of light and acquisition of CO_2 which may more than compensate for the relatively lower A_{net} values of *L. cuneata*. Multiplying monthly mean photosynthetic rate by monthly mean leaf area estimates the greatest monthly carbon gain in June and July for *L. cuneata* and the greatest monthly carbon gain in August and September for *A. psilostachya* (data not shown). Increased plant carbon gain

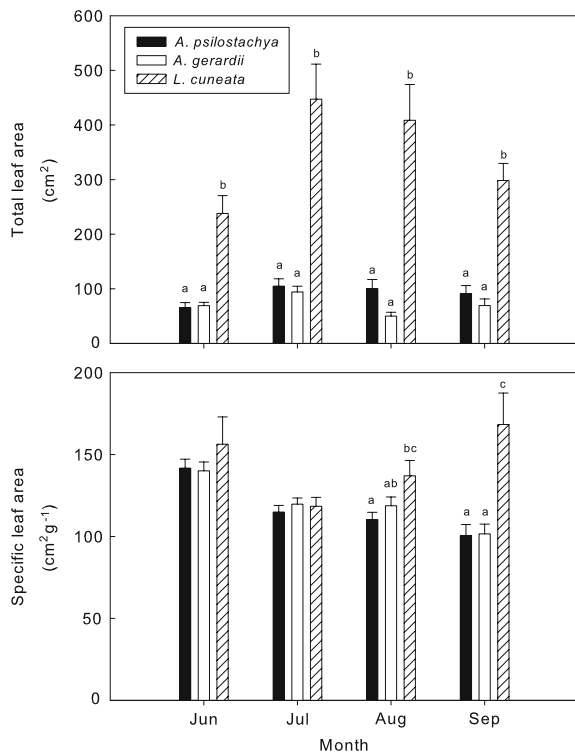


Fig. 7 Mean values (\pm SE) of total and specific leaf area for *A. psilostachya*, *A. gerardii*, and *L. cuneata* June–September 2007. Differing letters indicate significant differences within month ($P < 0.05$) using Tukey's HSD

early in the season may allow for rapid growth and establishment, facilitating invasion. Canopy size and architecture not only determines the amount of light energy that is absorbed by the whole plant, but also the amount of energy deprived from competitors. Our results agree with the findings of Brandon et al. (2004), suggesting that *L. cuneata* may suppress native plants by interfering with their light acquisition (i.e. shading). Although intercepted radiation was not measured, the large amount of leaf area from

a single plant of *L. cuneata* is likely to contribute to dense, light-limited canopies. Once monocultures of *L. cuneata* form, other plant species may be suppressed by the lack of light energy available. Additionally, lower R_d may reduce respiratory losses in *L. cuneata* during the night, conserving assimilated carbon. As low R_d may simply coincide with low A_{net} , additional work, through sampling and/or modeling of daily carbon balance is needed to determine the importance of lower R_d in relation to species life history strategies.

Specific leaf area also is an important determinant of plant function, including plant growth and carbon assimilation (Reich et al. 1997; Westoby 1998). Higher specific leaf area indicates more foliage area per investment in biomass. Toward the end of the growing season (September), specific leaf area was greater for *L. cuneata* than the native species, such that *L. cuneata* would have 40% more leaf area for every gram of carbon allocated to foliage. Greater specific leaf area may result in increased light absorption and shading of other species, increasing competitive ability in light limited environments. Others have also found that specific leaf area of exotic plants was higher than native plants (Baruch and Goldstein 1999; Lake and Leishman 2004; Smith and Knapp 2001). The combination of increased specific and total leaf area may be traits that contribute to the competitive strategy of *L. cuneata*.

Lespedeza cuneata also appears to possess traits that exhibit a strategy of tolerance. Contrary to other species examined, there were fewer reductions of A_{net} , g_s , and F_v/F_m in *L. cuneata* due to time of day. The ability to maintain relatively constant A_{net} may be advantageous and enhance overall plant success. Analogous to the familiar parable of the tortoise and the hare, slow and steady may eventually help win the

Table 1 Mean values (SE) for total aboveground dry biomass and leaf nitrogen in *A. psilostachya*, *A. gerardii*, and *L. cuneata*

	June	July	August	September
Total aboveground biomass (g)				
<i>A. psilostachya</i>	1.19 (0.15) ^a	2.60 (0.35) ^a	3.31 (0.64) ^a	3.97 (0.51) ^a
<i>A. gerardii</i>	0.76 (0.07) ^a	2.99 (0.37) ^a	4.51 (0.61) ^a	6.91 (0.78) ^{ab}
<i>L. cuneata</i>	2.68 (0.32) ^b	4.85 (0.66) ^b	9.13 (1.60) ^b	9.01 (1.43) ^b
Leaf N (% weight)				
<i>A. psilostachya</i>	1.91 (0.05) ^a	2.00 (0.03) ^a	2.30 (0.04) ^a	2.42 (0.07) ^a
<i>A. gerardii</i>	0.96 (0.01) ^b	1.06 (0.04) ^b	1.07 (0.01) ^b	1.17 (0.03) ^b
<i>L. cuneata</i>	1.94 (0.02) ^a	1.78 (0.05) ^c	1.97 (0.03) ^c	2.16 (0.04) ^c

Differing letters indicate significant differences within month ($P < 0.05$) using Tukey's HSD

race. While the daily consistency of physiological traits in *L. cuneata* may assist in tolerance, the seasonal consistency is similar, or less so (e.g. AQY) to other species examined. At this temporal scale, with such a lack of consistency, no particular advantages are gained. High specific leaf area, however, may also aid in tolerance of adverse conditions. Though this study was conducted during a relatively wet year, the efficient use of biomass allocated to foliage may indicate the ability to tolerate stressful situations. If resources become limiting for all species during a growing season (e.g. drought), the high specific leaf area (more leaf area for less biomass investment) of *L. cuneata* may sustain growth and/or light and carbon acquisition compared to other species. Anecdotally, *L. cuneata* is known to tolerate and persist during periods of drought (Ohlenbusch et al. 2001; Vermeire et al. 2005).

In this study, we examined such traits of the exotic and invasive *L. cuneata*, native C₃ forb *A. psilostachya*, and native C₄ grass *A. gerardii*. These particular species were chosen because of their dominance and abundance in tallgrass prairie vegetation, respective to their functional groups (invasive plant, forb, and grass, respectively). While differences in the traits examined were found (and were overwhelming in some cases), our small sample of three species makes it difficult to state that the specific traits looked at are key to successful invasion. Further studies should include additional species to confirm that such differences are vital to the success of *L. cuneata*, and also not necessarily an effect of functional group. Examining native species from similar functional groups (i.e. a native legume) would determine if traits are peculiar to the invasive or common with species of that group. With specific regard to total leaf area of *L. cuneata*, however, there appear to be few (if any) native legumes that compare (B. Allred, personal observation). Nonetheless, it is apparent that differences do exist between the invasive and dominant/abundant vegetation types and that such differences may be advantageous in the establishment and success of this tallgrass invasive.

Invasive plants are often generalized as having favorable differences in physiological and/or morphological traits that lead to their success over native species. However, it is important to study invasive species individually and within their particular

environments to determine specific characteristics that may assist in their victory over native vegetation (Smith and Knapp 2001). Previous work shows that shading, allelopathy, resource availability, and resistance to herbivory (Brandon et al. 2004; Kalburtji and Mosjidis 1992; Sanders et al. 2007; Schutzenhofer and Knight 2007) may contribute to and be important in successful invasions of *L. cuneata*. We add to that list, showing the *L. cuneata* possesses physiological and morphological characteristics that support strategies of competition and tolerance, which can help in invasion. Perhaps the most influential traits, total and specific leaf area, may simply increase productivity and allow it to aggressively invade into native vegetation. A combination of such traits and the other abovementioned mechanisms is likely responsible for the successful invasion and persistence of *L. cuneata* into tallgrass prairie.

Acknowledgments We thank Jonathan Kelly and Chris Stansberry for field work assistance and logistical support. We also thank two anonymous reviewers for suggestions that improved this manuscript. B. Allred thanks A. Allred for support and encouragement. This research was supported by the Oklahoma Agricultural Experiment Station and the National Research Initiative of the U.S. Department of Agriculture Cooperative State Research, Education and Extension Service, grant numbers 2003-35101-12928 and 2006-35320-17476.

References

- Aerts R (1995) The advantages of being evergreen. *Trends Ecol Evol* 10:402–407. doi:[10.1016/S0169-5347\(00\)89156-9](https://doi.org/10.1016/S0169-5347(00)89156-9)
- Baruch Z, Goldstein G (1999) Leaf construction cost, nutrient concentration, and net CO₂ assimilation of native and invasive species in Hawaii. *Oecologia* 121:183–192. doi:[10.1007/s004420050920](https://doi.org/10.1007/s004420050920)
- Baruch Z, Pattison RR, Goldstein G (2000) Responses to light and water availability of four invasive Melastomataceae in the Hawaiian islands. *Int J Plant Sci* 161:107–118. doi:[10.1086/314233](https://doi.org/10.1086/314233)
- Brandon AL, Gibson DJ, Middleton BA (2004) Mechanisms for dominance in an early successional old field by the invasive non-native *Lespedeza cuneata* (Dum. Cours.) G. Don. *Biol Invasions* 6:483–493. doi:[10.1023/B:BINV.0000041561.71407.f5](https://doi.org/10.1023/B:BINV.0000041561.71407.f5)
- Brock FV, Crawford KC, Elliott RL, Cuperus GW, Stadler SJ, Johnson HL, Eilts MD (1995) The Oklahoma Mesonet: a technical overview. *J Atmos Ocean Technol* 12:5–19. doi:[10.1175/1520-0426\(1995\)012<0005:TOMATO>2.0.CO;2](https://doi.org/10.1175/1520-0426(1995)012<0005:TOMATO>2.0.CO;2)
- Cummings DC, Fuhlendorf SD, Engle DM (2007) Is altering grazing selectivity of invasive forage species with patch burning more effective than herbicide treatments?

- Rangeland Ecol Manag 60:253–260. doi:[10.2111/1551-5028\(2007\)60\[253:AGSOI\]2.0.CO;2](https://doi.org/10.2111/1551-5028(2007)60[253:AGSOI]2.0.CO;2)
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass fire cycles, and global change. *Annu Rev Ecol Syst* 23:63–87
- D'Antonio CM, Hughes RF, Vitousek PM (2001) Factors influencing dynamics of two invasive C₄ grasses in seasonally dry Hawaiian woodlands. *Ecology* 82:89–104
- Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88:528–534. doi:[10.1046/j.1365-2745.2000.00473.x](https://doi.org/10.1046/j.1365-2745.2000.00473.x)
- Donnelly ED (1954) Some factors that affect palatability in sericea lespedeza, *L. cuneata*. *Agron J* 46:96–97
- Durand LZ, Goldstein G (2001) Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. *Oecologia* 126:345–354. doi:[10.1007/s004420000535](https://doi.org/10.1007/s004420000535)
- Feng Y-L, Auge H, Ebeling S (2007) Invasive *Buddleja davidii* allocates more nitrogen to its photosynthetic machinery than five native woody species. *Oecologia* 153:501–510. doi:[10.1007/s00442-007-0759-2](https://doi.org/10.1007/s00442-007-0759-2)
- Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through reassembly: plant traits and invasion resistance. *Trends Ecol Evol* 23:695–703. doi:[10.1016/j.tree.2008.07.013](https://doi.org/10.1016/j.tree.2008.07.013)
- Garten CT, Classen AT, Norby RJ, Brice DJ, Weltzin JF, Souza L (2008) Role of N₂-fixation in constructed old-field communities under different regimes of [CO₂], temperature, and water availability. *Ecosystems* (N Y, Print) 11:125–137. doi:[10.1007/s10021-007-9112-1](https://doi.org/10.1007/s10021-007-9112-1)
- Harrington RA, Brown BJ, Reich PB (1989) Ecophysiology of exotic and native shrubs in southern Wisconsin I. Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. *Oecologia* 80:356–367. doi:[10.1007/BF00379037](https://doi.org/10.1007/BF00379037)
- Heywood VH (1989) Patterns, extents and modes of invasions by terrestrial plants. In: Drake JA, Mooney HA (eds) *Biological invasions: a global perspective*. Wiley, Chichester, New York, pp 31–60
- Hill JP, Germino MJ, Wraith JM, Olson BE, Swan MB (2006) Advantages in water relations contribute to greater photosynthesis in *Centaurea maculosa* compared with established grasses. *Int J Plant Sci* 167:269–277. doi:[10.1086/499505](https://doi.org/10.1086/499505)
- Kalbertji KL, Mosjidis JA (1992) Effects of sericea lespedeza residues on warm-season grasses. *J Range Manag* 45:441–444. doi:[10.2307/4002899](https://doi.org/10.2307/4002899)
- Kalbertji KL, Mosjidis JA, Mamos AP (2001) Allelopathic plants. 2. *Lepedeza cuneata*. *Allelopathy J* 8:41–49
- Knapp AK, Bargmann N, Maragni LA, McAllister CA, Bremer DJ, Ham JM, Owensby CE (1999) Elevated CO₂ and leaf longevity in the C₄ grassland-dominant *Andropogon gerardii*. *Int J Plant Sci* 160:1057–1061. doi:[10.1086/314202](https://doi.org/10.1086/314202)
- Lake JC, Leishman MR (2004) Invasion success of exotic in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biol Conserv* 117:215–226. doi:[10.1016/S0006-3207\(03\)00294-5](https://doi.org/10.1016/S0006-3207(03)00294-5)
- Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv Ecol Res* 23:187–261. doi:[10.1016/S0065-2504\(08\)60148-8](https://doi.org/10.1016/S0065-2504(08)60148-8)
- Lodge DM (1993) Biological invasions: lessons for ecology. *Trends Ecol Evol* 8:133–137. doi:[10.1016/0169-5347\(93\)90025-K](https://doi.org/10.1016/0169-5347(93)90025-K)
- Mack RN (1996) Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biol Conserv* 78:107–121. doi:[10.1016/0006-3207\(96\)00021-3](https://doi.org/10.1016/0006-3207(96)00021-3)
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710. doi:[10.1890/1051-0761\(2000\)010\[0689:BICEGC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2)
- McAlpine KG, Jesson LK, Kubien DS (2008) Photosynthesis and water-use efficiency: a comparison between invasive (exotic) and non-invasive (native) species. *Austral Ecol* 33:10–19
- McDowell SCL (2002) Photosynthetic characteristics of invasive and noninvasive species of *Rubus* (Rosaceae). *Am J Bot* 89:1431–1438. doi:[10.3732/ajb.89.9.1431](https://doi.org/10.3732/ajb.89.9.1431)
- Nagel JM, Griffin KL (2004) Can gas-exchange characteristics help explain the invasive success of *Lythrum salicaria*? *Biol Invasions* 6:101–111. doi:[10.1023/B:BINV.0000010125.93370.32](https://doi.org/10.1023/B:BINV.0000010125.93370.32)
- Ohlenbusch PD, Bidwell TG, Fick WH, Kilgore G, Scott W, Davidson J, Clubine S, Mayo J, Coffin M (2001) *Sericea lespedeza*: history, characteristics, and identification. Kansas State Extension MF-2408, Kansas State University Agricultural Experiment Station and Cooperative Extension Service, Manhattan
- Owens MK (1996) The role of leaf and canopy-level gas exchange in the replacement of *Quercus virginiana* (Fagaceae) by *Juniperus ashei* (Cupressaceae) in semiarid savannas. *Am J Bot* 83:617–623. doi:[10.2307/2445921](https://doi.org/10.2307/2445921)
- Pattison RR, Goldstein G, Ares A (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* 117:449–459. doi:[10.1007/s004420050680](https://doi.org/10.1007/s004420050680)
- Pfundel E (1998) Estimating the contribution of photosystem I to total leaf chlorophyll fluorescence. *Photosynth Res* 56:185–195. doi:[10.1023/A:1006032804606](https://doi.org/10.1023/A:1006032804606)
- Reich PB, Walters MB, Ellsworth DS (1997) From tundra to tundra: global convergence in plant functioning. *Proc Natl Acad Sci USA* 94:13730–13734. doi:[10.1073/pnas.94.25.13730](https://doi.org/10.1073/pnas.94.25.13730)
- Ritchie ME, Tilman D (1995) Responses of legumes to herbivores and nutrients during succession on a nitrogen-poor soil. *Ecology* 76:2648–2655. doi:[10.2307/2265835](https://doi.org/10.2307/2265835)
- Sanders NJ, Weltzin JF, Crutsinger GM, Fitzpatrick MC, Nunez MA, Oswalt CM, Lane KE (2007) Insects mediate the effects of propagule supply and resource availability on a plant invasion. *Ecology* 88:2383–2391. doi:[10.1890/06-1449.1](https://doi.org/10.1890/06-1449.1)
- Schutzenhofer MR, Knight TM (2007) Population-level effects of augmented herbivory on *Lepedeza cuneata*: implications for biological control. *Ecol Appl* 17:965–971. doi:[10.1890/06-1282](https://doi.org/10.1890/06-1282)
- Smith MD, Knapp AK (2001) Physiological and morphological traits of exotic, invasive exotic, and native plant species in tallgrass prairie. *Int J Plant Sci* 162:785–792. doi:[10.1086/320774](https://doi.org/10.1086/320774)

- Turner CL, Knapp AK (1996) Responses of a C₄ grass and three C₃ forbs to variation in nitrogen and light in tallgrass prairie. *Ecology* 77:1738–1749. doi:[10.2307/2265779](https://doi.org/10.2307/2265779)
- Vermeire LT, Bidwell TG, Stritzke J (2005) Ecology and management of sericea lespedeza. OSU Extension Facts F-2874, Oklahoma Cooperative Extension Service, Stillwater
- Vilà M, Weiner J (2004) Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. *Oikos* 105:229–238. doi:[10.1111/j.0030-1299.2004.12682.x](https://doi.org/10.1111/j.0030-1299.2004.12682.x)
- Vitousek PM, Dantonio CM, Loope LL, Rejmanek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. *N Z J Ecol* 21:1–16
- von Caemmerer S, Farquhar GD (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153:376–387. doi:[10.1007/BF00384257](https://doi.org/10.1007/BF00384257)
- Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199:213–227. doi:[10.1023/A:1004327224729](https://doi.org/10.1023/A:1004327224729)