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Responses of legumes and grasses to non-, moderate, and dense shade in Missouri, USA. I. Forage yield and its species-level plasticity

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Abstract Annual screenings of forage grasses and legumes for shade tolerance were conducted from 1996 to 2001 in the outdoor Shade Tolerance Screening Laboratory at the Horticulture and Agroforestry Research Center, University of Missouri. Forty-three forages were grown under non-shade (100% of full sunlight), moderate shade (45%), and dense shade (20%) without competition for water and nutrients. Annual forage yield (g pot^{-1}) was equal to or higher under moderate shade for all 43 forages and under dense shade for 31 forages than the non-shade control. Relative distance plasticity index (RDPI), a measure of a species' adaptability to different environments, ranged from 0.104 to 0.567. Cool season grasses had the lowest RDPI (0.183), followed by warm season grasses (0.252), warm season legumes (0.274), and cool season legumes (0.314), indicating grasses tend to be more shade tolerant than legumes in terms of forage yield. Overall, most grass and legume forages have the potential to produce equivalent or higher yields in agroforestry practices featuring light to moderate shade than forages in open pastures when competition from tree roots is minimized.

Keywords Shade tolerance · Relative distance plasticity index · Annual biomass · Warm-season forages · C4 grasses

Introduction

An agroforestry system, in which trees and forages or crops are intentionally integrated, has both economic and ecological benefits including diversifying sources of income for landowners, mitigating soil erosion, improving water quality, increasing biodiversity, and moderating microclimate extremes (Gold and Garrett 2009). The microclimate factors affected include humidity, soil and air temperature, soil moisture, and especially, light intensity and quality (Martsolf 1966; Callaway 2007). Consequently, the yield of forages grown in agroforestry systems are likely to differ from forages grown in open fields or pastures (Pearson 1983; Watson et al. 1984). Our knowledge about the

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shade tolerance of forage species is usually qualitative, i.e., whether they occur in shaded environment, while quantitatively how adaptive these forages are to reduced light remains little explored.

Investigations of shade tolerance for forages have been conducted under a wide range of environmental conditions, from green shade created by tree canopies to neutral shade produced by shade cloth or slats under which the distribution of light wavelengths remain unchanged. Examples include studies by Peri et al. (2002) on the photosynthetic response of cocksfoot (*Dactylis glomerata*) and white clover (*Trifolium repens*) in a silvopastoral setting, by Beard (1965) on qualitative differences in survival rate and visual quality of eight turf grass species under tree canopies, and by Varella et al. (2010) on alfalfa (*Medicago sativa*) responses to reduced light under both shade cloth/slats and tree canopies in agroforestry systems. Both light intensity and quality (i.e., red: far-red ratio) under tree canopies can vary depending on species, canopy density, and duration of sun flecks (Martsolf 1966; Varella et al. 2010), but light intensity under neutral shade is relatively easy to quantify and light quality remains unchanged. Researchers have evaluated the shade tolerance of forages using shade cloth suspended over field-grown plants (Watson et al. 1984; Devkota et al. 1997; Jiang et al. 2004; Ehret et al. 2015), as well as the shade tolerance of forages grown in well-watered, enriched potting medium under shade cloth inside greenhouses (Gaussoin et al. 1988; Yang et al. 2012; Abraham et al. 2014). Inside a greenhouse, the full sun treatment can be as low as 49–67% of the ambient sunlight depending on the infrastructure and covering (Wong et al. 1985a, b; Abraham et al. 2014; Albaugh et al. 2014). Using adequate irrigation, enriched potting medium, and shade cloth, Lin et al. (1999) evaluated yield responses of 30 forages grown within a hoop house under moderate, dense, and non-shade, and Semchenko et al. (2012) assessed the biomass production of 46 Estonian grassland species grown under 10, 25, 50, and 100% of ambient light.

There does not appear to be a clear, concise definition of shade tolerance or how to measure it when trying to rank plant species for shade tolerance. Beard (1965) defined shade tolerance of turf grasses as the ability to survive and maintain quality. When ranking multiple species, some species inherently yield more biomass per plant or unit of occupied area than others under certain shade levels, thus methods based on a species' relative ability to tolerate shade are required. Wong et al. (1985a) ranked the shade tolerance of 12 tropical grass forages grown under each of four shade levels based on the average scores of several agronomic characteristics. Van Sambeek et al. (2007) ranked 45 forages based on their percentage change in forage production under dense and moderate shade compared to non-shade.

A more comprehensive definition of shade tolerance is the capacity of plants to adapt morphologically and physiologically to maintain productivity under different light environments (Valladares et al. 2006; Valladares and Niinemets 2008). These authors proposed calculating the relative distance plasticity index (RDPI) for traits of plants when grown under at least three different light environments. Using the RDPI methodology, we can generate a single value for each species within each screening trial, thus multiple RDPIs estimated from multiple trials of different species can be statistically tested for differences among species (Valladares et al. 2006).

The objectives of our study were to: (1) assess the effect of non-, moderate, and dense shade on the annual cumulative yields of 43 forages grown with adequate water and nutrients and without root competition from other plants; (2) evaluate whether RDPI is a useful measure for quantifying shade tolerance.

Materials and methods

Study site

In spring 1996, an outdoor Shade Tolerance Screening Laboratory (STSL) was constructed at the Horticulture and Agroforestry Research Center (HARC) in New Franklin, Missouri (92° 46′W, 39° 01′N). The STSL sits on a 0.4 ha pad of limestone gravel laid over permeable weed barrier for weed control and drainage. A total of 72 posts (2.5 m tall) were set on a 4.9 × 4.9 m grid and connected by high tensile wires. Shade cloth made of black polypropylene fabric was hung over the top of the posts and wires, and along the sides 0.1 m above the gravel to create nine structures in a 3 × 3 array (Fig. O1 in Online Resource 1). Each structure is 14.6 m long (north to south) and 4.9 m wide, and 4.9 m away from other neighboring structures. Within each north–south block, three structures were randomly assigned to dense shade (80% shade cloth, i.e., 20% of full sunlight), moderate shade (55% shade cloth, 45% of full sunlight), and a non-shade control (100% of full sunlight). Valves on programmable timers controlled duration of daily drip irrigation to each pot. Each structure can hold 20 rows of six pots on a 0.7 m × 0.8 m spacing. Pots were filled with a well-drained potting medium consisting of composted pine bark, sphagnum peat moss, vermiculite, perlite, and sand (15:2:2:5:2 by volume), and supplemented with slow-release nitrogen (7.9 g N per 10-L pot), micronutrient fertilizer, and a wetting agent. During the growing season (May through September) from 1996 to 2001, the study site had an average daily temperature ranging from 16.6 °C to 27.7 °C. The minimum and maximum temperature inside the shade structures were recorded every 4 days from June to September in 2001. The average minimum temperatures within the non-, moderate, and dense shade structures were 17.6, 19.2, and 22.2 °C, respectively, and the average maximums were 35.2, 34.5, and 33.3 °C, respectively. Monthly precipitation during the same time period averaged 10.7 cm and ranged from 1.9 to 21.7 cm (http://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00236012/detail). The ambient photosynthetic active radiation (PAR) in an open field during the growing season ranged from 36 to 44 mol m^{-2} day^{-1} from June to September (unpublished data).

Plant material

Forages to be evaluated in the newly constructed STSL were initially selected to replicate the species screened by Lin et al. (1999). In subsequent years, forages were selected to repeat screenings of certain species, and new forages that were part of other ongoing agroforestry studies were also added. Seeds for our screening trials were obtained from a local farm supplier, the USDA Elsberry Plant Materials Center, or harvested from native savanna and prairies in Missouri. A total of 43 forages (39 species including 2 species having 2 cultivars each and 1 species with 3 cultivars) were chosen for our study (Table 1). These forages contain annual and perennial, both cool-season and warm-season, grasses and legumes that were introduced or are native to the temperate region of the United States based on information from the USDA PLANTS database (USDA NRCS 2016).

Seed germination and seedling propagation

Seeds of grass species were germinated in seed starter flats in a greenhouse in late March or early April each year except 2001. Seeds of legumes were soaked in 85% rubbing alcohol for 1 min, and rinsed with deionized water, then placed in petri dishes lined with wet filter paper. When grass seedlings had one or two true leaves, or legume seeds had emerging radicles, three germinants were transplanted to a 442 cm^3 pot filled with a soil medium (Scott's Metro Mix) until we had 54 pots for each forage. When the legume seedlings were established, a commercial rhizobial inoculum labelled for each species was watered into the potting medium. Both grasses and legumes were watered with 0.11 g/L of Peter's 20-20-20 NPK in the greenhouse until April or May when six pots of each cultivar were randomly transplanted into one row of six black plastic pots (10 L each) in every shade structure. In 2000, plants after the fall harvest were overwintered under white plastic film and polyfoam (Nursery blanket, Hummert Nursery, St. Louis) and moved back into the structures in spring 2001.

Annual forage yield determination

Forage to a 10-cm stubble height was harvested in summer at the boot stage (grasses) or early flowering (legumes) and again in September or October from 1996 through 2000. In 2001, forage was harvested when the majority of plants within a species started to boot or flower resulting in up to four harvests. Forage was oven dried at 70 °C for 72 h to minimize nitrogen loss. Summer and fall yield of each cultivar within a structure were summed to determine annual forage yield (g pot^{-1}) for statistical analysis.

Experimental design and data analysis

Annual yields from 1996 through 1999 were analyzed using PROC Mixed in SAS 9.4 (SAS Inc., Gary, NC) for each forage (Eq. O1 in Online Resource 1). Each analysis is a split plot design with a randomized complete blocking arrangement for shade (the whole-plot) and year as the split-plot factor. Shade, year, shade*year are fixed effects, and block, block*shade, block*shade*year (residuals) are random effects. A diagonal covariance structure (type = vc) was applied. The forages screened in 2000 and 2001 were

Table 1 Descriptive characteristics for 43 forages screened from 1996 to 2001 for forage yield under three shade treatments at the Horticulture and Agroforestry Research Center (HARC), New Franklin, Missouri

Common name[a]	Scientific name[a]	Type[b]	Origin[c]	Lifecycle	Years tested					
					96	97	98	99	00	01
Italian ryegrass	*Lolium perenne* L. subsp. *multiflorum* (Lam.) Husnot	CSG	I	Annual	√	√	√	√		
Cheatgrass	*Bromus tectorum* L.	CSG	I	Annual					√	
Clustered fescue	*Festuca paradoxa* Desv.	CSG	N	Perennial					√	√
Red fescue	*Festuca rubra* L. subsp. *rubra*	CSG	N	Perennial					√	√
Kentucky bluegrass	*Poa pratensis* L.	CSG	Both	Perennial		√	√	√		
Orchardgrass ‘Benchmark’	*Dactylis glomerata* L.	CSG	I	Perennial		√	√	√		
Perennial ryegrass	*Lolium perenne* L. subsp. *perenne*	CSG	I	Perennial					√	√
Redtop	*Agrostis gigantea* Roth	CSG	I	Perennial	√	√	√	√		
Reed canarygrass	*Phalaris arundinacea* L.	CSG	N	Perennial	√	√	√	√		
Smooth brome	*Bromus inermis* Leyss.	CSG	Both	Perennial		√	√	√		
Timothy	*Phleum pratense* L.	CSG	I	Perennial		√	√	√		
Alfalfa ‘Nitro’	*Medicago sativa* L.	CSL	I	Perennial					√	√
Alfalfa ‘Victoria’	*Medicago sativa* L.	CSL	I	Perennial					√	√
Alsike clover	*Trifolium hybridum* L.	CSL	I	Perennial					√	√
Crimson clover	*Trifolium incarnatum* L.	CSL	I	Annual					√	
Crownvetch ‘Penngift’	*Securigera varia* (L.) Lassen	CSL	I	Perennial					√	√
Kura clover	*Trifolium ambiguum* M. Bieb.	CSL	I	Perennial					√	√
Red clover	*Trifolium pratense* L.	CSL	I	Perennial		√	√	√		
Sainfoin	*Onobrychis viciifolia* Scop.	CSL	I	Perennial					√	√
Subterranean clover	*Trifolium subterraneum* L.	CSL	I	Annual					√	
White clover	*Trifolium repens* L.	CSL	I	Perennial	√	√	√	√		
Atra paspalum ‘Suerte’	*Paspalum atratum* Swallen	WSG	I	Perennial	√	√				
Bahiagrass ‘Argentine’	*Paspalum notatum* Flueggé	WSG	Both	Perennial			√	√		
Bahiagrass ‘Pensacola’	*Paspalum notatum* Flueggé	WSG	Both	Perennial	√		√	√		
Bahiagrass ‘Tifton-9’	*Paspalum notatum* Flueggé	WSG	Both	Perennial	√		√	√		
Bermudagrass	*Cynodon dactylon* (L.) Pers.	WSG	I	Perennial		√	√	√		
Eastern gamagrass	*Tripsacum dactyloides* (L.) L.	WSG	N	Perennial					√	√
Prairie cordgrass	*Spartina pectinata* Bosc ex Link	WSG	N	Perennial			√	√		
Prairie dropseed	*Sporobolus heterolepis* (A. Gray) A. Gray	WSG	N	Perennial					√	√
Rhodes grass ‘Callide’	*Chloris gayana* Kunth	WSG	I	Perennial	√	√				
Switchgrass ‘Cave-in-rock’	*Panicum virgatum* L.	WSG	N	Perennial		√	√	√		
Bird’s-foot trefoil ‘Norcen’	*Lotus corniculatus* L.	WSL	I	Perennial					√	√
Bird’s-foot trefoil ‘rhizomatous’	*Lotus corniculatus* L.	WSL	I	Perennial					√	√
Hoary ticktrefoil	*Desmodium canescens* (L.) DC.	WSL	N	Perennial		√	√	√		
Illinois bundleflower	*Desmanthus illinoensis* (Michx.) MacMill. ex B.L. Rob. & Fernald	WSL	N	Perennial	√	√	√	√		
Korean clover	*Kummerowia stipulacea* (Maxim.) Makino	WSL	I	Annual					√	
Japanese clover	*Kummerowia striata* (Thunb.) Schindl.	WSL	I	Annual		√	√			
Panicledleaf ticktrefoil	*Desmodium paniculatum* (L.) DC.	WSL	N	Perennial		√	√	√		
Purple prairie clover	*Dalea purpurea* Vent.	WSL	N	Perennial	√					

Table 1 continued

Common name[a]	Scientific name[a]	Type[b]	Origin[c]	Lifecycle	Years tested					
					96	97	98	99	00	01
Roundhead lespedeza	*Lespedeza capitata* Michx.	WSL	N	Perennial	√					
Showy ticktrefoil	*Desmodium canadense* (L.) DC.	WSL	N	Perennial	√					
Slender lespedeza	*Lespedeza virginica* (L.) Britton	WSL	N	Perennial	√					
Strawberry clover	*Trifolium fragiferum* L.	WSL	Both	Perennial	√	√	√	√		

[a] Both common and scientific names followed the information in USDA PLANTS database (USDA NRCS 2016)

[b] *CSG* cool season grasses (C3), *WSG* warm season grasses (C4), *CSL* cool season legumes, WSL warm season legumes

[c] *N* native to US, *I* introduced to US

analyzed using an additional autocorrelated covariance structure—AR (1) to address the potential correlation between first year and the second year forage yields of the same plants.

Annual yield was also analyzed across years by grouping forages as the following types: warm season grasses (WSG, C4), cool season grasses (CSG, C3), warm season legumes (WSL, C3), or cool season legumes (CSL, C3), using Eq. O2 (Online Resource 1). Shade, type, shade*type are fixed effects, species (type), i.e., species nested in type, and the residuals are random effects. Annual forage yields were natural-log transformed before analysis, and then back-transformed for data presentation. Tukey method ($\alpha = 0.05$) was applied for the mean separations.

RDPIs were calculated according to Valladares et al. (2006) as the pairwise comparisons across replications of annual forage yield under non-, moderate, and dense shade:

$$\mathrm{RDPI} = \sum \frac{\left|X_{jm} - X_{j'm'}\right|}{X_{jm} + X_{j'm'}} \Big/ n \qquad (1)$$

where X_{jm} or $X_{j'm'}$ is the forage yield; m or m′ is the mth block (m or m′ = 1, 2, 3, but $m \neq m'$) subjected to light treatment j or j′ (j or j′ = 1, 2, 3, but $j \neq j'$), and *n* is the total number of all possible pairs of block and shade treatment in a given year. Missing yield values of each forage were imputed as the average of the other two replicates of the same treatment, thus $n = 27$. RDPIs were calculated for each cultivar in each year it was screened. For multiple-cultivar species, cultivars were treated as replicates, and the RDPI estimated for that species is the average across all cultivars and years. To include more forages and increase the accuracy of estimation, RDPIs were also calculated from the original data for 27 forages (22 species with 5 species having 2 cultivars each) screened by Lin et al. (1999) under the same shade treatments as in this study. RDPIs were natural-log transformed and compared both among species and forb types in PROC MIXED, and Tukey method ($\alpha = 0.05$) was used for the mean separations.

Results

Annual forage yield

Annual forage yield differed among shade treatments for 30 of 43 forages ($p < 0.05$, Table 2). Year effect was also significant ($p < 0.05$, Table 2) and differences in yield among years existed for 31 out of the 35 forages screened for more than 1 year (Table O1 in Online Resource 1). For forages that were tested between 1996 and 1999, average forage yield across all shade treatments was generally highest in 1997 (except Rhodes grass 'Callide' had higher yield in 1996 than in 1997). No differences in yield were found among the same forages tested in 1996 and 1998 except Illinois bundle flower with higher yield in 1996 than 1998. Forage yields were equal for 10 forages in 1998 and 1999 with another nine forages yielding less in 1999 than in 1998. In the two-consecutive-growing-season trials (2000, 2001), annual forage yields in 2001 of overwintered plants across all shade treatments were higher in 11 out of 13 forages than the yields of plants started as seedlings in 2000. For the remaining two forages, alfalfa 'Nitro' had equal

Table 2 Probability of significant F-value of the fixed effects in the mixed effects models for each forage, the average annual forage yield (g pot^{-1}), and 95% confidence interval (CI) for 43 forages grown under non-, moderate, and dense shade between 1996 and 2001

Forages	Number of years tested[a]	F[b]			Non-shade (full sun)		Moderate shade (45% of full sun)		Dense shade (20% of full sun)	
		Shade (S)	S*Y	Year (Y)	Biomass[c] (g pot^{-1})	95% CI	Biomass (g pot^{-1})	95% CI	Biomass (g pot^{-1})	95% CI
Group 1: 45% = 100% = 20%										
Clustered fescue	2,C	1.05^{NS}	0.05^{NS}	193.71***	22.6a	18.2–28.1	24.9a	20.1–30.9	20.7a	16.7–25.7
Eastern gamagrass	2,C	1.15^{NS}	0.87^{NS}	68.23***	26.6a	18.3–38.7	38.2a	26.3–55.6	31.5a	21.7–45.8
Cheatgrass	1	1.63^{NS}	–	–	16.2a	11.0–23.7	15.8a	10.8–23.1	11.0a	7.5–16.1
Kura clover	2,C	2.24^{NS}	4.50^{NS}	151.24***	8.2a	5.3–12.6	7.9a	5.2–12.2	5.6a	3.6–8.6
Slender lespedeza	1	2.29^{NS}	–	–	8.4a	5.2–13.6	11.8a	7.3–19.1	6.9a	4.3–11.1
Showy ticktrefoil	1	3.25^{NS}	–	–	27.4a	19.5–38.4	46.8a	33.3–65.7	33.7a	24.0–47.4
Atra paspalum ‘Suerte’	2	3.32^{NS}	1.00^{NS}	23.29**	120.9a	105.4–138.6	136.2a	118.8–156.2	148.3a	129.4–170.1
Roundhead lespedeza	1	3.75^{NS}	–	–	6.8a	5.2–9.0	9.9a	7.5–13.1	6.9a	5.2–9.1
Sainfoin	2,C	3.94^{NS}	5.07^{NS}	121.10***	20.0a	12.6–31.8	16.2a	10.2–25.8	9.0a	5.7–14.3
Perennial ryegrass	2,C	4.63^{NS}	1.10^{NS}	55.49***	23.1a	14.7–36.4	21.5a	13.6–33.8	18.3a	11.6–28.9
Redtop	4	5.57^{NS}	2.34^{NS}	17.64***	43.2a	34.8–53.6	59.2a	47.7–73.4	38.2a	30.8–47.3
Orchardgrass ‘Benchmark’	3	5.83^{NS}	0.67^{NS}	27.61***	34.1a	30.4–38.3	43.4a	38.7–48.7	36.6a	32.6–41.1
Subterranean clover	1	6.40^{NS}	–	–	7.1a	2.5–20.2	11.6a	4.0–33.0	3.4a	1.2–9.7
Group 2: 45% > 20%; 100% > 20%										
Bird’s-foot trefoil ‘rhizomatous’	2,C	12.32^{*}	0.09^{NS}	174.88***	44.6a	33.5–59.3	51.2a	38.5–68.2	22.1b	16.6–29.4
Korean clover	1	12.19^{*}	–	–	47.1a	30.0–73.9	37.6a	24.0–58.9	16.2b	10.3–25.4
Illinois bundleflower	4	14.51*	0.93^{NS}	10.80***	33.7a	26.9–42.2	41.4a	33.1–51.8	20.1b	16.1–25.2
Bermudagrass	3	17.10*	1.47^{NS}	3.08^{NS}	125.3a	101.9–154.1	140.1a	113.9–172.4	78.6b	63.9–96.7
Alsike clover	2,C	25.56**	6.31*	15.42**	24.1a	18.0–32.4	30.2a	22.5–40.4	11.3b	8.4–15.2
Rhodes grass ‘Callide’	2	86.72***	1.06^{NS}	58.53***	101a	81.4–125.3	91.1a	73.5–113	57.1b	46.0–70.8
Japanese clover	2	33.19**	1.18^{NS}	34.71**	41.2a	30.4–55.8	50.3a	37.1–68.1	13.4b	9.9–18.2
Purple prairie clover	1	35.25**	–	–	8.0a	5.0–12.7	6.3a	3.9–10.0	0.9b	0.6–1.4
Red fescue	2,C	54.82**	26.00**	11.01*	35.1a	26.5–46.3	34.5a	26.1–45.7	12.7b	9.6–16.8
Prairie cordgrass	2	57.18**	3.49^{NS}	0.08^{NS}	35.1a	24.8–49.8	35.0a	24.7–49.6	11.9b	8.4–16.9

Table 2 continued

Forages	Number of years tested[a]	F[b]			Non-shade (full sun)		Moderate shade (45% of full sun)		Dense shade (20% of full sun)	
		Shade (S)	S*Y	Year (Y)	Biomass[c] (g pot^{-1})	95% CI	Biomass (g pot^{-1})	95% CI	Biomass (g pot^{-1})	95% CI
Switchgrass ‘Cave-in-Rock’	3	57.41**	1.13^{NS}	11.90**	89.2a	77.4–102.8	85.9a	74.5–99.0	38.5b	33.4–44.4
Prairie dropseed	2,C	77.87***	0.01^{NS}	40.16***	37.3a	27.8–49.9	26.0a	19.4–34.8	6.0b	4.5–8.0
Group 3: 45% = 100%, 100% = 20%, 45% > 20%										
Alfalfa ‘Nitro’	2,C	9.06*	0.24^{NS}	5.42^{NS}	45.2ab	29.4–69.7	48.7a	31.6–75.1	18.5b	12.0–28.5
Alfalfa ‘Victoria’	2,C	7.41*	0.71^{NS}	133.78***	43.7ab	30.2–63.1	54.1a	37.4–78.1	22.7b	15.7–32.8
Bird’s-foot trefoil ‘Norcen’	2,C	7.55*	1.47^{NS}	111.07***	41.8ab	29.3–59.6	57.9a	40.6–82.6	24.2b	17.0–34.5
Bahiagrass ‘Argentine’	2	18.85**	1.22^{NS}	12.66*	61.8ab	53.9–70.9	77.8a	67.8–89.2	49.7b	43.3–57.0
Bahiagrass ‘Pensacola’	3	7.05*	2.45^{NS}	11.14**	69.6ab	55.1–87.8	82.3a	65.2–103.9	48.0b	38.0–60.5
Bahiagrass ‘Tifton-9’	3	13.70*	1.15^{NS}	2.33^{NS}	71.5ab	60.8–84.1	86.2a	73.3–101.3	50.8b	43.2–59.8
Crimson clover	1	10.56*	–	–	13.0ab	4.8–35.0	26.5a	9.8–71.2	4.3b	1.6–11.5
Red clover	3	13.64*	1.38^{NS}	21.12***	36.7ab	26.5–50.7	62.1a	44.9–85.9	21.3b	15.4–29.4
Timothy	3	8.89*	0.82^{NS}	22.73***	29.6ab	20.3–43.3	41.4a	28.3–60.6	18.7b	12.8–27.4
Group 4: 45% > 100%, 100% = 20%, 45% > 20%										
Smooth brome	3	11.35*	1.48^{NS}	68.26***	30.6b	27.6–33.9	40.4a	36.4–44.8	31.2b	28.1–34.6
Panicledleaf ticktrefoil	3	12.26*	0.66^{NS}	8.09**	44.8b	35.7–56.1	75.0a	59.8–94.0	45.4b	36.2–56.8
Italian ryegrass	4	17.31*	8.83***	49.74***	35.1b	30.6–40.3	54.1a	47.1–62.0	35.7b	31.1–40.9
Kentucky bluegrass	3	23.85**	17.73***	203.71***	19.1b	16.9–21.6	31.4a	27.8–35.5	20.7b	18.3–23.4
White clover	4	26.59**	4.55**	40.82***	28.9b	22.1–37.8	53.6a	41.0–70.1	27.3b	20.9–35.7
Strawberry clover	4	31.51**	2.49^{NS}	33.92***	24.4b	18.8–31.6	58.6a	45.1–75.9	23.1b	17.8–30.0
Group 5: 45% = 20%, 45% > 100%, 20% > or = 100%										
Reed canarygrass	4	7.03*	1.80^{NS}	8.41**	40.5b	34.4–47.6	57.7a	49.0–67.9	47.9ab	40.7–56.4
Hoary ticktrefoil	3	18.87**	1.51^{NS}	41.51***	25.9b	21.7–31.0	48.6a	40.6–58.1	36.5ab	30.5–43.6
Crownvetch ‘Penngift’	2,C	13.84*	1.56^{NS}	109.85***	28.3b	22.9–35.0	37.9a	30.7–46.8	37.8a	30.6–46.7

[a] C: consecutively grown from 2000 to 2001

[b] NS: not significant ($p \geq 0.05$); * $0.01 \leq p < 0.05$; ** $0.001 \leq p < 0.01$; *** $p < 0.0001$

[c] Means with same designation letters within a row are not significantly different ($\alpha = 0.05$) by Tukey’s test. Values were back transformed from natural logarithm to original scale

biomass in 2000 and 2001, and alsike clover had higher biomass in 2000 than in 2001.

Among the 43 forages, five forages showed an interaction between shade and year ($p < 0.05$, Table 2). Mostly, the interaction occurred due to more variable yields in the non-shade control (Fig. 1) that may have been in response to ineffective irrigation during hot dry weather in some years. Although pots were automatically irrigated, evidence suggests the soil surface may have formed a crust so that irrigation water flowed over the surface without adequately wetting the soil. Light, long duration precipitation usually eliminated these crusts. Overall, forage yields were the least during the growing season (May to September) in 1999, which also had the least precipitation: 16 days of ≥5 mm and 11 days of ≥10 mm (Fig. 2) compared to the average 24.5 and 17.7 days, respectively. The 1999 season also had the second highest number of days (70 days) with a maximum temperature ≥30 °C (Fig. 2). The 1998 growing season had the most days (75) with a maximum temperature ≥30 °C; however, it had more frequent precipitation with 29 days of ≥5 mm and 21 days of ≥10 mm (Fig. 2).

The shade responses of forage yield showed five major patterns (Table 2). Forages in group 1 showed no yield differences under all three shade treatments, indicating these species have a high degree of shade tolerance. This group included cheat grass, slender lespedeza, showy ticktrefoil, roundhead lespedeza, subterranean clover, clustered fescue, eastern gamagrass, Kura clover, atra paspalum, sainfoin, perennial ryegrass, redtop, and orchardgrass.

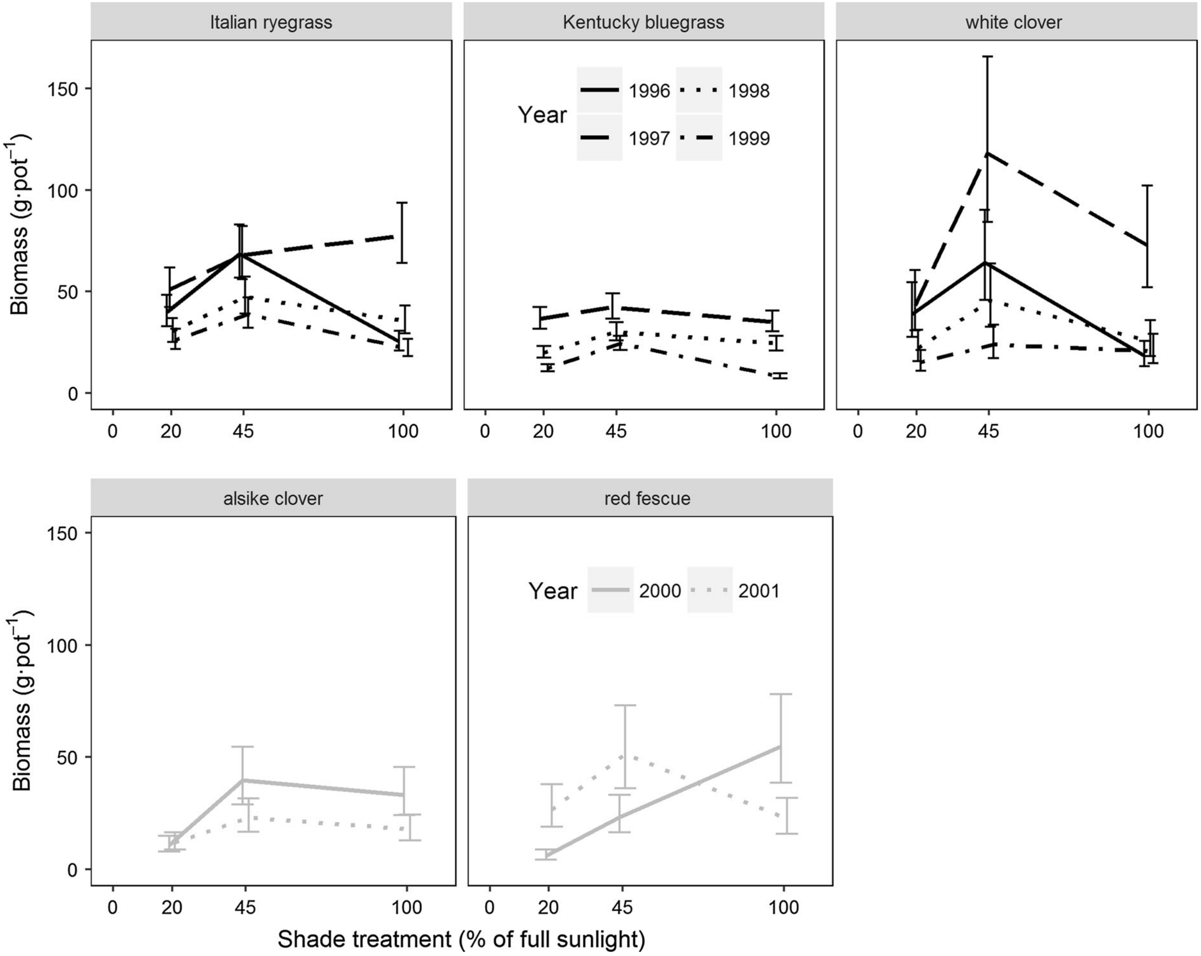
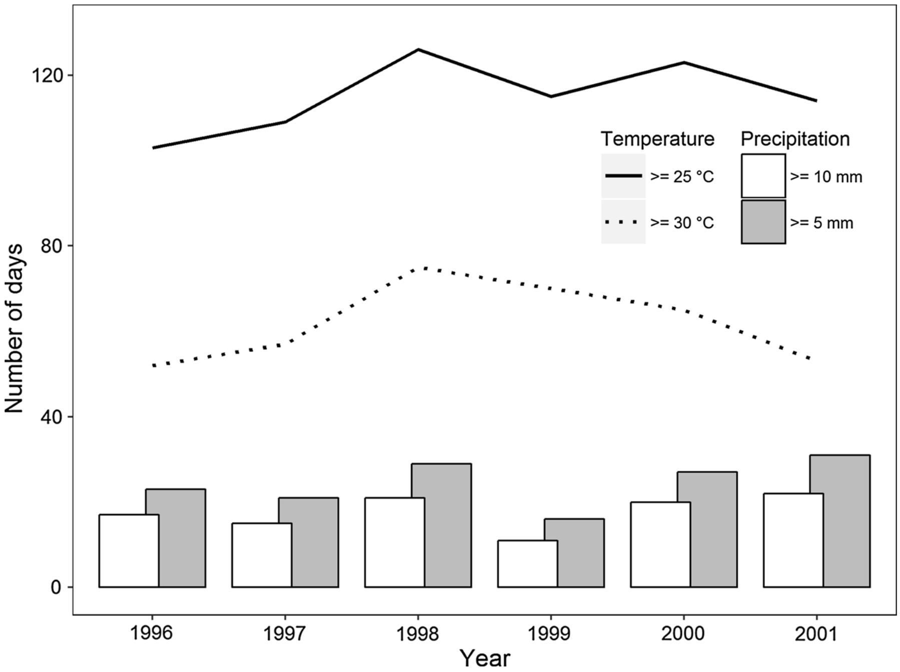


Fig. 1 Annual biomass yield (g pot^{-1}) responses to non-, moderate, and dense shade of the five forages among the 43 forages with significant interactions ($p < 0.05$) between shade and year from 1996 to 2001

Fig. 2 Number of days with maximum air temperature ≥25 or ≥30 °C and number of days with rainfall ≥5 or ≥10 mm from May to September in 1996–2001 in New Franklin, Missouri



The forages in group 2 had equal yields between moderate shade and the non-shade control, but yield under dense shade averaged 40% of that under moderate shade and the control. This suggests group 2 is tolerant to moderate, but not dense shade. This group included bird's-foot trefoil 'rhizomatous', Illinois bundleflower, Bermudagrass, alsike clover, Rhodes grass, Japanese clover, red fescue, prairie cordgrass, switchgrass, purple prairie clover, prairie drop seed, and Korean clover.

In group 3, forage yield was greater under moderate than under dense shade with no differences between the control and dense shade nor between the control and moderate shade. This group, of which the yield under dense shade averaged 44% of that under moderate shade, included crimson clover, the two alfalfa cultivars, bird's-foot trefoil 'Norcen', all 3 bahiagrass cultivars, red clover, and timothy.

In group 4, forages grown under moderate shade had higher yield than the control or dense shade with no differences between the latter two treatments. Yields under the control and dense shade averaged about 59 and 60% of that under moderate shade, respectively. Forages in this group included white clover, strawberry clover, Italian ryegrass, Kentucky bluegrass, smooth brome, and panicledleaf ticktrefoil.

For group 5, forages under moderate shade grew better than the control, while plants under dense shade had biomass growth equal to or exceeding that of the control. The yield of the forages in the control was 66%, on average, of that under moderate shade, and 77% of dense shade. Forages in this group included crownvetch, reed canary grass, and hoary ticktrefoil.

A shade effect was detected when grouping forages by forb types ($p < 0.0001$, Table O2 in Online Resource 1). Although an interaction existed between forb types and shade treatments ($p < 0.0001$), all four forb types performed best under moderate shade, followed by the control and dense shade (Fig. 3). Grasses generally yielded higher biomass than legumes. Average forage yields declined from warm season grasses, cool season grasses, and then to warm season legumes and the cool season legumes as the two least productive types ($p = 0.018$).

Relative distance plasticity index

Relative distance plasticity indices for forage yield ranged from 0.104 to 0.567 for 45 species (Table 3) with differences existing among species ($p < 0.0001$). The 13 species with the lowest RDPIs and presumably the most shade tolerant in terms of forage production

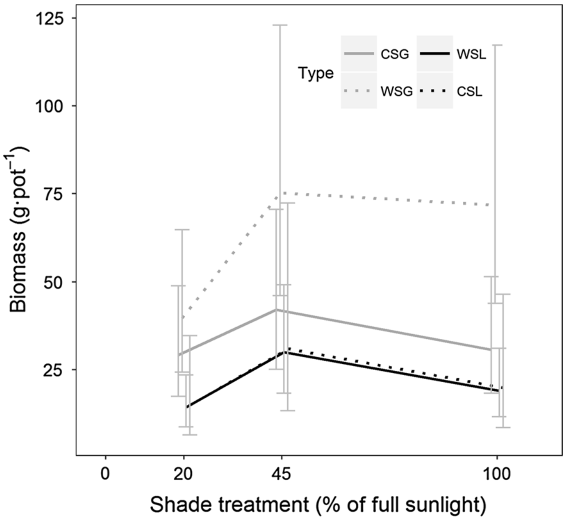


Fig. 3 Annual biomass yield (g pot^{-1}) responses to non-, moderate, and dense shade between 1996 and 2001 by forage types: *CSG* cool season grasses, *WSG* warm season grasses, *WSL* warm season legumes, and *CSL* cool season legumes

were clustered fescue, atra paspalum, crownvetch, smooth brome, cheatgrass, orchardgrass, roundhead lespedeza, reed canarygrass, hoary ticktrefoil, bahiagrass, eastern gamagrass, panicledleaf ticktrefoil, and perennial ryegrass (Table 3).

Analysis of the four forage types showed that grasses have lower RDPI than legumes ($p < 0.0001$), with the CSG (C3) having the lowest average RDPI followed by the WSG (C4), then the WSL (C3), and, finally, the CSL (C3) having the highest average RDPI (Table 3).

Discussion

Shade effects on forage yield

Compared to the non-shade control, 34 of the 43 forages showed no differences and nine forages had greater yields when grown under moderate shade (Table 2). Likewise, 30 forages showed no differences and one forage had greater yield than the control when grown under dense shade (Table 2). In a similar study by Lin et al. (1999), 13 forages (out of 27) in the two summer-fall trials, and nine forages in the spring–summer trial produced no differences between moderate shade and the control, and three forages in the summer-fall trials had higher yields under moderate shade than the control. Three forages in the summer-fall trials and five forages in the spring–summer trial showed no differences in forage yield between dense shade and the control. Forages that performed equally well under moderate shade and the control from both studies included smooth brome, hoary ticktrefoil, panicledleaf ticktrefoil, Kentucky bluegrass, orchardgrass, perennial ryegrass, timothy, and alfalfa 'Victoria'. Semchenko et al. (2012) discovered that 43 out of 46 temperate grassland species in Estonia grew more biomass under moderate shade (50% of full sunlight) than non-shade. These Estonian species include many grasses, among which some are forages or closely related to the forages tested in our study, such as soft brome (*Bromus hordeaceus*), sweet vernalgrass (*Anthoxanthum odoratum*), Kentucky bluegrass, colonial bentgrass (*Agrostis capillaris*), creeping bentgrass (*Agrostis stolonifera*), orchardgrass, red fescue, tall fescue (*Schedonorus arundinaceus*, syn. *Festuca arundinacea* in their original text), timothy, and reed canarygrass.

Similar shade response patterns, i.e., biomass either plateaued or peaked at moderate shade, have been found with seedlings of temperate tree species. Loach (1970) reported that seedlings of five species, both shade tolerant (*Fagus grandifolia* and *Acer rubrum)* and intolerant (*Liriodendron tulipifera*, *Quercus rubra*, and *Populus tremuloides*), had comparable or higher root, stem, and leaf biomass under moderate shade (44% of full sun) than the control; but biomasses were lowest under dense shade (17 and 3% of full sun).

Other studies, however, have reported shade responses that do not plateau or peak at moderate shade. Devkota (1997) reported a linear increase in shoot dry weight of ten pasture species across five shade levels from 14 to 78% of ambient PAR in a greenhouse study. A similar linear increase was found in biomass of shade-treated orchardgrass from 10, 30, to 100% of full sun inside a greenhouse (Abraham et al. 2014). Both aboveground and belowground biomass of switchgrass 'Alamo' increased when grown inside a greenhouse as light intensity increased from 11, to 23, to 31, to 49%, and to 100% of full sun (Albaugh et al. 2014). Jiang et al. (2004) found biomass of seashore paspalum (*Paspalum vaginatum* Swartz) and hybrid Bermudagrass (*Cynodon dactylon* L. × C. *transvaalensis* Burtt Davy) cultivars increased from 10 to 30%, and then to 100% of full sun.

Table 3 Relative distance plasticity index (RDPI), 95% confidence interval (CI), and rank for annual forage yield (g pot^{-1}) of 45 forage species tested between 1994 and 2001

Species	Group[a]	RDPI[b]	95% CI	Rank	Number of cultivars[c]	
					1996–2001	1994–1995
Clustered fescue	CSG	0.104df	0.063–0.171	1	1	0
Atra paspalum	WSG	0.128abcd	0.078–0.210	2	1	0
Crownvetch	CSL	0.134abcd	0.081–0.220	3	1	0
Smooth brome	CSG	0.136d	0.102–0.181	4	1*	1
Cheatgrass	CSG	0.145abcd	0.088–0.238	5	1	0
Orchardgrass	CSG	0.148d	0.117–0.187	6	1*	2
Roundhead lespedeza	WSL	0.160abcd	0.079–0.323	7	1	0
Reed canarygrass	CSG	0.161bcd	0.114–0.229	8	1	0
Hoary ticktrefoil	WSL	0.162cde	0.122–0.216	9	1*	1
Bahiagrass	WSG	0.163cd	0.127–0.208	10	3	0
Eastern gamagrass	WSG	0.172abcd	0.104–0.282	11	1	0
Panicledleaf ticktrefoil	WSL	0.174bcd	0.131–0.232	12	1*	1
Perennial ryegrass	CSG	0.175abcd	0.128–0.240	13	1*	1
Showy ticktrefoil	WSL	0.189abcd	0.094–0.380	14	1	0
Italian ryegrass	CSG	0.194abcd	0.137–0.276	15	1	0
Redtop	CSG	0.197abcd	0.139–0.279	16	1	0
Kentucky bluegrass	CSG	0.208abcd	0.156–0.277	17	1*	1
Tall fescue	CSG	0.226abcd	0.170–0.301	18	0	2
Rhodes grass	WSG	0.228abcd	0.139–0.374	19	1	0
Slender lespedeza	WSL	0.247abcd	0.150–0.406	20	1*	1
Kura clover	CSL	0.249abcd	0.152–0.409	21	1	0
Sericea lespedeza[d]	WSL	0.254abcd	0.155–0.418	22	0	1
Timothy	CSG	0.257abcd	0.193–0.343	23	1*	1
Bermudagrass	WSG	0.263abcd	0.185–0.373	24	1*	1
Illinois bundleflower	WSL	0.267abcd	0.188–0.379	25	1	0
Sainfoin	CSL	0.269abcd	0.164–0.443	26	1	0
White clover	CSL	0.275abcd	0.211–0.359	27	1*	1
Alfalfa	CSL	0.281abcd	0.225–0.351	28	2	2
Switchgrass	WSG	0.322abcf	0.242–0.429	29	1*	1
Big bluestem	WSG	0.322abcd	0.215–0.483	30	0	1
Prairie cordgrass	WSG	0.33abcd	0.201–0.542	31	1	0
Japanese clover	WSL	0.331abcf	0.242–0.453	32	1*	1
Bird's–foot trefoil	WSL	0.336abe	0.269–0.419	33	2*	2
Indiangrass[e]	WSG	0.34abcd	0.226–0.509	34	0	1
Strawberry clover	WSL	0.343abcd	0.242–0.487	35	1	0
Red clover	CSL	0.382abe	0.269–0.477	36	1*	1
Alsike clover	CSL	0.394abe	0.279–0.523	37	1*	1
Red fescue	CSG	0.401abcd	0.240–0.647	38	1	0
Korean clover	WSL	0.358a	0.307–0.523	39	1*	2
Crimson clover	CSL	0.432abcd	0.263–0.710	40	1	0
Berseem clover[f]	CSL	0.459ab	0.306–0.689	41	0	1
Buffalograss[g]	WSG	0.468abcd	0.232–0.945	42	0	1

Table 3 continued

Species	Group[a]	RDPI[b]	95% CI	Rank	Number of cultivars[c]	
					1996–2001	1994–1995
Subterranean clover	CSL	0.494abc	0.301–0.811	43	1	0
Prairie dropseed	WSG	0.494abc	0.301–0.812	44	1	0
Purple prairie clover	WSL	0.567abcd	0.281–1.144	45	1	0
Forb types	CSG	0.183B	0.163–0.206	I		
	WSG	0.252A	0.217–0.292	II		
	WSL	0.274A	0.242–0.311	III		
	CSL	0.314A	0.274–0.360	IV		

* indicates the number of cultivars of that species shared with Lin et al. (1999)

[a] *CSG* cool season grasses, *WSG* warm season grasses, *CSL* cool season legumes, *WSL* warm season legumes

[b] RDPIs with the same lower case or upper case letters in the same column are not significantly different ($a = 0.05$). RDPIs and CIs are all back transformed from natural log to original scale

[c] Number of cultivars tested in each period of time

[d–f] Forages that are from Lin et al. (1999) but their scientific names do not appear in the text other than this table. sericea lespedeza: *Lespedeza cuneate*; Indiangrass: *Sorghastrum nutans*; berseem clover: *Trifolium alexandrinum*; buffalograss: *Bouteloua dactyloides*

Plant responses to decreasing light can range from linear decreases in forage yield to those that plateau or peaked under moderate shade as found in Lin et al. (1999), Semchenko et al. (2012), and our study. Because net assimilation in C3 plants saturates around 50–60% of maximum sunlight, it is possible plants grown under moderate shade achieved maximum net assimilation on most days, while plants grown without shade absorbed surplus light resulting in high rates of dark respiration which reduced photosynthetic efficiency. Maximum air temperatures in the non-shade structures were 0.7 and 1.9 °C higher than under moderate and dense shade which were covered with black shade cloth, further increasing dark respiration rates for plants exposed to full sun. Similar temperature differences among shade structures compared with the non-shade control was also noted by Semchenko et al. (2012).

Interactions between shade and year occurred for five species (Fig. 1) in part due to variable responses in forage yield from year to year, especially in the non-shade control. Lower biomass in 2000 was in part because most species were planted late and harvested only in the fall of 2000, while in 2001 most species had 2–4 harvests depending on harvest recovery time and initiation of flowering. Of the 13 perennial forages screened in 2000 and 2001, only red fescue and alsike clover showed an interaction between shade treatment and year, suggesting yield response to shade does not change as most perennial forages mature from first-year seedlings to established plants.

Relative distance plasticity index

Forage species that show the least differences in biomass yield across non-, moderate, and dense shade (group 1), or at least the latter two treatments (group 5), should in theory have the lowest RDPIs and ought to be the most shade tolerant species. Among the top 13 species with the lowest RDPIs (Table 3), clustered fescue, atra paspalum, cheatgrass, orchardgrass, roundhead lespedeza, eastern gamagrass, and perennial ryegrass are in group 1, while crownvetch, reed canarygrass, and hoary ticktrefoil are in group 5. Species with reduced biomass under dense shade compared to moderate and/or non-shade (groups 2, 3, and 4) should have higher RDPIs. None of the 12 species in group 2, only bahiagrass out of nine species in group 3, and smooth brome and panicledleaf ticktrefoil out of six species in group 4 have low RDPIs. The calculation of RDPI of smooth brome (0.136) and panicledleaf ticktrefoid (0.174) included biomass data from Lin et al. (1999), which showed smaller differences in biomass than our study across all three shade levels.

RDPIs confirm relative shade tolerance of reported observations for several forages. Orchardgrass is reported to be productive under a wide range of light conditions and is recognized as a shade tolerant species (Blake et al. 1966; Christie and McElroy 1995). Our RDPI calculated as the average of two cultivars across several trials (six trials for 'Benchmark' and three for 'Justus') was 0.148, which ranked orchardgrass as the 6th most shade tolerant out of the 45 species examined. Atra paspalum, a shade tolerant C4 grass recommended for tropical agroforestry systems had a low RDPI (0.128), placing it the 2nd out of 45 species. White clover, reported to be shade intolerant by Christie and McElroy (1995), has a relatively high RDPI (0.275) and ranked 27th on the list of 45 species.

We also assessed the usefulness of RDPI to rank forage species for shade tolerance by comparing published relative ranks to our estimated RDPIs. RDPIs align well with the rankings by Feldhake and Belesky (2009) for orchardgrass (0.148) being more shade tolerant than tall fescue (0.226). RDPI and rankings do not align so well for the shade tolerance rankings reported by Beard (1965) for red fescue (0.394) > perennial ryegrass (0.175) > tall fescue (0.226) > Kentucky bluegrass (0.208), or by Kephart et al. (1992) for tall fescue (0.226) > reed canarygrass (0.161) > switchgrass (0.322). RDPIs support the rankings by Devkota et al. (1997) of orchardgrass (0.148) being more shade tolerant than perennial ryegrass (0.175) but not for subterranean clover (0.494) being more shade tolerant than white clover (0.275). Discrepancies among relative rankings may be in part due to measuring different growth responses, i.e., survival and plant health; amount of root competition (pasture compared to a few plants in a large pot); or study duration (a couple months compared to multiple harvests over an entire growing season). Van Sambeek et al. (2007) investigated species with widely differing shade tolerance from multiple screening trials by comparing the relative changes in forage yields from plants under moderate and dense shade to those under non-shade, and then ranked them on a scale between 0 (least tolerant) and 100% (most tolerant). There is reasonable agreement between the reported percentile ranks and RDPIs of our study except for bahiagrass, Bermudagrass, switchgrass, and red clover.

C3 and C4 species generally have different degrees of shade tolerance. Kephart et al. (1992) found that in response to reduced irradiance, C3 grasses like tall fescue, reed canarygrass, and deertongue grass (*Dichanthelium clandestinum*) have smaller relative reductions in biomass than C4 grasses such as switchgrass and big bluestem (*Andropogon gerardii*), indicating more shade tolerance within C3 grasses than C4. This is in agreement with our finding that C3 grasses (cool season) are more resilient to shade (lower RDPI) in forage yield than C4 grasses (warm season). However, there was no difference for RDPIs between legumes (all C3) and C4 grasses.

Conclusion

Multiple screenings evaluating responses of forages to moderate and dense shade showed most forages did not change or increased in forage yield, when grown with adequate water and nutrients in the absence of root competition from other plants. RDPI that measures the resilience of a plant to adapt when grown along an environmental gradient has acceptable concordance with known shade tolerance rankings. Low RDPIs indicate small changes in yield for forage species that can adapt to moderate and dense shade.

Several agroforestry systems are characterized by continuums from moderate to dense shade in the presence of trees. Our results indicate that for most forages, yield can be maintained or improved under moderate shade compared to open grown forages when tree root competition is minimized. RDPI can be a useful and convenient indicator for shade tolerance. Agroforestry practitioners may want to choose forages with low RDPIs, because these species are more likely to maintain biomass yield in their agroforestry practices as trees grow and canopies close.

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