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

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Abstract From a series of shade tolerance screening trials conducted in an outdoor Shade Tolerance Screening Laboratory, 22 forages (16 grasses and 6 legumes) were selected for quality evaluation. The forages were grown under non-shade (100% of full sun, the control), moderate shade (45%), and dense shade (20%) with adequate water and nutrients and free of competition from other plants. All 22 forages had equal or higher percent crude protein (%CP) and CP yield (g pot^{-1}) under moderate shade than in the control. Under dense shade, 22 and 18 forages had equal or higher %CP and CP yield than in the control, respectively. Under moderate and dense shade, 14 and 15 forages, respectively, maintained relative feed value (RFV) equal to that in the control. Legumes had higher %CP and RFV than grasses with no differences for CP yield. Relative distance plasticity index (RDPI), an indicator of a species' adaptability to different environments, suggested grasses maintained RFV better than legumes under shade, while legumes were more resilient under shade in maintaining %CP than grasses. Our results suggest most grass and legume forages will maintain or have improved quality when grown in agroforestry practices with light to moderate shade compared to forages grown in open pastures.

Keywords Shade tolerance · Crude protein · Relative feed value · Relative distance plasticity index

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Introduction

Agroforestry systems, in which trees and forages or crops are integrated, feature lightly- to moderately-shaded environments with modified microclimates. Compared to open fields, the altered microclimatic factors in shaded environments include moderated air and soil temperatures, higher humidity and more soil moisture, and most importantly, reduced light quantity and altered quality (Martsolf 1966; Callaway 2007). Consequently, plants grown under shade are likely to show changes in nutritive quality in addition to biomass yield (Pang et al. 2017).

Forage quality is usually measured as a combination of feed intake, nutrient content, and digestibility (Saha et al. 2010; Hancock et al. 2014). Hight et al. (1968) found that shade reduced the total soluble carbohydrates and voluntary feed intake of perennial ryegrass (*Lolium perenne*). Chabot and Chabot (1977) reported shade lowered the ratio of easily digested mesophyll tissue to the less digestible epidermis. The responses of dry matter digestibility to increasing shade were found to be variable and mostly fluctuated within a small range in buffalo grass (*Stenotaphrum secundatum*), mat grass (*Axonopus compressus*), kikuyu grass (*Pennisetum clandestinum*) (Samarakoon et al. 1990), and orchardgrass (*Dactylis glomerata*) (Peri et al. 2007). Hight et al. (1968) and Masuda (1977) reported slightly decreased dry matter digestibility in perennial ryegrass and forage oats (*Avena sativa*), respectively, while Garrett and Kurtz (1983) concluded percentage digestible dry matter increased in tall fescue (*Schedonorus arundinaceus*) and orchardgrass grown under shade than those in full sun possibly due to cell wall content decline. Norton et al. (1991) discovered that moderate shade (50% of full sun) had little effect on the intake and digestibility of five grass forages, although there were changes in the chemical composition of plant cell walls and nitrogen content. Both acid detergent fiber (ADF) and neutral detergent fiber (NDF) of most forages were found to be either not impacted or increased by shade (Lin et al. 2001; Kyriazopoulos et al. 2013). Plants grown under shade frequently have increased percent crude protein (%CP) (Allard et al. 1991; Lin et al. 2001; Kyriazopoulos et al. 2013; Abraham et al. 2014).

No single chemical analysis can adequately determine forage quality, although relative feed value (RFV), %CP, and CP yield compose a comprehensive set of indicators (Ball et al. 2001; Redfearn et al. 2010). Relative feed value of a forage compared to the nutritive value of full bloom alfalfa can be derived from digestible dry matter (DDM) and dry matter intake (DMI): $RFV = DDM \times DMI \times 0.775$, where $DDM = 88.9 - (0.779 \times ADF)$, and $DMI = 120/NDF$ (Redfearn et al. 2010). Lower ADF indicates higher digestibility, lower NDF means higher intake, and both ADF and NDF are inversely related to RFV. The advantage of using RFV to assess forage quality is that it combines ADF and NDF into a single value representing both the digestibility and the amount of the forage that will be consumed. RFV also can be used to compare forages for their energy content (Henning et al. 1991). Relative feed value is linearly related to relative feed quality, which is the current most frequently used measure of forage quality (Jeranyama and Garcia 2004). However, RFV does not include the protein content in its calculation. Crude protein yield is not commonly evaluated in shade tolerance screening, but is very informative on the total CP mass contained within different forage yields.

The objectives of our study were to: (1) assess whether the quality (%CP, CP yield, and RFV) of 22 forages (16 grasses and 6 legumes) grown under moderate and dense shade differ from the non-shade control, given adequate soil moisture and nutrients, and (2) assess the plasticity of different forage species or forb types to maintain quality across 3 levels of shaded environments: non-, moderate, and dense shade.

Materials and methods

Study site

Forages were grown in the outdoor Shade Tolerance Screening Laboratory (STSL, Fig O1 in Online Resource 1) at the Horticulture and Agroforestry Research Center (HARC) in New Franklin, Missouri (92° 46′W, 39° 01′N). The STSL consisted of 3 blocks of 3 shade structures (structure dimensions: 4.9 m × 14.6 m × 2.5 m high) which were randomly assigned to dense shade (80% black shade cloth, i.e., 20% of full sun), moderate shade (55% shade cloth, 45% of full sun), and the non-shade control (100% of full sun). Each forage screened was grown in a row of 6 widely spaced pots with enriched potting medium and automated drip irrigation. The average ambient photosynthetic active radiation in an adjacent open field ranged from 36 to 44 mol m^{-2} day^{-1} during the May through September growing season.

Plant material

This study is the second part of a shade tolerance screening project that was designed to repeatedly evaluate the shade tolerance of a diverse selection of grasses and legumes (Pang et al. 2017). After the forage yield responses to non-, moderate, and dense shade were assessed, 19 forages from 1999, and 3 forages from 2000 to 2001 were chosen to determine their forage quality (Table 1). Forages were chosen to include cool and warm season perennial legumes and grasses that were introduced or are native to the temperate region of the United States according to the USDA PLANTS database (USDA NRCS 2016).

Seed germination, seedling propagation, and harvesting

Seeds were germinated in seed starter flats or petri dishes before 3 germinants of each forage were transplanted to 45 starter pots (442 cm^3 each) in late March or early April. All seedlings were grown in a greenhouse (equal to 50% of full sunlight) until late April or May when seedlings in starter pots were transplanted into 10-L black pots and moved to the STSL. Forages were harvested in the summer at the early reproductive stage (early bloom for legumes; boot to early head for grasses) and then the regrowth was harvested again in the fall. The above ground biomass from 6 pots for each forage within a shade structure were oven-dried at 70 °C for 72 h, weighed, and then combined before grinding to pass a 2-mm screen. After the fall harvest in 2000, plants were overwintered and moved back to the STSL in 2001 spring.

Table 1 Descriptive characteristics for 22 forages evaluated for forage quality in 1999 or 2000–2001 under non-, moderate, and dense shade in the Shade Tolerance Screening Laboratory at New Franklin, Missouri

Common name[a]	Scientific name[a]	Type	Origin	Years tested	
				1999	2000–2001
Italian ryegrass	*Lolium perenne* L. subsp. *multiflorum* (Lam.) Husnot	CSG	I	√	
Clustered fescue	*Festuca paradoxa* Desv.	CSG	N		√
Kentucky bluegrass	*Poa pratensis* L.	CSG	Both	√	
Orchardgrass ‘Benchmark’	*Dactylis glomerata* L.	CSG	I	√	
Redtop	*Agrostis gigantea* Roth	CSG	I	√	
Reed canarygrass	*Phalaris arundinacea* L.	CSG	N	√	
Smooth brome	*Bromus inermis* Leyss.	CSG	Both	√	
Timothy	*Phleum pratense* L.	CSG	I	√	
Red clover	*Trifolium pratense* L.	CSL	I	√	
White clover	*Trifolium repens* L.	CSL	I	√	
Bahiagrass ‘Argentine’	*Paspalum notatum* Flueggé	WSG	Both	√	
Bahiagrass ‘Pensacola’	*Paspalum notatum* Flueggé	WSG	Both	√	
Bahiagrass ‘Tifton-9’	*Paspalum notatum* Flueggé	WSG	Both	√	
Bermudagrass	*Cynodon dactylon* (L.) Pers.	WSG	I	√	
Eastern gamagrass	*Tripsacum dactyloides* (L.) L.	WSG	N		√
Prairie cordgrass	*Spartina pectinata* Bosc ex Link	WSG	N	√	
Prairie dropseed	*Sporobolus heterolepis* (A. Gray) A. Gray	WSG	N		√
Switchgrass ‘Cave-in-rock’	*Panicum virgatum* L.	WSG	N	√	
Hoary ticktrefoil	*Desmodium canescens* (L.) DC.	WSL	N	√	
Illinois bundleflower	*Desmanthus illinoensis* (Michx.) MacMill. ex B.L. Rob. & Fernald	WSL	N	√	
Panicledleaf ticktrefoil	*Desmodium paniculatum* (L.) DC.	WSL	N	√	
Strawberry clover	*Trifolium fragiferum* L.	WSL	Both	√	

CSG cool season grasses (C3), *WSG* warm season grasses (C4), *CSL* cool season legumes (C3), *WSL* warm season legumes (C3), *N* native to US, *I* introduced to US

[a] Common names and scientific names followed the information in USDA PLANTS database (USDA NRCS 2016). All forages are perennials and Italian ryegrass is annual/perennial depending on climate and length of growing season

Forage quality determination

Oven-dried forage from 16 grasses and 6 legumes from harvests in 1999, 2000, or 2001 were chemically analyzed to determine %CP, NDF, and ADF. To estimate %CP, 0.05 to 0.1 g samples were analyzed on a LECO FP-248 Nitrogen Analyzer to determine N and multiplied by 6.25 (Rivera and Parish 2010). The CP yield (g pot^{-1}) was determined by multiplying forage yield by the %CP for summer and fall harvest, respectively. A 0.5 to 1 g sample was put into a 600 mL Berzelius beaker with 100 mL of NDF or ADF solution and boiled for an hour. The solutions were then filtered, oven-dried overnight at 105 °C, re-weighed, and analyzed for NDF or ADF. Relative feed value was determined following the equations in the introduction.

Experimental design and data analysis

The experiment was a split plot design with a randomized complete block arrangement of 3 replications for shade (whole plot) and harvest time as the subplot factor for each forage. Main plots were the non-shade control, moderate shade, and dense shade. Percent CP, CP yield, and RFV were analyzed using PROC Mixed in SAS 9.4 (SAS Inc., Gary, NC). In each model, Shade, Harvest, and the Shade*Harvest interaction are fixed effects, and the whole-plot error (Block*Shade) and the split-plot error (Block*Shade*Harvest, i.e., the residual) are random effects (Eq. O1 in Online Resource 1). In the random portion, the default diagonal covariance structure (type = vc) was used. An auto-correlated covariance structure (AR(1)) was applied to address potential correlations between repeated harvests on the same plants. Each quality parameter was further analyzed across harvest times by grouping forages into 4 forb types (Eq. O2 in Online Resource 1): warm season grasses (C4), cool season grasses (C3), warm season legumes (C3), and cool season legumes (C3). Values for %CP, CP yield, and RFV were natural-log transformed before analysis, and then back-transformed for data presentation. Tukey method ($\alpha = 0.05$) was applied for the mean separations.

An equation to calculate Relative Distance Plasticity Index (RDPI) proposed by Valladares et al. (2006) was applied as it was for our earlier analyses (Pang et al. 2017). For each quality parameter, an RDPI value was estimated at each harvest time for each species across the 3 blocks and 3 shade levels. For species with multiple cultivars, cultivars were used as replicates for that species. To include more forages and increase the accuracy of estimation, RDPI values were also calculated from the original data for 18 forages (14 species with 4 of them having 2 cultivars each) screened in 1994 and 1995 by Lin et al. (2001) under similar shade treatments as in our study. For each forage quality parameter, RDPI was natural-log transformed and compared both among species and forb types using PROC MIXED. Tukey method ($\alpha = 0.05$) was used for the mean separations.

Results

Forage quality

When grown under non-, moderate, and dense shade, %CP was the same for 6 of the 22 forages, including bahiagrass 'Argentine', eastern gamagrass, Kentucky bluegrass, Illinois bundleflower, hoary ticktrefoil, and strawberry clover (Table 2). The remaining 16 forages on average were 43% higher in %CP when grown under dense shade than in the control. Only smooth brome had higher %CP under moderate shade than the non-shade control with no differences for the other 21 forages. A general trend of increasing %CP as shade increased was observed even though interactions between shade and harvest time were found for 8 forages (Table 2; Fig. 1). For most forages, this interaction occurred because the change in %CP between forages grown under moderate and dense shade was greater for the summer harvest than the fall harvest. For strawberry clover, %CP declined under dense shade in the fall but not in the summer harvest in 1999.

CP yield (g pot^{-1}) for 8 of the 22 forages was the same under non-, moderate, and dense shade (Table 3). This group included hoary ticktrefoil, white clover, eastern gammagrass, 2 bahiagrass cultivars ('Argentine' and 'Pensacola'), clustered fescue, Bermudagrass, and timothy. For the remaining 14 forages, 5 of them did not differ in CP yield between the control and moderate shade, while 9 had higher CP yields when grown under moderate shade than in the control. Five forages under dense shade had higher CP yields than the non-shade control, including Italian ryegrass,

Table 2 F-value and its level of significance for the fixed effects in the models for each forage, the least square means and 95% confidence interval (CI) of %CP across harvests for 22 forages grown under non-, moderate, and dense shade

Forages	F[a]			Non-shade (full sun)		Moderate shade (45% of full sun)		Dense shade (20% of full sun)	
	Shade (S)	Harvest (H)	S*H	CP[b] (%)	95% CI	CP (%)	95% CI	CP (%)	95% CI
Illinois bundleflower	0.93[NS]	10.93*	1.79[NS]	14.5a	13.28–15.87	14.55a	13.31–15.91	13.61a	12.45–14.88
Bahiagrass 'Argentine'	1.36[NS]	45.12***	1.73[NS]	7.89a	6.65–9.36	7.27a	6.13–8.62	8.23a	6.94–9.76
Hoary ticktrefoil	2.45[NS]	0.43[NS]	2.89[NS]	12.99a	11.57–14.58	13.69a	12.20–15.37	15.06a	13.41–16.90
Eastern gamagrass[c]	3.12[NS]	17.20***	1.43[NS]	6.01a	5.27–6.85	5.02a	4.40–5.72	–	–
Strawberry clover	4.03[NS]	81.42***	5.79*	14.81a	13.48–16.26	17.38a	15.83–19.09	16.62a	15.13–18.25
Kentucky bluegrass	4.45[NS]	9.90*	4.67[NS]	18.71a	16.74–20.90	16.23a	14.53–18.14	19.69a	17.62–21.99
Clustered fescue[c]	5.21*	41.30***	3.39*	7.17b	6.39–8.06	7.67ab	6.83–8.62	9.34a	8.32–10.49
White clover	7.93*	22.44**	5.97*	18.09b	16.89–19.37	19.50ab	18.21–20.88	21.51a	20.08–23.04
Panicledleaf ticktrefoil	10.83*	8.14*	1.27[NS]	12.43b	10.88–14.19	13.89ab	12.16–15.86	14.52a	12.71–16.58
Red clover	13.74*	72.48***	10.66*	15.65b	14.52–16.88	17.46ab	16.19–18.82	19.66a	18.24–21.20
Bermudagrass	15.85*	2.09[NS]	2.28[NS]	4.98b	4.15–5.97	5.42b	4.52–6.49	9.11a	7.60–10.92
Bahiagrass 'Tifton–9′	16.14*	36.48***	0.37[NS]	6.47b	5.97–7.00	6.67b	6.16–7.22	8.43a	7.79–9.13
Italian ryegrass	16.30*	4.62[NS]	6.88*	11.32b	10.07–12.72	12.64b	11.25–14.20	15.78a	14.05–17.73
Bahiagrass 'Pensacola'	16.58*	50.48***	4.05[NS]	6.79b	6.06–7.61	7.21b	6.43–8.07	10.00a	8.93–11.20
Reed canarygrass	17.2*	1.92NS	2.44[NS]	11.23b	10.38–12.14	10.89b	10.08–11.78	14.21a	13.14–15.36
Prairie dropseed[c]	17.35*	50.95***	0.61[NS]	5.60b	4.82–6.52	7.03b	6.05–8.18	9.79a	8.29–11.56
Orchardgrass 'Benchmark'	30.01**	61.47***	1.09[NS]	11.67b	10.65–12.79	11.99b	10.94–13.14	16.22a	14.79–17.77
Prairie cordgrass	48.20**	9.59*	7.09*	8.18b	7.57–8.84	8.57b	7.93–9.26	11.64a	10.77–12.58
Timothy	58.59**	80.85***	11.17**	11.50b	10.74–12.32	12.99b	12.13–13.91	17.61a	16.45–18.86
Redtop	65.11***	0.00[NS]	17.47**	12.24b	11.45–13.08	11.94b	11.17–12.77	16.24a	15.19–17.35
Switchgrass 'Cave-in-Rock'	66.54***	11.78*	0.05[NS]	6.54b	5.93–7.22	7.03b	6.37–7.76	11.39a	10.32–12.57
Smooth brome	64.57***	11.80*	1.62[NS]	11.22c	10.47–12.02	13.25b	12.37–14.19	17.32a	16.17–18.55

[a] *NS* not significant ($P \geq 0.05$); * $0.01 \leq P < 0.05$; ** $0.001 \leq P < 0.01$; *** $P < 0.0001$

[b] Means within a row with same designation letters are not significantly different at $\alpha = 0.05$ level. Means and CI values are all back transformed from natural log to original scale

[c] These three forages were harvested in fall 2000, summer 2001, and fall 2001, and all other forages were harvested in summer and fall 1999

orchardgrass 'Benchmark', smooth brome, reed canarygrass, and Kentucky bluegrass. Interactions existed between shade and harvest time for prairie cordgrass, panicledleaf ticktrefoil, and orchardgrass largely because of their variable responses when grown without shade (Fig. 2).

RFV was the same for 12 of the 22 forages grown under non-, moderate, and dense shade (Table 4). This group included red clover, white clover, panicledleaf ticktrefoil, reed canarygrass, redtop, smooth brome, prairie dropseed, clustered fescue, orchardgrass, Kentucky bluegrass, and 2 bahiagrass cultivars ('Pensacola' and 'Tifton-9'). For the other 10 forages, 8 of them showed a decline in RFV from control to moderate shade, while 5 forages had no differences between moderate and dense shade. Only prairie cordgrass showed a continuous decline in RFV from non- to moderate to dense shade. Interactions between shade and harvest time were found for 8 forages (Table 4; Fig. 3). Despite the interactions between shade and harvest time, the overall trend for RFV of eastern gamagrass, hoary ticktrefoil, and Illinois

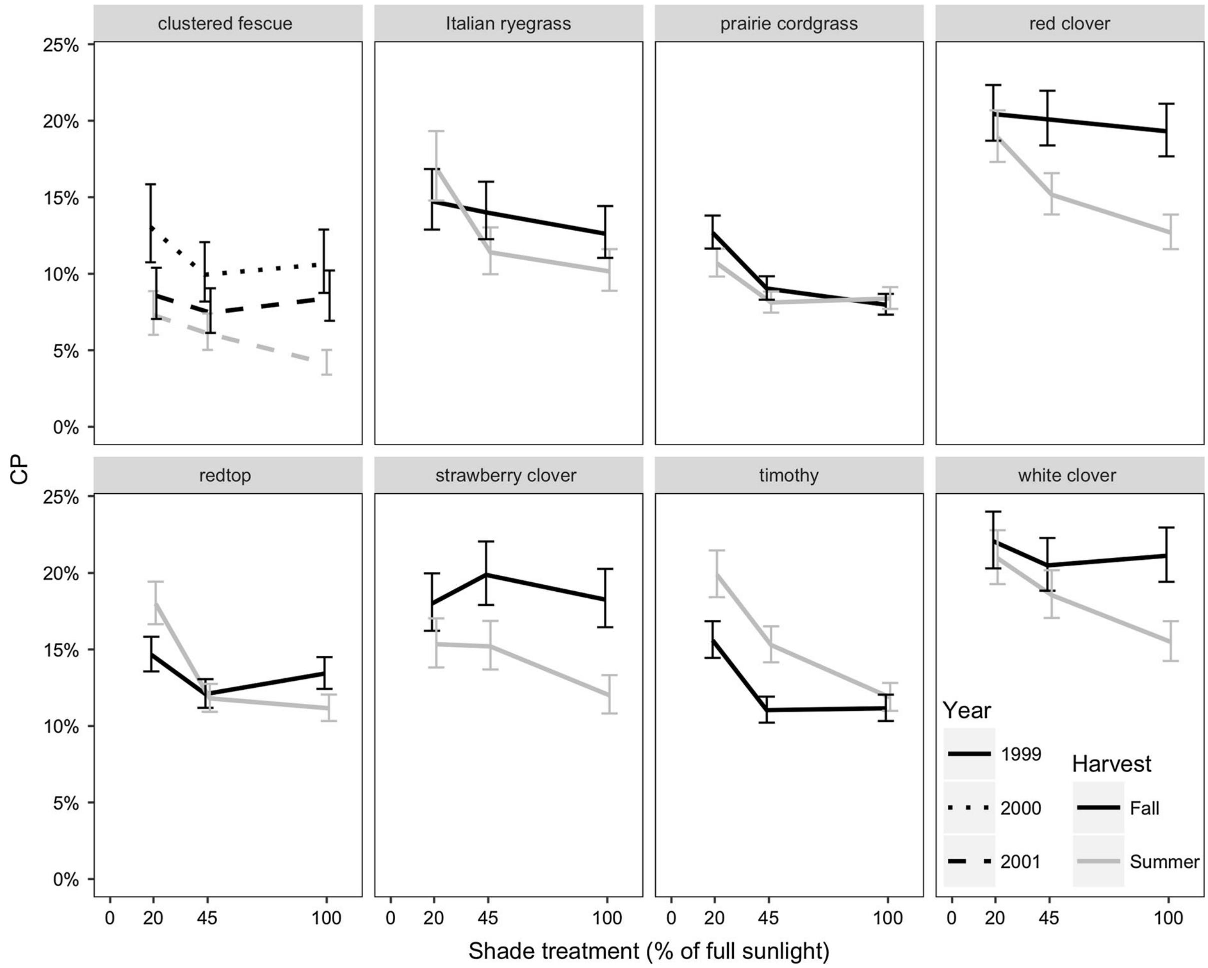

Fig. 1 Interactions between shade and harvest time on percent crude protein (CP) for the 8 (p's < 0.05) among the 22 tested under non-, moderate, and dense shade in 1999 or 2000–2001

bundleflower showed a decrease as light was reduced (Fig. 3). For bahiagrass "Argentine" and "Pensacola", panicledleaf ticktrefoil, and redtop, RFV increased as shade increased in the 1999 summer harvest, but remained unchanged or decreased as shade increased in the fall harvest (Fig. 3). The RFV of switchgrass in the 1999 fall harvest showed little change when shade increased, but for the 1999 summer harvest, switchgrass had high RFV's under both control and dense shade, but relatively low RFV under moderate shade (Fig. 3).

Forage quality parameters showed different trends between summer and fall harvests (Table O1-O3 in Online Resource 1). Six out of 22 forages had equal and 10 out of 22 had higher %CP in summer harvests than fall harvests. For CP yield, 4 out of 22 forages did not differ between summer and fall harvests, and 16 out of 22 had higher CP yield in summer than fall harvests in 1999. Six out of 22 forages showed no difference in RFV between summer and fall, while 13 out of 22 forages had higher RFV's in fall than in summer.

When forages were grouped by forb types, %CP, RFV, and CP yields were affected by shade (p's < 0.0001, Table O4 in Online Resource 1). Overall, %CP increased, but RFV remained unchanged or decreased slightly within each group when shade increased. All 4 types achieved higher CP yield under moderate shade than the control or dense shade, similar to the forage yield responses shown on

Table 3 F-value and its level of significance for the fixed effects in the models for each forage, the least square means and 95% confidence interval (CI) of CP yield (g pot^{-1}) across harvests for 22 forages grown under non-, moderate, and dense shade

Forages	F[a]			Non-shade (full sun)		Moderate shade (45% of full sun)		Dense shade (20% of full sun)	
	Shade (S)	Harvest (H)	S*H	CP yield[b] (g pot^{-1})	95% CI[1]	CP yield (g pot^{-1})	95% CI	CP yield (g pot^{-1})	95% CI
Hoary ticktrefoil	0.30[NS]	33.49**	1.47[NS]	0.95a	0.54–1.68	0.97a	0.55–1.71	0.77a	0.44–1.36
Eastern gamagrass[c]	0.69[NS]	10.43**	0.73[NS]	1.16a	0.88–1.53	1.41a	1.07–1.86	–	–
White clover	0.91[NS]	42.03***	0.45[NS]	2.04a	1.36–3.06	2.11a	1.40–3.17	1.54a	1.02–2.31
Bahiagrass 'Pensacola'	1.14[NS]	52.11***	0.02[NS]	1.76a	1.24–2.49	2.26a	1.60–3.21	2.03a	1.43–2.88
Clustered fescue[c]	1.50[NS]	14.72***	1.51[NS]	1.02a	0.72–1.43	1.38a	0.98–1.95	1.42a	1.00–2.00
Bermudagrass	2.25[NS]	109.44***	0.03[NS]	2.41a	1.78–3.26	3.13a	2.31–4.24	2.26a	1.67–3.06
Bahiagrass 'Argentine'	2.75[NS]	14.00**	0.07[NS]	1.83a	1.42–2.36	2.31a	1.79–2.97	1.88a	1.46–2.42
Timothy	5.48[NS]	0.26[NS]	1.89[NS]	1.11a	0.72–1.74	1.86a	1.19–2.90	1.04a	0.66–1.61
Illinois bundleflower	40.40**	246.93***	4.40[NS]	1.60a	1.30–1.97	2.15a	1.75–2.64	0.73b	0.59–0.90
switchgrass 'Cave-in-Rock'	15.90*	144.05***	1.95[NS]	1.83a	1.36–2.46	2.14a	1.59–2.87	1.35b	1.01–1.82
prairie dropseed[c]	45.44***	6.31*	0.95[NS]	1.63a	1.40–1.89	1.41a	1.21–1.64	0.53b	0.42–0.66
Prairie cordgrass	8.64*	62.00***	5.62*	1.15ab	0.93–1.42	1.30a	1.06–1.61	0.80b	0.65–0.99
Strawberry clover	12.05*	13.79**	0.23[NS]	1.15ab	0.80–1.65	2.24a	1.56–3.20	0.74b	0.52–1.06
Red clover	10.26*	2.59[NS]	1.25[NS]	1.27b	0.80–2.00	3.22a	2.04–5.07	1.27b	0.80–2.00
Bahiagrass 'Tifton-9'	14.71*	116.18***	0.12[NS]	1.96b	1.66–2.30	2.58a	2.19–3.04	2.00b	1.70–2.36
Panicledleaf ticktrefoil	18.21**	113.23***	5.55*	2.03b	1.06–3.89	3.28a	1.72–6.28	1.75b	0.91–3.34
Italian ryegrass	35.48**	90.28***	0.02[NS]	1.15b	1.00–1.32	2.28a	1.99–2.62	2.02a	1.76–2.31
Orchardgrass 'Benchmark'	37.74**	67.63***	8.10*	1.42b	0.81–2.51	2.01a	1.14–3.54	2.11a	1.19–3.71
Smooth brome	38.73**	23.20**	4.33[NS]	1.08b	0.83–1.40	2.13a	1.64–2.78	1.87a	1.44–2.44
Reed canarygrass	40.61**	83.07***	4.02[NS]	1.52b	1.25–1.84	2.75a	2.26–3.34	2.27a	1.87–2.76
Redtop	10.73*	265.27***	0.25[NS]	1.80b	1.44–2.25	2.57a	2.06–3.21	2.40ab	1.92–3.00
Kentucky bluegrass	48.45**	2.51[NS]	1.83[NS]	0.75c	0.62–0.89	2.02a	1.69–2.42	1.19b	0.99–1.42

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

[b] Means within a row with same designation letters are not significantly different at $\alpha = 0.05$ level. Means and CI values are all back transformed from natural log to original scale

[c] These three forages were harvested in fall 2000, summer 2001, and fall 2001, and all other forages were harvested in summer and fall 1999

the top left of Fig. 4. Legumes had higher quality (%CP and RFV, p's < 0.0001, Table O4 in Online Resource 1) than grass forages under shade, although legumes yielded less biomass than grasses. No differences in CP yield were found among the 4 forb types (Table O4 in Online Resource 1). Because CP yield is the product of biomass and %CP (2 parameters showing opposite trends and offsetting each other), CP yield had similar trends to forage yield when shade increased in all 4 forb types. An interaction between

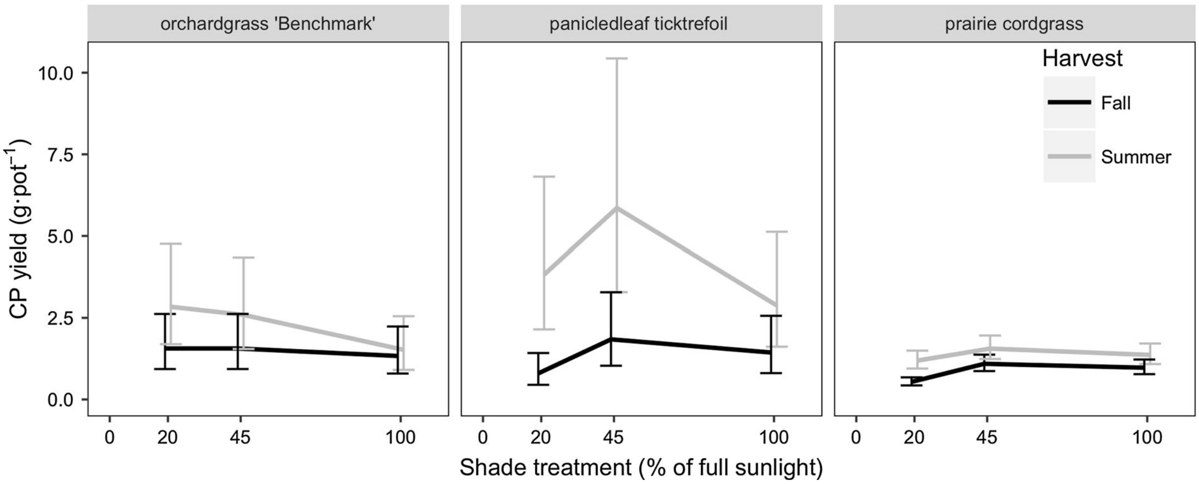

Fig. 2 Interactions between shade and harvest time on crude protein (CP) yield (g pot^{-1}) for the three temperate forages (p's < 0.05) among the 22 tested under non-, moderate, and dense shade in 1999 or 2000–2001

forb type and shade for RFV was minimal ($p = 0.0471$), while the interaction for %CP ($p < 0.0001$) was due to the low %CP of warm season legumes under dense shade (Fig. 4).

Relative distance plasticity index at species level

Average RDPI was determined for %CP, CP yield, and RFV for 20 out of 39 species that were evaluated for forage yield between 1996 and 2001 (Pang et al. 2017) and for 14 species assessed between 1994 and 1995 by Lin et al. (1999, 2001). RDPI values ranged from 0.025 to 0.204 for %CP, 0.121 to 0.353 for CP yield, and 0.027 to 0.123 for RFV for 25 species (Table 5). Differences exist among species in RDPI values for %CP ($p < 0.0001$), but not for CP yield ($p = 0.0428$) or RFV ($p = 0.1065$). RDPI values for RFV showed no differences likely due to the small variation observed in RFV within and among species. The species with the lowest RDPI values for %CP were Japanese clover, alfalfa, white clover, panicledleaf ticktrefoil, and hoary ticktrefoil; and the species with the highest RDPI values were Bermudagrass, switchgrass, and prairie dropseed (Table 5).

Grasses and legumes had different RDPI tendencies for individual parameters when responding to shade. With relatively low RFVs, grasses are more resilient to different levels of shade than legumes based on lower RDPI values (Table 5, $p = 0.0032$). Low RDPI values indicated that legumes changed less in %CP than grasses as light conditions changed ($p < 0.0001$). However, grasses and legumes did not differ in their RDPI values for CP yield ($p = 0.1263$).

Discussion

Shade effects on forage quality

As found in our studies, other studies have reported forages grown in shade have similar or slightly higher %CP than when grown in full sun. Lin et al. (2001) reported that %CP of all 15 forages tested either remained unchanged or increased as shade increased. Houx et al. (2009) found that hoary ticktrefoil, showy ticktrefoil, and Illinois bundleflower had equal or higher nitrogen concentration under 80% shade cloth than under 55% shade cloth or without shade cloth in a greenhouse that reduced ambient light by 40–50%. Nitrogen concentration also increased as shade increased in green panic (*Panicum maximum*) and kikuyu (*Pennisetum clandestinum*) at low-nitrogen availability (Samarakoon 1988). Burton et al. (1959) found %CP increased as shade level increased in coastal Bermudagrass (*Cynodon dactylon*) at both low- and high-nitrogen soil fertility levels. In contrast, %CP decreased in Siratro (*Macroptilium atropurpureum*) as shade increased if defoliated every 4 or 8 weeks (Wong and Wilson 1980). Kallenbach et al. (2006) reported increased %CP for Italian ryegrass

Table 4 F-value and its level of significance for the fixed effects in the models for each forage, the least square means and 95% confidence interval (CI) of RFV across harvests for 22 forages grown under non-, moderate, and dense shade

Forages	F[a]			Non-shade (full sun)		Moderate shade (45% of full sun)		Dense shade (20% of full sun)	
	Shade (S)	Harvest (H)	S*H	RFV[b]	95% CI	RFV	95% CI	RFV	95% CI
Red clover	0.08[NS]	26.49**	4.92[NS]	211a	177-251	202a	170–241	205a	172–243
White clover	0.45[NS]	36.86***	1.68[NS]	276a	259–295	285a	267–304	275a	258–293
Reed canarygrass	0.68[NS]	9.64*	0.66[NS]	126a	118–134	121a	114–129	120a	113–129
Redtop	1.14[NS]	0.87[NS]	8.00*	130a	121–140	122a	113–131	127a	118–137
Smooth brome	1.43[NS]	39.37***	4.34[NS]	139a	130–149	134a	125–144	130a	122–139
Panicledleaf ticktrefoil	1.44[NS]	24.63**	29.79***	161a	147–175	148a	136–162	151a	139–165
Prairie dropseed[c]	1.58[NS]	11.09**	2.70[NS]	75a	72–79	74a	71–78	71a	68–75
Clustered fescue[c]	1.87[NS]	114.27***	1.68[NS]	82a	78–86	86a	81–90	87a	83–92
Orchardgrass ‘Benchmark’	3.37[NS]	193.12***	1.35[NS]	134a	125–144	131a	123–141	122a	114–131
Kentucky bluegrass	3.50[NS]	0.31[NS]	2.28[NS]	117a	111–122	112a	107–118	108a	103–113
Bahiagrass ‘Pensacola’	4.93[NS]	3.84[NS]	8.19*	99a	95—103	93a	90–97	94a	90–97
Bahiagrass ‘Tifton–9’	6.80[NS]	6.42*	1.88[NS]	115a	103–129	94a	84–105	92a	83–103
Bahiagrass ‘Argentine’	10.78*	6.85*	13.51**	103a	94–114	98b	89–107	94b	85–103
timothy	11.70*	7.36*	2.56[NS]	141a	135–148	129b	124–135	127b	121–132
Hoary ticktrefoil	15.97*	21.09**	10.65*	170a	160–182	142b	133–152	137b	128–146
Illinois bundleflower	32.87**	1.9[NS]	11.29**	234a	213–257	181b	165–199	156b	142–172
Bermudagrass	55.71**	22.96**	1.44[NS]	118a	115–120	107b	104–109	102b	100–105
Prairie cordgrass	41.12**	146.08***	1.15[NS]	98a	95–100	92b	89–94	86c	84–88
Eastern gamagrass[c]	14.05**	19.84***	4.41*	93a	90–97	88b	84–91	–	–
Switchgrass ‘Cave-in-Rock’	19.83**	292.37***	30.74***	108a	103–114	101b	96–107	109a	103–115
Italian ryegrass	21.59**	7.31*	0.76[NS]	125a	120–130	108b	103–113	122a	117–127
Strawberry clover	14.83*	4.63[NS]	2.33[NS]	217b	207–228	246a	234–258	213b	202–223

[a] *NS* not significant ($P \geq 0.05$); * $0.01 \leq P < 0.05$; ** $0.001 \leq P < 0.01$; *** $P < 0.0001$

[b] Means within a row with same designation letters are not significantly different at $\alpha = 0.05$ level. Means and CI values are all back transformed from natural log to original scale

[c] These three forages were harvested in fall 2000, summer 2001, and fall 2001, and all other forages were harvested in summer and fall 1999

and cereal rye (*Secale cereale* L.) in silvopastures compared to open pastures after the walnut trees leafed out.

We found most forages maintained CP yields under moderate and dense shade, and some were even higher than plants grown without shade. Lin et al. (2001) found that 9 out of 15 forages under moderate shade and 6 forages under dense shade had equal CP yields compared to their non-shade control. In addition, 5 of the 15 forages under moderate shade and 3 forages under dense shade had higher CP yields than forages grown in the full sun treatment (Lin et al. 2001).

Because ADF and NDF in Lin et al. (2001) and our studies (data available on request) were either unchanged or slightly increased by shade, RFV, which is derived from ADF and NDF, also showed minimal responses to shade. Moderate and dense shade resulted in no change in RFV for 13 and 15 of 22 forages, respectively, compared to the non-shade control in our study. Likewise, the RFV’s calculated from the original ADF and NDF values in the Lin et al. (2001) study, changed for only 3 of 14 forages when grown under shade. In our study, 13 out of 22 forages had higher RFV in fall than in summer harvest

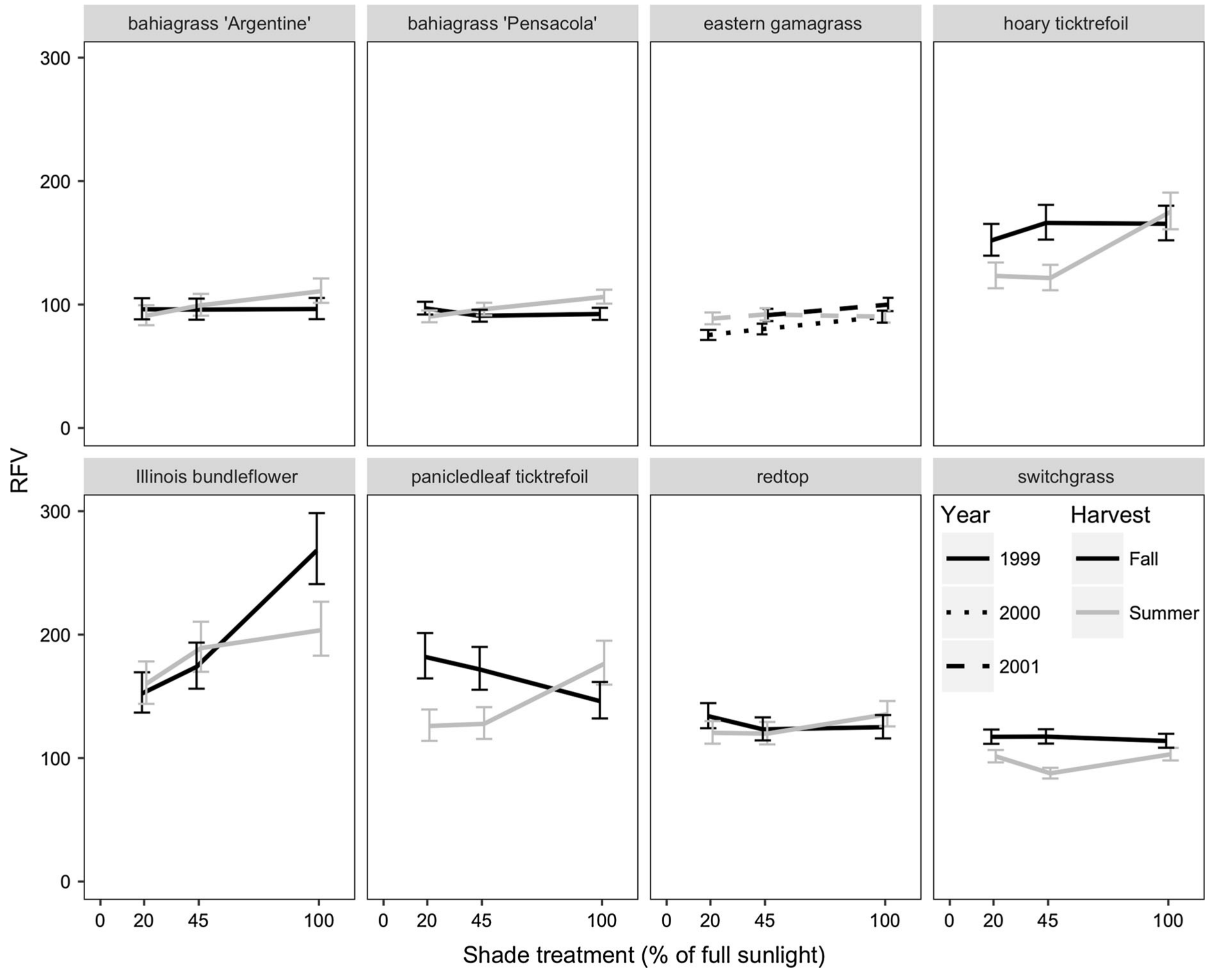

Fig. 3 Interactions between shade and harvest time on relative feed value (RFV) for the eight temperate forages (p's < 0.05) among the 22 tested under non-, moderate, and dense shade in 1999 or 2000–2001

possibly due to higher temperatures before the summer harvest (June, July, and August) than the fall harvest (September and October). Ball et al. (2001) indicated forages grown at lower temperatures had higher quality than plants grown at high temperatures. Contreras-Gove and Albrecht (2006) reported oat (*Avena sativa*) had lower ADF and NDF (hence higher RFV) in the fall than the summer.

Legume forages usually have both higher RFV and %CP than grasses due to lower concentrations of fiber (Ball et al. 2001; Bonin and Tracy 2011). Likewise, we found both warm and cool season legumes had higher RFV and %CP than grass forages. Warm season grasses usually have a higher fiber content and lower nutritive quality in terms of lower %CP than cool season grasses (Reid et al. 1988; Ball et al. 2001; Bonin and Tracy 2011). This is consistent with our findings that warm season grasses had lower %CP and RFV than cool season grasses across non-, moderate, and dense shade.

Differences in shade responses and resilience between grasses and legumes

Grass and legume forages responded to shade differently as reflected by their differences in biomass (Pang et al. 2017), %CP, CP yields, and RFV under the 3 shade levels (Fig. 4), and the different degrees of resilience (RDPI) of each aforementioned forage quality trait (Table 3 in Pang et al. 2017, and Table 5). These

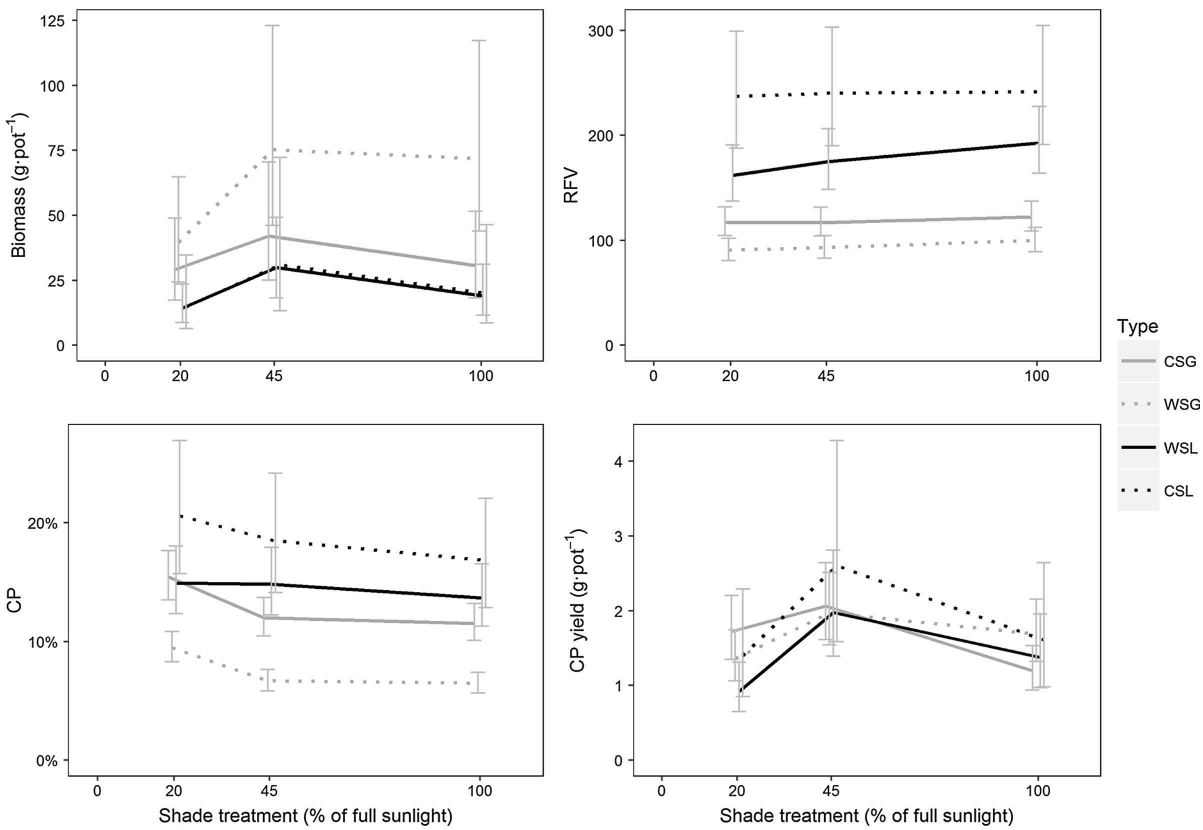

Fig. 4 Interaction between shade and forage type for average annual forage yield (biomass) across years (Pang et al. 2017) and forage quality parameters averaged across summer and fall harvests: *CP* percent crude protein, *RFV* relative feed value, and CP yield (g pot^{-1}) for *CSG* cool season grasses, *WSG* warm season grasses, *WSL* warm season legumes, *CSL* cool season legumes

differences may be consequences of the difference in physiological and life history traits between grasses and legumes. As also found by Bonin and Tracy (2011), warm season grasses yielded more biomass than other groups of forages including legumes. Del Pozo et al. (2000) suggested that legumes have lower rates of carbon gain than annual C3 grasses at stand level, short time scale, and leaf level, explaining the lower biomass generally found in legumes compared to grasses; however, the nitrogen concentration (%CP) in vegetative organs was higher in legumes than in grasses. High resilience of %CP (low RDPI) for legumes may be due to the nitrogen fixing ability of legumes and their using feedback mechanisms to determine the amount of photosynthate to allocate for N fixation and growth, while grasses are dependent solely on available soil nitrogen. Lin et al. (2001) also found %CP was less affected by shade in legumes than in grasses. Although plant growth rate is dependent on nitrogen concentration in vegetative organs, high %CP in legumes may not be contributing to carbon sequestration, but rather stored for future seed production, a trade-off common in legumes (Del Pozo et al. 2000). Therefore, it is possible that the tendency of legume species' preserving stronger nitrogen sinks is at the expense of their low carbon gain rate and low resilience on biomass (Pang et al. 2017). Conversely, the opposite may be true for grasses.

Conclusion

Our study showed most forages remain unchanged or increased in aboveground biomass and CP yields when grown under moderate or dense shade, if supplied with adequate water and nutrients and free of root competition from other plants. Likewise, for all 22 forages %CP either did not change or increased under both

Table 5 Least square means, confidence interval (CI), and rank for relative distance plasticity index (RDPI) values for percent crude protein (%CP), CP yield, and relative feed value (RFV) for 25 forages and 4 forage types

Species	Group	%CP			CP yield			RFV			# of cultivars[b]	
		RDPI[a]	95% CI	Rank	RDPI	95% CI	Rank	RDPI	95% CI	Rank	1999–2001	1994–1995
Japanese clover	WSL	0.025bd	0.013–0.047	1	0.290a	0.165–0.512	21	0.074a	0.038–0.147	23	0	1
Alfalfa	CSL	0.030bc	0.016–0.057	2	0.159a	0.090–0.280	7	0.064a	0.033–0.127	22	0	1
White clover	CSL	0.031b	0.020–0.049	3	0.209a	0.140–0.313	16	0.043a	0.027–0.070	14	1*	1
Panicledleaf ticktrefoil	WSL	0.049ab	0.031–0.077	4	0.169a	0.113–0.252	12	0.047a	0.029–0.076	19	1*	1
Hoary ticktrefoil	WSL	0.053ab	0.034–0.084	5	0.165a	0.110–0.246	10	0.045a	0.028–0.073	16	1*	1
Slender lespedeza	WSL	0.059ab	0.024–0.145	6	0.255a	0.114–0.570	20	0.027a	0.010–0.072	2	0	1
Red clover	CSL	0.059ab	0.031–0.112	7	0.319a	0.181–0.563	22	0.111a	0.056–0.219	24	1	2
Kentucky bluegrass	CSG	0.060ab	0.038–0.095	8	0.248a	0.166–0.371	19	0.033a	0.020–0.053	6	1*	1
Strawberry clover	WSL	0.061ab	0.032–0.116	9	0.353a	0.200–0.624	25	0.060a	0.031–0.119	21	1	0
Illinois bundleflower	WSL	0.064ab	0.034–0.121	10	0.348a	0.197–0.614	24	0.123a	0.062–0.243	25	1	0
Perennial ryegrass	CSG	0.065ab	0.034–0.124	11	0.162a	0.092–0.286	8	0.040a	0.020–0.078	12	0	1
Tall fescue	CSG	0.086ab	0.054–0.135	12	0.187a	0.125–0.280	14	0.030a	0.019–0.049	4	0	2
Reed canarygrass	CSG	0.096ab	0.050–0.181	13	0.200a	0.114–0.354	15	0.033a	0.017–0.066	7	1	2
Smooth brome	CSG	0.096ab	0.061–0.151	14	0.187a	0.125–0.279	13	0.035a	0.022–0.057	8	1*	1
Bahiagrass	WSG	0.097acd	0.067–0.141	15	0.121a	0.087–0.167	1	0.046a	0.031–0.068	18	3	0
Redtop	CSG	0.102ab	0.054–0.193	16	0.130a	0.074–0.230	2	0.041a	0.021–0.081	13	1	0
Italian ryegrass	CSG	0.105ab	0.055–0.200	17	0.223a	0.127–0.394	18	0.055a	0.028–0.108	20	1	0
Clustered fescue	CSG	0.106ab	0.063–0.179	18	0.137a	0.086–0.218	4	0.029a	0.016–0.050	3	1	0
Eastern gamagrass	WSG	0.106ab	0.063–0.179	19	0.150a	0.095–0.239	6	0.039a	0.023–0.069	11	1	0
timothy	CSG	0.113ac	0.072–0.178	20	0.217a	0.145–0.324	17	0.036a	0.022–0.057	10	1*	1
Orchardgrass	CSG	0.122ac	0.084–0.176	21	0.137a	0.099–0.190	3	0.035a	0.024–0.053	9	1*	2
Prairie cordgrass	WSG	0.122ab	0.064–0.232	22	0.162a	0.092–0.286	9	0.043a	0.022–0.086	15	1	0
Prairie dropseed	WSG	0.173a	0.102–0.292	23	0.323a	0.203–0.514	23	0.027a	0.016–0.047	1	1	0
Switchgrass	WSG	0.186a	0.098–0.353	24	0.168a	0.095–0.296	11	0.031a	0.016–0.061	5	1	0
Bermudagrass	WSG	0.204a	0.108–0.388	25	0.150a	0.085–0.265	5	0.046a	0.023–0.090	17	1	0
Forb types	CSL	0.036B	0.026–0.050	I	0.217A	0.159–0.296	III	0.060A	0.043–0.085	IV		
	WSL	0.049B	0.039–0.063	II	0.225A	0.180–0.282	IV	0.056A	0.044–0.072	III		
	CSG	0.095A	0.081–0.111	III	0.178A	0.153–0.208	II	0.035B	0.030–0.041	I		
	WSG	0.130A	0.105–0.162	IV	0.162A	0.132–0.199	I	0.039AB	0.031–0.049	II		

CSG cool season grasses, *WSG* warm season grasses, *CSL* cool season legumes, *WSL* warm season legumes

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

[b] Number of cultivars tested in each period of time. * indicates the number of cultivars of that species shared with Lin et al. (2001)

moderate and dense shade. RFV was similar for most forages under moderate and dense shade compared to the non-shade control. Low RDPI values indicate small changes in %CP, CP yield, or RFV across non-, moderate, and dense shade, thus greater adaptability to light change in the environment.

Our results indicate that for most temperate forages, their quality (RFV, %CP, and CP yield) will be retained or increased under moderate shade compared to open conditions along with their aboveground biomass (Pang et al. 2017). Several agroforestry practices are characterized by continuums from moderate to dense shade as the trees grow. Agroforestry practitioners may want to choose forages with low RDPI values for biomass, CP yield, %CP, and RFV, because these species are more likely to maintain biomass and quality in their agroforestry practices. Landowners may also want to consider a mixture of both legumes and grasses to ensure high production and quality using grasses with high shade tolerance for forage production and legumes that are capable of maintaining forage quality under increasing shade.

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