Tree canopy effect on grass and grass/legume mixtures in eastern Nebraska

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Agroforest Syst (2009) 77:23–35
DOI 10.1007/s10457-009-9234-x

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Received: 5 April 2008 / Accepted: 8 May 2009 / Published online: 9 June 2009

Abstract A study to determine the feasibility of producing forage for grazing livestock under trees was conducted as a step toward evaluating the potential for silvopasture systems in the northern and central Great Plains. The effects of overstory leaf area index (LAI), percentage understory light transmittance (LT), and soil moisture (SM) on yield and crude protein (CP) of big bluestem [*Andropogon gerardii* Vitman; (BB)], smooth bromegrass [*Bromus inermis* Leyss.; (SB)], and mixtures with birdsfoot trefoil [*Lotus corniculatus* L.; (BFT)] were examined. The study was conducted in both Scotch pine (*Pinus sylvestris* L.) and green ash (*Fraxinus pennsylvancia* Marsh.) tree plantations, at the University of Nebraska Agriculture Research and Development Center near Mead, Nebraska. Thirty-six plots representing a wide range of canopy cover were selected at each location and seeded in April 2000 to BB, SB, or mixtures with BFT. Measurements of LAI, LT, and SM were taken throughout the 2001-growing season and plots were harvested in June and September 2001. Soil moisture generally did not explain much of the variability in yield or CP for BB, SB, or BFT. Cumulative LAI or LT averaged over the growing season was the best predictor of yield or CP, particularly under the pine. Yields of BB and SB increased as LAI decreased or LT increased. Conversely, the CP of BB and SB increased as LT decreased for both the June and September harvests. Both BB and SB maintain relatively high productivity under partial shading; however, BFT yields were low at LT levels below 75%.

Keywords *Andropogon gerardii* Vitman · *Bromus inermis* Leyss. · Leaf area index · Light transmittance · *Lotus corniculatus* L. · Silvopasture

Introduction

Silvopasture is a type of agroforestry that intentionally combines trees, forage crops, and livestock production into a structural system of planned interactions. These

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are managed intensively to produce simultaneously wood products, high quality forage, and livestock on an environmentally sustainable basis (Clason and Sharrow 2000). A silvopasture system provides an overall greater economic return for the landowner per hectare than either timber or cattle alone (Pearson and Whitaker 1974; Clason 1995; Gold et al. 2000). In the United States, the majority of research with silvopasture systems has been conducted in the southeast and northwest, and has focused on forage and/or animal performance under various canopy covers of different conifer tree species or the forage response to different light levels, whether imposed by shade cloth or tree canopy (Pearson and Whitaker 1974; Garrett and Kurtz 1983; Lewis et al. 1985; Kephart et al. 1992; Kephart and Buxton 1993).

Most warm-season grasses utilize the C_4 photosynthetic pathway of carbon fixation whereas cool-season grasses use the C_3 pathway (Waller and Lewis 1979). The C_4 species are adapted to full sunlight and generally possess a higher light saturation point, higher photosynthetic capacity, and show a greater reduction in photosynthetic capacity under shade than C_3 species (Björkman 1981). At light saturation, C_3 grasses have a maximum photosynthetic rate about one-half that of C_4 grasses (Moser and Hoveland 1996). Cool-season plants generally respond to shade by investing a greater proportion of synthetic capacity into increasing overall leaf chlorophyll content (Boardman 1977), whereas warm-season plants respond by increasing specific leaf area (Murchie and Horton 1997). Even with greater specific leaf area, shaded leaves of C_4 plants intercept less light than full sunlight leaves and net photosynthesis declines because of low irradiance (Kephart et al. 1992).

Forage quality is modified by the plant environment, and temperature and soil moisture may have a more profound effect on overall quality than light flux (Buxton and Fales 1994; Henderson and Robinson 1982). Shading, with the associated lower temperatures, however, may cause lower cell wall concentrations and increased nutrient content because of slower rate of plant maturity (Allard et al. 1991; Kephart and Buxton 1993). Soil water deficiency also can have a positive influence on forage quality (Misra and Singh 1982; Wilson 1983). Seasonal water deficits generally slow the rate of plant maturity, and dry matter (DM) production, thereby increasing the nutrient content and digestibility of plant tissue.

Forage production in silvopasture systems with different tree canopy covers has not been documented in the eastern prairie region of the Great Plains. Warm-season grasses may not be well suited for understory conditions because of their high light requirements, but big bluestem (*Andropogon gerardii* Vitman; BB), a common native warm-season grass, is adapted to a wide range of environments (Stubbendieck et al. 1997). In the tall-grass prairie in the eastern Great Plains, BB is the most abundant and highest-quality species present in good to excellent condition range (Moser and Vogel 1995). Of the tall grasses found in Nebraska, BB is the most shade tolerant (Weaver 1965). Cool-season grasses that are shade tolerant and well adapted to the eastern Great Plains, such as smooth bromegrass (*Bromus inermis* Leyss.; SB), appear to be excellent candidates. Smooth bromegrass is adapted to many environments and soil types and tolerates moderate shade conditions (Fulbright et al. 1982; Lin et al. 1999). Smooth bromegrass is highly palatable, is high in crude protein (CP) content, relatively low in fiber and produces excellent hay for livestock and fall regrowth may produce enough biomass for fall grazing programs (Casler and Calrson 1995; Stubbendieck et al.1997). Legumes are important components of pastures because of positive impacts on forage quality and quantity as well as providing soil nitrogen (N). Birdsfoot trefoil (*Lotus corniculatus* L.; BFT) is a legume adapted to a wide range of environmental conditions and is used commonly in grass/legume mixtures in the central and northern Great Plains. Birdsfoot trefoil can tolerate many growing conditions, can grow where soil properties or environmental conditions make alfalfa production difficult, and will grow under drought conditions (Beuselinck and Grant 1995; Undersander et al. 1993). The nutritive value of BFT has been suggested to be equal to or greater than that of alfalfa (Langilee and Calder 1971; Marten and Jordan 1979). The purpose of this study was to evaluate tree and forage species common to the central Great Plains, as to their potential in silvopasture systems.

The objective of this study was to determine dry matter yield and CP content of seeded understory forage species in response to a range of overstory leaf area or percentage understory light transmittance (LT), and their interactions with soil moisture.

Materials and methods

Study area

The study was conducted in two tree plantations at the University of Nebraska Agricultural Research and Development Center (ARDC) near Mead, Nebraska in 2001. The tree plantations were a stand of Scotch pine (*Pinus sylvestris* L.) trees (96°33′ W, 41°11′ N, and 315 m elevation) and green ash (*Fraxinus pennsylvancia* Marsh.) trees (96°30′ W, 41°08′ N, and 366 m elevation). The prominent soil type at the Scotch pine location is a Tomek silt loam (fine, smectitic, mesic Pachic Argiudolls) of loess origin; whereas, the soils of the green ash location are of loess origin and consists of Filbert silt loams (fine, smectitic, mesic Vertic Argialbolls) and Tomek silt loams (fine, smectitic, mesic Pachic Argiudolls). The soils at both locations are relatively fertile with pH ranging from 6.04 to 6.63 and organic matter content of the topsoil between 2.55 and 4.43% (Perry 2004). The long-term (1968–2001) mean annual precipitation was 675 mm with about 75% coming during the growing season, April through September (HPRCC 2002; Table 1). The precipitation in 2000 and 2001 was 587 and 695 mm, respectively. Rainfall amount for May 2001 (233 mm) exceeded the 31-year long-term average for this month (107 mm), with 137 mm falling the first 5 days of the month. Average temperatures from May through September in 2000 and 2001 were 21.4 and 21.1°C, respectively, and were near the long-term (1968–2001) average of 20.8°C (HPRCC 2002). The first killing frost of fall 2000 was October 5, 2000, and the last of 2001 was April 24, 2001.

The Scotch pine trees were planted at a spacing of 6.1 × 6.1 m in 1971 and 1972 as a seed orchard with branches grafted from various sources. Trees had been pruned most recently in winter 1989/1990. Canopy cover of the Scotch pine location was relatively uniform, except where groups of trees had died, resulting in scattered openings. Tree basal diameters ranged from 18 to 76 cm. The understory was not seeded at tree planting, and no effort was made to control the establishment of invading species. Smooth bromegrass and tall fescue (*Festuca arundinacea*, Schreb.) were the principal plant species under dense canopy cover and transition areas, while the open areas were dominated by green foxtail [*Setaria viridis* (L.) Beauv]. The most common understory forb was creeping woodsorrel (*Oxalis corniculata* L.).

A site was selected at the Scotch pine location that included an open area with little to no overhead canopy, a dense canopy of trees, and an area of intermediate canopy density. There were no trees in the open area but branches of the neighboring trees partially shaded the area, especially on the south side. Thirty-six contiguous plots were located within this site with 12 plots each in the open area, in the dense canopy area, and in the intermediate canopy area. Each plot measured 3.0 × 4.6 m. In mid-summer 2001, average plot LAI ranged from 0 in the plots of the open area (although the LAI of some plots was as high as 0.5–1.0 because of surrounding trees) to 5.3 in dense canopy plots. Basal area of trees in the intermediate and dense canopy areas was as high as 30 m^2 ha^{-1}.

The green ash trees were from sources throughout the Great Plains. They were planted at a spacing of

Table 1 Monthly meteorological measurements for the Agricultural Research and Development Center near Mead, NE, 2001

Month	Maximum temperature (°C)	Minimum temperature (°C)	Relative humidity (%)	Solar radiation (MJ/m^2)	Total precipitation (mm)
Monthly averages					
Mar	7.05	−3.77	81.9	12.1	20.0
Apr	19.8	4.43	66.4	15.7	55.0
May	23.4	11.1	65.9	16.4	233.0[a]
June	27.7	14.9	68.7	21.0	42.0
July	31.4	19.2	78.9	19.1	5.58
Aug	30.3	16.6	74.6	19.9	58.4
Sept	24.8	11.0	73.9	15.5	60.1

[a] In May 137 mm of rainfall was recorded in the first 5 days of the month

3.7 m in 1981 at the ARDC as part of a drought resistance study. The understory was seeded to 'KY31' tall fescue following tree establishment. Tree canopy cover within the stand varied greatly because of variable tree size and death of some trees since planting. Tree basal diameters ranged from 3.3 to 28 cm. Existing differences in tree density and growth were used in selecting areas of low, intermediate, and dense tree canopy cover in August 1999. Within each area, there were 12 contiguous plots (3.7 × 3.7 m) with a tree at each corner. In midsummer 2001, average plot LAI and basal area of the trees at plot corners ranged from 1.7 and 5.7 m^2 ha^{-1} in low canopy plots to 2.7 and 11 m^2 ha^{-1} in dense canopy plots, respectively.

Experiment layout

Each of four different grass/legume mixtures was allocated randomly to three of the 12 plots within each of the canopy cover areas at the two locations. The mixtures were BB, BB/BFT, SB, and SB/BFT. Preparation of plots for seeding began in September 1999 when all understory vegetation was sprayed with glyphosate (4-amino-3,5,6-trichloropicolinic acid) at a rate of 1.1 kg a.i. ha^{-1} using a backpack sprayer. Prescribed fire was used in late March 2000 to remove all aboveground herbaceous plant material and suppress cool-season plants that had begun to grow. The plots were rototilled in early April to prepare a seedbed for seeding in mid-April. Big bluestem was seeded at 5.6 kg pure live seed (PLS) ha^{-1}; and SB was seeded at 8.9 kg PLS ha^{-1}. Big bluestem and SB were seeded at the same rates in mixtures with BFT which was seeded at 6.7 kg ha^{-1}.

Plots were irrigated twice weekly in May and June 2000 to ensure stand establishment. Weed density was high in 2000. To minimize the effect of weeds on stand establishment, each plot was hand-weeded once in June and July. Plots were not weeded or irrigated in 2001. Plots were mowed to a height of 7.6 cm in April 2001 to remove dead plant material before the second growing season.

Measurements and laboratory analysis

In each plot, LAI of the tree canopy was estimated using the LI-COR LAI-2000 plant canopy analyzer (LI-COR Incorporated, Lincoln, NE). Measurements were taken on a monthly basis from May through August 2001. All LAI measurements were taken on cloudy mornings or at dawn when the azimuth angle of the sun was no greater than 76° (Gower and Norman 1991). Measurements were taken at 1.0 m above the soil surface from each corner of a plot, facing the opposite corner. Reference measurements were taken two or more times on each collection day in an open field near each location. To mask out the operator, an opaque cover to restrict the viewing area to 45° or 90° was placed over the LAI sensor at the Scotch pine or green ash locations, respectively. The LAI data were downloaded to a computer following each collection period and processed using the C2000 program provided by LI-COR to correct the LAI values with respect to reference readings.

Percentage understory light transmittance was calculated following the method described by Constabel and Lieffers (1996). Measurements were taken on a monthly basis from May through August near solar noon (between 1,200 and 1,400 h). When possible, LT was measured within a few days of the LAI measurements. The LT measurements were taken on days with few or no clouds. Measurements were taken at 1.5 m above the soil surface in eight directions (cardinal and ordinal) from the center of each plot. Data collection per plot took approximately 30 s. The data were downloaded to a computer following each collection period. The eight data points per plot were averaged together then matched up with the LI-190SA Quantum Sensor data that was closest in time to determine % understory LT. Percentage understory LT was calculated by dividing the understory PAR readings for each plot by the unattenuated PAR readings (Constabel and Lieffers 1996) taken in the open.

Soil moisture (SM) was estimated with the Trase Time Domain Reflectrometry (TDR) System Model 6050X1 (Soil Moisture Equipment Corp., Santa Barbara, CA). Soil moisture was measured at the center of each plot at depth intervals of 0–15 cm, 0–30 cm, 0–45 cm, and 0–60 cm using stainless steel rods. Rods were installed and remained for the duration of the study; however, the 15-cm depth interval was measured by inserting a pair of 15-cm rods into the soil at the time of measurement. Soil moisture measurements were taken from April through July and were made in conjunction with LAI and LT measurements (Table 2).

Table 2 Number of observations (*N*), mean, and standard deviation (SEM) of % soil moisture content measurements from 2001

Depth increment (cm)	Scotch pine			Green ash		
	N	Mean	SEM	*N*	Mean	SEM
Soil moisture content (%)[a]						
April 0–15	–	–	–	35	32.2	0.52
May 0–15	36[b]	25.9	0.41	35	25.8	0.58
June SM 0–15	36	27.3	0.52	35	31.8	0.41
July SM 0–15	35	17.3	0.41	35[b]	23.5	0.55
April 0–30	–	–	–	32	33.4	0.25
May 0–30	36[b]	29.0	0.31	32	28.4	0.41
June SM 0–30	36	26.1	0.49	32	26.3	0.46
July SM 0–30	36	18.5	0.34	32[b]	21.1	0.46
April 0–45	–	–	–	32	33.8	0.40
May 0–45	36[b]	30.4	0.26	32	30.0	0.48
June SM 0–45	36	27.5	0.40	32	27.7	0.50
July SM 0–45	36	19.9	0.36	32[b]	20.6	0.64
April 0–60	–	–	–	32	35.4	0.62
May SM 0–60	36[b]	33.0	0.98	32	32.9	1.07
June SM 0–60	35	31.2	1.33	32	30.4	1.19
July SM 0–60	23	20.5	0.86	32[b]	20.6	0.73

[a] Percentage soil moisture was a volumetric measurement

[b] Soil moisture measurements were taken twice during the month, but were averaged together

Above-ground yields were estimated in all plots in early June 2001 and mid-September 2001 using a quadrat method. The June and September sampling dates coincided with the reproductive stage of BB and SB, respectively. To avoid sampling a point in a plot more than once, quadrat (25 × 100 cm) locations were identified within each plot and marked with flags before the first sampling date. At each sampling date, vegetation in each quadrat was clipped at ground level, separated into plant groups (i.e., BB, SB, BFT, or non-seeded species), and placed in separate paper bags.

Samples were dried in a forced-air oven at 60°C to a constant dry weight. After drying, BB and SB plants from each bag were separated into leaf and stem fractions. Leaf blades were separated at the collar, and the sheaths remained with the stems. The leaf fraction and stem fraction for each grass species from each quadrat were weighed and then composited by plot. The BFT bags also were composited for each plot. Composited samples were ground initially using a Wiley mill (Arthur Thomas Co., Philadelphia, PA) fitted with a 2-mm screen. Later, samples were ground using a cyclone mill (Udy Analyzer Company, Boulder, CO) fitted with a 1-mm screen in preparation for forage quality analysis. The nitrogen (N) content of each sample was estimated using a FP-428 N determination system 601-700-300 (Leco Corporation, St. Joseph, MI) in the University of Nebraska-Lincoln Soil and Plant Analysis Laboratory. The N content of each sample was then converted to CP using the conversion factor of 6.25.

Data analysis

Data from the two locations in 2001 were analyzed separately. Multiple linear regression analysis was used to model the dependent variables (i.e., dry matter yield or CP) as a function of the independent variables (i.e., LAI, LT, or SM). Leaf area index and LT were analyzed separately in model development. Soil moisture was tested as a significant variate in model development with LAI and LT separately. Analyses were conducted using a manual selection of significant variables from the variance table in the GLM procedure of SAS (SAS Institute Inc 1999) at $\alpha = 0.05$ level. The BFT data were omitted from the analysis of the June and September harvests at the green ash location because establishment was poor and sporadic.

An average of each independent variable over the sampling dates was used as another independent variable in the analysis. The average LAI (AVGLAI), LT (AVGLT), and SM (AVGSM) measurements for the June harvest at both locations included sampling dates in May and June. Soil moisture was measured in April at the green ash, but plots were wet and inaccessible at the Scotch pine in April. Average measurements for the September harvest at both locations included sampling dates from May through August; however, SM measurements at the Scotch pine location included only May, June, and July measurements, whereas, April was included at the green ash location.

In the interpretation of interactions, only interactions between light variables and SM within the same month or averaged over the same months were examined. Interactions between light variables and SM were graphed using the dependent variable as a function of the changing light levels while SM was

held constant. The constant SM values were the maximum, mean, and minimum SM values specific to the plant species and sampling dates. To assist in interpreting the interactions involving the SM data, soil field capacity (FC) and permanent wilting point (PWP) at both locations were estimated based on soil textural analysis using the Decision Support System for Agrotechnology Transfer (DSSAT) program (Hunt et al. 1994; Jones et al. 1998).

Results and discussion

Scotch pine location

Grass and BFT yields

Variability of BB June yields was not effectively explained by May and June light conditions. Yields of BB were relatively low in June (Table 3) because BB growth did not begin until the later half of May; consequently, the overstory canopy did not have a significant impact on June BB yields. September BB yields were explained largely by AVGLT, as an integration of growing season light conditions (Fig. 1). Yield of BB ranged from 0.82 to 1.0 Mg DM ha^{-1} between 20 and 75% LT. Yield at full sunlight was over two times greater than that at 20–75% LT range. An inverse polynomial model was analyzed and found to fit the data well. The rapidly increasing BB yield at higher LT agrees with the findings of Kephart et al. (1992) and Lin et al. (1999), although they reported points of inflection at lower light levels than what we found. The relationship described in Fig. 1 was substantiated by other significant relationships between light and September yield regardless of light (LAI or LT) and month (Table 4, Eqs. 2–8). These responses showed a relatively flat line between 20 and 75% LT and LAI levels of 2–5.

Variability in SB yields in June and September was explained by light conditions and the relationship between yield and LT was linear; however, the full range of LT was not analyzed for SB. All SB plots located in the open area were partially shaded by surrounding trees and LT did not exceed 75%

Table 3 Yields (Mg DM ha^{-1}) in June and September 2001 at the Scotch pine and green ash locations for big bluestem (BB), smooth bromegrass (SB), and birdsfoot trefoil (BFT)

Treatment	Species	June harvest			September harvest		
		Range (Mg DM ha^{-1})	Mean (Mg DM ha^{-1})	SEM (Mg DM ha^{-1})	Range (Mg DM ha^{-1})	Mean (Mg DM ha^{-1})	SEM (Mg DM ha^{-1})
Scotch pine							
BB	BB	0.22–1.5	0.61	0.16	0.72–2.6	1.2	0.26
BB/BFT	BB	0.04–0.74	0.32	0.08	0.39–0.80	0.59	0.05
	BFT	0.01–0.99	0.31	0.12	<0.01–0.99	0.34	0.01
	Total	0.09–1.6	0.63	0.19	0.43–1.8	0.93	0.16
SB	SB	0.09–1.4	0.81	0.14	0.17–1.4	0.96	0.13
SB/BFT	SB	0.12–1.7	0.67	0.17	0.20–1.7	0.76	0.13
	BFT	<0.01–1.4	0.25	0.16	<0.01–1.3	0.30	0.20
	Total	0.13–2.0	0.92	0.22	0.20–2.0	1.1	0.25
Green ash							
BB	BB	0.87–2.0	1.4	0.11	1.3–2.1	1.6	0.08
BB/BFT	BB	0.36–0.97	0.64	0.07	0.62–2.0	1.2	0.16
	BFT	<0.01–1.1	0.47	0.14	<0.01–1.5	0.48	0.19
	Total	0.45–1.8	1.1	0.13	0.99–2.8	1.7	0.22
SB	SB	0.98–1.9	1.5	0.09	1.4–2.0	1.6	0.07
SB/BFT	SB	0.94–1.9	1.4	0.09	1.4–1.8	1.6	0.05
	BFT	<0.01–1.3	0.33	0.15	0.01–0.56	0.19	0.07
	Total	0.94–2.6	1.8	0.18	1.4–2.1	1.8	0.07

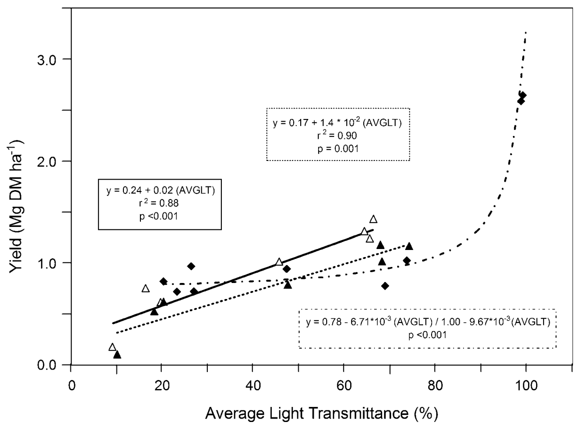

Fig. 1 Fitted curves for yield of big bluestem (*BB*) in September (Sept, ◆–◆) from monoculture plots, and smooth bromegrass (*SB*) in June (▲–▲) and Sept (Δ–Δ) from monoculture plots, at the Scotch pine location, in response to average light transmittance (*AVGLT*)

(Fig. 1). The increasing SB yields with increased light levels were in accordance with other studies that reported linear increases of cool-season grasses as light levels increased (Kephart et al. 1992; Lin et al. 1999).

June yields of BFT in the SB/BFT plots were correlated to LAI measurements taken on 4 June 2001 (Table 4, Eq. 20). Yield of BFT increased on average by 0.24 Mg DM ha^{-1} as LAI decreased by increments of 0.5 between levels of 3.0 and 1.0; whereas, BFT yield remained near 0 from LAI levels of 3.0–5.0. Poor yield response of legumes to low light intensity has been reported in other studies (Lin et al. 1999; McGraw et al. 2008). June BFT yields in the BB/BFT plots were not correlated to LAI or LT. September BFT yields in the BB/BFT and SB/BFT plots increased linearly as AVGLT increased. September yields of BFT in the BB/BFT and SB/BFT plots increased by 0.15 or 0.12 Mg ha^{-1}, respectively, with each 10% increase in AVGLT (Table 4, Eqs. 11 and 23). Total yield in the BB/BFT and SB/BFT plots generally increased linearly as AVGLT increased (data not shown).

Grass and BFT CP

Leaf and stem CP of BB in the BB plots in June and September (Table 5) were correlated to light conditions and increased as light levels decreased. The quadratic response of June CP of BB leaves to AVGLT (Fig. 2) demonstrated that CP of BB leaves remained above 150 g kg^{-1} at low to moderate levels of LT (<75%), but decreased to 110 g kg^{-1} at full sunlight. June CP of BB stems in the BB plots was not correlated to LAI or LT as main effects. In September, CP of BB leaves and stems in the BB plots decreased by 4.5 and 2.3 g kg^{-1}, respectively, as the AVGLT increased by 10% (Fig. 2). The CP of BB leaves and stems in the BB plots in September was predicted to increase by 4.7 and 2.5 g kg^{-1}, respectively, as AVGLAI increased by increments of 0.5 (Fig. 3).

The relationship between light and the CP of SB leaves and stems in June and September were similar to those previously described for the CP of BB leaves and stems. June CP of SB leaves was not correlated to LAI or LT as main effects. The CP of SB leaves and stems in September increased as LT decreased or overstory LAI increased. In September there was a quadratic relationship between CP of SB leaves and AVGLAI in the SB plots (Fig. 3). The response with AVGLAI demonstrated that CP of SB leaves at LAI levels below 0.5 almost reached 80 g kg^{-1}, but CP remained above 250 g kg^{-1} when the overstory LAI was greater than 3.0. The response of leaf CP to light levels corresponds with other studies (Allard et al. 1991; Kephart and Buxton 1993; Lewis et al. 1983). Although shading appears to have a positive influence on tissue CP content, shading is commonly reported to lower soluble carbohydrate level in plants contributing to a decline in herbage dry matter digestibility (Wilson 1984; Buxton and Casler 1993).

Crude protein content of BFT did not appear to respond to light level. The lack of variability was probably related to poor stand establishment and the absence of plant material over the full range of light levels for proper CP analysis.

Green ash location

Grass and BFT yields and CP

The average June and September yields of BB and SB were greater than the observed yields at the Scotch pine location (Table 1); however, BFT yields were similar at both locations. The difference in average yield between the two locations likely was related to the denser overstory of the Scotch pine trees. The relationship between yield of BB or SB in

Table 4 Regression equations for the Scotch pine and green ash locations for yield (Mg DM ha^{-1}) and crude protein concentration (CP; g kg^{-1}) of big bluestem (BB), smooth bromegrass (SB), and birdsfoot trefoil (BFT). Table includes equations not presented in figures

Location	Variable	Trt	Harvest	Eq	Regression equations	*df*	r^2	*P*
Scotch pine	BB yield	BB	June	1	$Y = 1.2 - 0.31$ (MayLAI)	7	0.57	0.030
Scotch pine	BB yield	BB	September	2	$Y = 3.0 - 1.3$ (MayLAI) $+ 0.17$ $(\text{MayLAI})^2$	8	0.93	0.002
Scotch pine	BB yield	BB	September	3	$Y = 2.0 - 0.06$ (MayLT) $+ 6.7 \times 10^{-4}$ $(\text{MayLT})^2$	8	0.95	0.001
Scotch pine	BB yield	BB	September	4	$Y = 3.2 - 1.7$ (JuneLAIB) $+ 0.30$ $(\text{JuneLAIB})^2$	8	0.90	0.008
Scotch pine	BB yield	BB	September	5	$Y = 3.0 - 1.5$ (JulyLAI) $+ 0.23$ $(\text{JulyLAI})^2$	8	0.90	0.003
Scotch pine	BB yield	BB	September	6	$Y = 1.9 - 0.06$ (JulyLT) $+ 7.0 \times 10^{-4}$ $(\text{JulyLT})^2$	8	0.92	0.003
Scotch pine	BB yield	BB	September	7	$Y = 3.9 - 1.9$ (AugustLAI) $+ 0.27$ $(\text{AugustLAI})^2$	7	0.79	0.029
Scotch pine	BB yield	BB	September	8	$Y = 1.2 - 0.28$ (AugustLT) $+ 4.2 \times 10^{-4}$ $(\text{AugustLT})^2$	8	0.96	0.002
Scotch pine	CP leaves	BB	June	9	$Y = 1.7 - 0.67$ (MayLAI) $- 0.02$ (MaySM15B) $+ 0.03$ (MayLAI) (MaySM15B)	8	0.85	0.028
Scotch pine	BB yield	BB/BFT	June	10	$Y = -4.6 \times 10^{-3} + 9.1 \times 10^{-3}$ (AVGLT)	8	0.80	0.001
Scotch pine	BFT yield	BB/BFT	September	11	$Y = -9.5 \times 10^{-2} + 1.2 \times 10^{-2}$ (AVGLT)*	7	0.79	0.003
Scotch pine	Plot yield	BB/BFT	June	12	$Y = -0.19 + 1.9 \times 10^{-2}$ (MayLT)	7	0.88	<0.001
Scotch pine	Plot yield	BB/BFT	September	13	$Y = 0.41 + 0.02$ (JulyLT)	7	0.61	0.022
Scotch pine	SB yield	SB	June	14	$Y = 1.4 - 0.25$ (AVGLAI)	8	0.60	0.014
Scotch pine	SB yield	SB	September	15	$Y = 1.9 - 0.28$ (AugustLAI)	7	0.73	0.007
Scotch pine	SB yield	SB	September	16	$Y = 0.26 + 1.7 \times 10^{-2}$ (AugustLT)	8	0.81	0.001
Scotch pine	CP stems	SB	June	17	$Y = 59 + 2.0$ (JuneLT) $- 2.8 \times 10^{-2}$ $(\text{JuneLT})^2$	7	0.93	0.002
Scotch pine	CP stems	SB	September	18	$Y = 45 + 7.6$ (JulyLAI)	8	0.92	<0.001
Scotch pine	CP stems	SB	September	19	$Y = 71 + 1.0$ (AVGLT) $- 2.0 \times 10^{-2}$ $(\text{AVGLT})^{2}$*	8	0.86	0.046
Scotch pine	BFT yield	SB/BFT	June	20	$Y = 1.7 - 0.79$ (JuneLAIA) $+ 0.09$ $(\text{JuneLAIA})^{2}$*	8	0.96	0.003
Scotch pine	BFT yield	SB/BFT	June	21	$Y = 1.6 - 0.76$ (JuneLAIB) $+ 0.08$ $(\text{JuneLAIB})^{2}$*	8	0.97	0.002
Scotch pine	BFT yield	SB/BFT	June	22	$Y = 0.11 - 0.01$ (JuneLT) $+ 2.2 \times 10^{-4}$ $(\text{JuneLT})^{2}$*	7	0.97	0.001
Scotch pine	BFT yield	SB/BFT	September	23	$Y = -0.26 + 0.01$ (AVGLT)	8	0.92	<0.001
Scotch pine	Plot yield	SB/BFT	June	24	$Y = 0.27 + 0.02 \times 10^{-2}$ (JuneLT)	7	0.72	0.007
Scotch pine	Plot yield	SB/BFT	September	25	$Y = 0.43 + 0.02$ (AVGLT)	8	0.74	0.003
Green ash	CP leaves	BB	June	26	$Y = 89 + 18$ (MayLAI)	8	0.77	0.002
Green ash	CP stems	BB	September	27	$Y = -196 + 98$ (AVGLAI) $+ 8.6$ (AVGSM45) $- 3.6$ (AVGLAI) (AVGSM45)	7	0.90	0.033
Green ash	CP leaves	SB	June	28	$Y = 124 + 17$ (MayLAI)	8	0.62	0.012
Green ash	CP leaves	SB/BFT	June	29	$Y = -704 + 445$ (JuneLAI) $+ 32$ (JuneSM30) $- 17$ (JuneLAI) (JuneSM30)	6	0.91	0.019
Green ash	CP stems	SB/BFT	September	30	$Y = 44 + 5.3$ (JulyLAI)	7	0.76	0.005

Trt treatment, *Eq* equation, *LAI* leaf area index, *LT* light transmittance, *A* first sampling date, *B* second sampling date, *AVGLAI* or *AVGLT* average measurements for May and June or May, June, July, and August, *SM* soil moisture, *AVGSM* average measurements for May, June, July, August

* Linear regression equation also was significant at $P < 0.05$

Table 5 Leaf and stem crude protein (CP) concentrations (g kg^{-1}) in June and September 2001 at the Scotch pine and green ash locations for big bluestem (BB), smooth bromegrass (SB), and birdsfoot trefoil (BFT)

Treatment	Species	June harvest			September harvest		
		Range (g kg^{-1})	Mean (g kg^{-1})	SEM (g kg^{-1})	Range (g kg^{-1})	Mean (g kg^{-1})	SEM (g kg^{-1})
Scotch pine							
BB	BB leaves	106–170	145	7.0	69–110	94	5.3
	BB stems	60–118	87	6.7	31–53	44	3.0
BB/BFT	BB leaves	135–165	148	4.2	95–124	109	2.7
	BB stems	75–106	90	4.2	45–59	50	2.0
	BFT[a]	149–224	181	9.9	101–155	134	8.3
SB	SB leaves	144–217	174	8.7	82–271	214	19.0
	SB stems	56–93	78	4.6	52–87	67	4.7
SB/BFT	SB leaves	144–231	186	10.0	208–263	234	6.0
	SB stems	69–95	83	2.7	51–90	74	4.0
	BFT	147–209	179	16.5	102–146	131	8.9
Green ash							
BB	BB leaves	110–144	124	4.0	70–93	85	2.3
	BB stems	65–87	75	2.7	32–54	41	2.3
BB/BFT	BB leaves	115–161	133	5.3	0.08–105	89	2.7
	BB stems	65–92	76	3.3	39–49	43	1.3
	BFT	172–203	192	3.8	83–116	150	4.5
SB	SB leaves	137–171	155	4.7	160–209	182	5.0
	SB stems	66–84	75	2.7	47–64	55	1.7
SB/BFT	SB leaves	144–184	165	5.0	170–246	197	8.1
	SB stems	75–93	86	2.5	51–63	55	1.8
	BFT	172–212	191	5.7	62–117	92	6.4

[a] Birdsfoot trefoil was not separated into leaf and stem fractions

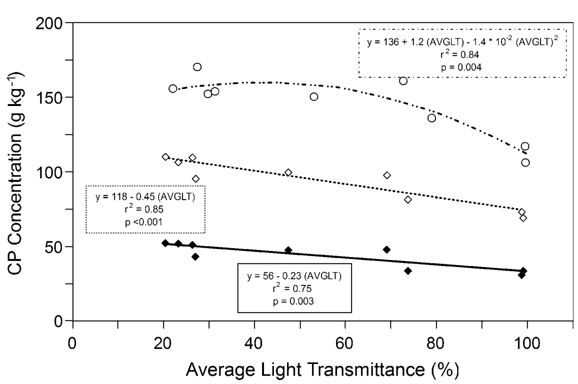

Fig. 2 Fitted curves for crude protein (*CP*) concentration of big bluestem (*BB*) leaves in June (○–○) and September (Sept, ◇–◇) from monoculture plots, and BB stems in Sept (◆–◆) from monoculture plots, at the Scotch pine location, in response to average light transmittance (*AVGLT*)

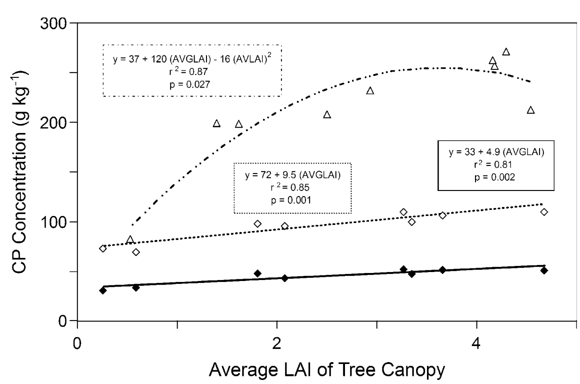

Fig. 3 Fitted curves for crude protein (*CP*) content of big bluestem (*BB*) leaves (◇–◇), BB stems (◆–◆), and smooth bromegrass (*SB*) leaves (Δ–Δ) in September (Sept) from monoculture plots, at the Scotch pine location, in response to average leaf area index (*AVGLAI*)

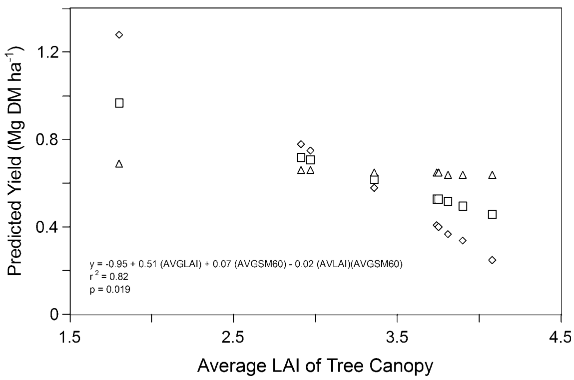

Fig. 4 Fitted curves for yield of big bluestem (*BB*) in the BB/birdsfoot trefoil plots in September (Sept) in response to average leaf area index (*AVGLAI*) and average soil moisture (*AVGSM60*) measured at the 0–60-cm interval at the Scotch pine location. Predicted yield was based on the maximum (◇), mean (□), and minimum (Δ) AVGSM values (41.4, 31.6, and 22.8%, respectively) as overstory tree LAI increased

June or September and any of the individual light main effects, AVGLT or AVGLAI were not significant. Characterizing canopy cover and light conditions in green ash plots was challenging because of the spatial irregularity of the overstory within each plot. Tree canopy was not uniformly distributed over a plot; therefore, LT measurements at plot centers or LAI measurements at plot corners did not necessarily characterize canopy cover or light conditions of a plot. The lack of correlation between light conditions and yield likely was related to this spatial irregularity of the overstory. Field observations, however, suggested that BB, SB, and BFT yields tended to respond to the range of canopy cover found over the study site.

Leaf and stem CP of BB and SB in June and September also were poorly correlated to light conditions of the deciduous tree overstory. There were a few instances, however, where light conditions did relate to CP (Table 4). Leaf CP of BB in the BB plots in June was predicted to increase by 9.0 g kg^{-1} as May LAI increased at increments of 0.5 (Table 4, Eq. 26). Leaf CP of SB in the SB plots in June was predicted to increase by 8.7 g kg^{-1} as May LAI increased at increments of 0.5 (Table 4, Eq. 28). In September, stem CP of SB in the SB/BFT plots was predicted to increase by 2.6 g kg^{-1} as July LAI increased at increments of 0.5 (Table 4, Eq. 30). The relatively poor correlation between light conditions and CP of the understory forage likely was caused by the spatial variability of the tree canopy within plot.

Interactions between light and soil moisture

There were light and SM interactions in predicting yield and CP of BB, SB, and BFT at both the Scotch pine and green ash locations. We hypothesized that yield of the understory forage plants would increase with increasing light levels when SM was favorable, but that yield would not necessarily respond to increasing light when SM was not favorable. There were several interactions between light variables and SM (Table 4, Eqs. 9, 27, 29) where SM was a significant part of equations explaining DM yield variability. September yields of BB in the BB/BFT plots at the Scotch pine location generally decreased as AVGLAI increased; however, AVGSM at the 0–60 cm interval influenced the rate of yield decline (Fig. 4). The greatest BB yield was at low LAI and maximum AVGSM (41.4%). Yield of BB was predicted to decrease at the mean (31.6%) and maximum SM with increasing LAI. Yield of BB was relatively low at the full range of LAI (1.8–4.1) at the minimum AVGSM (22.8%). Soil moisture of plots at the minimum SM (22.8%) was below the estimated PWP of 29.3%, which suggests that physiological development and growth of BB would stop below the PWP and would not respond to light levels. Predicted yields at high LAI (4.1) were lower at maximum SM than the minimum. We did not collect complementary data that would help explain this result, but our visual observations supported this finding. We did not measure soil temperature but Wong and Wilson (1980) reported that soil temperatures decreased on average 3 and 2°C at depths of 5-cm and 13-cm, respectively, as light levels decreased from full sunlight to 40% of full sunlight. Although we have no measure of this, wet, cool/cold soils favor some root and seedling diseases (Brady and Weil 2002). The wet soil found in some of the high canopy cover plots could have created favorable conditions for plant disease, resulting in very little plant growth—even when compared to plots with a combination of dry soil and high canopy cover. Although there were other interactions between light and SM in predicting yields of BB and SB, SM tended not to be a significant part of equations explaining yield variability in the understory of trees.

Summary and management implications

Yields of BB, SB, and BFT frequently were correlated to overstory LAI and LT at the Scotch pine location. The relationship between yield and light was generally linear with yield increasing incrementally as light levels increased. The infrequent occurrence of quadratic responses indicates that yield thresholds generally were not reached where yield was no longer affected by changing light conditions. The increase in BB yield as light increased was not surprising because BB is a warm-season species and does not reach a light saturation point where CO_2 uptake is limited (Hopkins 1999). The linear relationship between SB yields and light levels demonstrates that light saturation, even at full sunlight, of a cool-season grass such as SB does not occur on a stand basis. Within the canopy of a SB stand, most leaves are shaded by other SB leaves; therefore, light saturation for the stand as a whole does not occur and plant production increases incrementally with increasing light. Relationships between light and BFT yield in the BB/BFT or SB/BFT plots were quadratic in most cases. The response of total plot yield was similar to those already described for the BB, SB, and BFT relationships. Yield of BB, SB, and BFT at the green ash location were not highly correlated to the narrower range of light levels; however, a few significant relationships were found.

Crude protein of leaves and stems of BB and SB and whole-plant BFT generally decreased as light levels increased and was predicted to be the lowest for all three species at full sunlight. The relationship between light and CP was not consistently linear or quadratic. Plants growing in the shade tended to be at earlier stages of development with lower yields and higher CP. At the Scotch pine location, AVGLT for May and June was a good predictor of June BB yield as well as CP of BB leaves and stems (Table 4). Such relationships were found in a few instances where yield and leaf CP and/or stem CP were predicted effectively by the same measure of light (e.g., LAI, AVGLAI, LT, or AVGLT).

The relationship between most measures of light and yield or CP was not significant at either location. The reasons for this can be explained by a number of design, methodology, and environment factors. Individual month measurements generally were not correlated to yield or CP and infrequently explained a significant portion of the variability in yield or CP in June or September. Average LAI or LT was usually the light-related variable that was correlated to June or September yields or CP. June or September yields and CP apparently were the result of the cumulative effect of light conditions rather than of a particular month.

Measuring light quality was not part of this study; however, light quantity and quality affects plant morphology and dry matter allocation (Belesky 2005) and carbohydrate partitioning (Frank and Hofmann 1994). As a result, far-red enriched light under tree canopies likely impacts forage yield and nutritive value. Conifers potentially provide much less far-red enrichment compared to deciduous trees because they reflect and scatter much less far-red light (Gates 1980). Awada et al. (2003) completed an accompanying study at the green ash location, during the same time frame as this study, to determine the physiological responses of BB and SB to various canopy levels in May and July. Chlorophyll content and leaf N of SB was greater than BB under all light levels. As overstory canopy cover and shade increased, stomatal conductance and dark respiration of both species declined. Species response to increasing shade showed an increase in specific leaf area, with a greater increase for SB at all light levels than for BB (Awada et al. 2003).

Results of this study demonstrate that measures of light can be used to predict forage yield and CP in the understory of Scotch pine and, to a lesser extent, green ash trees. Yield and CP of the understory forages was more commonly correlated to the LT measurements; however, there were acceptable equations with LAI as the independent variable. The two methods and instruments used as measures of light conditions under a tree canopy probably are not appropriate for most landowners operating silvopasture systems. The instruments are relatively expensive and the methods require close attention to detail, including the timing and location of measurements. The LT equipment and methods used in this study required measurements be taken at solar noon on sunny days and between the trees in eight different directions (Constabel and Lieffers 1996). Overstory LAI is a relatively rapid measure of canopy cover, but requires taking measurements on cloudy days, or at dawn, when the azimuth angle of the sun is no greater than 76° (Gower and Norman 1991). The LI-COR

LAI-2000 also is a very complex instrument and an understanding of the physics behind the instrument is crucial to acquiring data that is reliable. Other simpler methods of estimating green crown length or area and diffuse non-intercepted radiation could be identified and adapted to the needs of producers in silvopasture systems (Addendum to Water Quality Monitoring Technical Guide Book 2000).

There does not appear to be an optimum time during the growing season to measure overstory LAI or LT. Light measurements averaged over several months best predicted yield and CP. Two or more measures of LAI or LT distributed over time are likely to be a better predictor of yield and CP of the species because of a number of reasons. Over a period of 2 months or more, while understory plants are growing, the overstory LAI and/or LT changes because of canopy development dynamics and changes in sunlight incidence. This is especially true at the green ash location where the canopy was not fully established until mid- to late May. Plant growth during this time is a result of the integration of these changes rather than light conditions at a specific point in time. There also is error associated with each measurement point in time; therefore, multiple measurements should provide (1) a more accurate estimate of light conditions rather than a single measurement and (2) a better estimate of light conditions when dealing with irregular tree canopies. Results of this study indicate that there is not a single point in time that represents the most opportune time to measure overstory LAI or LT. This study is similar to what has been found in other regions, that additional studies on silvopasture systems in the central Great Plains region are warranted.

Acknowledgments The authors express appreciation to Richard Carmen, Michael Guderjan, Jeremy Hiller, Ann Koehler, Dr. Lowell Moser, Dr. David Nielsen, Elena Perry, and Dr. Michele Schoeneberger for their excellent technical assistance during the experiment. Without the assistance of these individuals, the completion of this research would not have been possible. This project was supported in part by the USDA Forest Service, Rocky Mountain Research Station, the USDA National Agroforestry Center, the McIntyre Stennis Forestry Research Fund, and the Center for Great Plains Studies.

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