Response of Four Perennial Southwestern Grasses to Shade[1]

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Highlight

A nursery plot study was conducted to determine if the observed relative abundance of Arizona cottontop, bush muhly, and plains bristlegrass under mesquite trees on native range was related to the ability of these grasses to adapt to shade. Plants of these species plus black grama which grows in open areas were subjected to shading only and shading after defoliation treatments using five levels of shade from 0 to 80%. Evaluation of morphological, physiological, and yield responses showed that all plants made their best growth in full sunlight; but Arizona cottontop, bush muhly, and plains bristlegrass displayed greater ability than black grama to adapt to shade.

On a protected area of desert grassland near Tucson, Arizona, Tiedemann (1970) found that differences in production of perennial grasses between areas under mesquite (*Prosopis juliflora*) trees and adjacent open areas were related to environmental variables. Three of the perennial grasses of interest, Arizona cottontop (*Trichachne californica*), plains bristlegrass (*Setaria macrostachya*), and bush muhly (*Muhlenbergia porteri*), had greater crown cover and forage production under mesquite canopies than in the open, while black grama (*Bouteloua eriopoda*) showed the opposite tendency and was most abundant in open spaces between mesquite trees. These observations suggest that three of these grasses can adapt to shade, whereas black grama is intolerant of shade. This experiment tests this hypothesis by evaluating the response of the four species to several levels of artificial shade in a nursery plot study.

Methods

Plants of the four grasses were collected from an upland desert grassland site with uniform soils at the Santa Rita Experimental Range south of Tucson, Arizona. Livestock had been excluded from the collection site for 30 years. Plants were selected for uniformity within species, excavated, placed in pots, and watered immediately.

The plants were transplanted to ten 1.8- by 2.4-m field plots in a 7.5- by 48.0-m border at the Tucson Plant Materials Center[3] on March 15, 1967. Location of four subsamples of each species on a 4×4 grid within each plot was randomly assigned. Two replications each of five levels of shade (0, 20, 40, 60, and 80%) were randomly assigned to the 10 plots. Mesquite trees in

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[3] Operated by the Soil Conservation Service, U. S. Department of Agriculture.

FIG. 1. Plot layout with shade structures in place at the Tucson Plant Materials Center, Tucson, Arizona.

full leaf provide approximately 55% shade at midday. On April 16 after plants had become established, shade structures were placed over the plots (Fig. 1). Shade was provided by saran shade cloth stretched over the top and sides of 1.8- by 2.4-m wooden frames 0.75 m high. The shade cloth was rated at 20, 43, 63, and 80% actual shade by the manufacturer.[4]

To assure adequate moisture for all plots, the entire border containing the plots was watered weekly. On May 1, the entire border was fertilized with 100 kg/ha of N and 30 kg/ha of P.

The effect of shade on plant morphology was evaluated by measuring number and length of inflorescences, distance between nodes, length of seedstalks (inflorescence included), and length and width of leaf blades. Upper and lower internodes of Arizona cottontop and plains bristlegrass appeared to vary in length. To account for this, the uppermost internode on a stem and the second internode above ground level were measured and recorded separately for these two species. Also, blades of the first and second leaves below the inflorescence on Arizona cottontop were shorter than other leaf blades on the stem. Measurements were confined to leaf blades below these. Measurements were taken when the majority of the seedheads were mature. This was done during the last week in June 1967 for Arizona cottontop and plains bristlegrass and the last week in July 1967 for bush muhly and black grama.

After the plants had matured and measurements for morphological features were completed, herbage samples were collected from two randomly selected plants of each species on each plot and dried 24 hours at 55 C to determine moisture content. All plants were then harvested to a stubble height of 8 cm and air dried to a constant weight. Immediately after the herbage was harvested, two randomly selected plants of each species on each plot were excavated for measurement of root weight, stubble weight, and total available carbohydrates. A 20-cm cube was taken for root systems. Soil was washed from the roots immediately. Plants were then brought to the laboratory, killed and dried in a forced-draft oven, separated into stubble and roots, and weighed. Total available carbohydrates in the roots were determined in finely ground samples (40 mesh) using the method described by Weinmann (1947) as modified by Araújo (1968).

The two remaining plants of each species in each plot were allowed to regrow until the first week in September 1967 for evaluation of the response of plants to shade after defoliation.[5] Weights of herbage, roots and stubble, and measurement of total available carbohydrates were made on plants allowed to regrow until September. Morphological characteristics were not re-examined.

Analysis of variance was used to evaluate the response of the four species (both singly and in combination) to shade and shade after defoliation. Analyses were conducted by the Statistical Laboratory of the Arizona Agricultural Experiment Station of the University of Arizona.

Results

Plants of all species grown under no-shade and 20% shade were more vigorous than those grown under higher levels of shade. As the level of shade increased, stems became thinner and less rigid; and at 60 and 80% shade, lodging became so pronounced that stems of Arizona cottontop and plains bristlegrass grew along the ground in a zig-zag fashion. Production of seedstalks was noticeably reduced with increasing shade for all species. At 60 and 80% shade, flowering lagged behind that for other levels of shade by a week or more. Many inflorescences of Arizona cottontop did not develop beyond the boot stage under 60 and 80% shade.

Morphological Responses

Neither all species nor all morphological characteristics showed similar responses to the shade treatments. For none of the species did length of seedstalks respond signifi-

[4] Shade cloth was donated by the Chicopee Manufacturing Company, Cornelia, Georgia.

[5] In this study defoliation refers to removal of culms and leaves to an 8-cm stubble height.

cantly, and only for one species did number and length of inflorescences and width of leaf blades respond. Length of leaf blades, however, responded significantly in three species. Trends were frequently apparent where significant responses were lacking, often accompanied by high coefficients of variation.

In all species except black grama, length of leaf blades was increased by shade. Length of leaf blades was more than doubled for bush muhly, increased by two-thirds for plains bristlegrass, and by one-third for Arizona cottontop. Increasing shade affected leaf width only in black grama; it caused width to decline from 2.1 mm with no shade to 1.8 mm at 80% shade.

Shade exerted a more pronounced effect on production of inflorescences of bush muhly than on any other species; there was a highly significant reduction from 1131 to 3 inflorescences per plant with increasing shade from 0 to 80%. Although the trend in number of inflorescences with increasing shade for the other three species was downward, differences among shade levels were not significant.

Shade significantly influenced internode length of the stems of two species, Arizona cottontop and bush muhly. For Arizona cottontop, length of the second internode above ground level increased from 5 cm with no shade to 7 cm with 40% shade, then declined to 5 cm with 80% shade. For bush muhly, internode length increased from 4 cm with no shade to 5 cm with 20% shade and remained unchanged with increases in shade to 80%. The trend for black grama internodes was similar to Arizona cottontop: length increased between 0 and 40% shade, then declined with 80% shade.

Shade had no influence on length of seedstalks and only in black grama did length of the inflorescences respond to shade. They increased from 24 cm with no shade to 29 cm with 20% shade, remained constant with intermediate shade, then declined to 18 cm with 80% shade.

Table 1. Influence of shade on weight (g) of herbage, roots, and stubble.

Species	Percent shade 0	20	40	60	80	Mean	Coeff. of variation	F[1]
Herbage								
Arizona cottontop	114	68	83	39	24	66	20	**
Bush muhly	172	175	64	97	65	115	99	NS
Black grama	90	64	49	23	11	48	72	*
Plains bristlegrass	196	226	132	142	61	151	97	NS
Species × shade interaction (combined analysis)						95	105	NS
Roots[2]								
Arizona cottontop	7	6	4	3	2	4	20	**
Bush muhly	14	11	7	8	5	9	42	*
Black grama	10	7	6	4	2	6	24	*
Plains bristlegrass	8	7	6	6	4	6	35	NS
Species × shade interaction (combined analysis)						6	46	NS
Stubble								
Arizona cottontop	36	24	19	9	8	19	15	**
Bush muhly	22	18	11	11	8	14	59	NS
Black grama	14	10	9	7	4	9	48	NS
Plains bristlegrass	44	22	18	16	6	22	87	NS
Species × shade interaction (combined analysis)						16	68	NS

[1] NS = not significant, ** = significant at the 0.01 level, and * = significant at the 0.05 level.

[2] Excavated from a 20-cm cube of soil.

Yield Responses

Herbage yield of black grama was reduced by eight times and that of Arizona cottontop by five times when shade was increased from 0 to 80% (Table 1). Similar but nonsignificant trends were apparent for bush muhly and plains bristlegrass. The trend in herbage yield between 0 and 20% shade for plains bristlegrass suggests that light shade may stimulate herbage production for this species.

Weight of stubble in only one species was significantly affected by shade. Stubble of Arizona cottontop weighed less than one-fourth as much under 80% shade as in no shade (Table 1). Response of stubble weight to increasing shade for the other species was similar but nonsignificant despite strong trends.

Increasing shade resulted in a significant reduction in root weight for three species (Table 1). Root weight decreased by about two-thirds for Arizona cottontop, bush muhly, and black grama between 0 and 80% shade. Although the effect of shade on root weight of plains bristlegrass was nonsignificant, the trend was similar to that for the other three species. The species × shade interaction was not significant, indicating that all four species responded similarly to shade. There was no significant difference in total available carbohydrates of the roots for any species among shade levels nor were there any evident trends in the data.

Moisture Content

The effect of shade on the moisture content of herbage (percent of tissue dry weight) varied among species. Moisture content of Arizona cottontop increased from 204 to 243% with increasing shade from 0 to 80%. The response of plains bristlegrass was even more pronounced: from 220 to 336%. In

Table 2. Effect of shade after defoliation on weight (g) of herbage, roots, and stubble.

Species	Percent shade 0	20	40	60	80	Mean	Coeff. of variation	F[1]
Herbage								
Arizona cottontop	230	140	189	58	20	127	17	**
Bush muhly	81	84	26	79	21	59	113	NS
Black grama	12	2	24	18	5	12	210	NS
Plains bristlegrass	261	387	174	183	24	206	84	NS
Species × shade interaction (combined analysis)						101	97	NS
Roots[2]								
Arizona cottontop	16	9	10	6	3	9	13	**
Bush muhly	24	15	17	10	5	14	30	**
Black grama	10	8	6	7	4	7	34	NS
Plains bristlegrass	18	12	10	9	5	11	20	**
Species × shade interaction (combined analysis)						10	30	NS
Stubble								
Arizona cottontop	78	39	53	16	7	39	20	**
Bush muhly	46	15	15	13	8	20	89	NS
Black grama	18	8	8	6	6	9	30	**
Plains bristlegrass	46	48	36	26	13	34	65	NS
Species × shade interaction (combined analysis)						25	57	*

[1] NS = not significant, ** = significant at the 0.01 level, and * = significant at the 0.05 level.
[2] Excavated from a 20-cm cube of soil.

contrast, moisture content of black grama was constant from 0 to 60% shade, then declined from 119 to 73% at 80% shade. Moisture content of bush muhly was not affected by shade. A significant species × shade interaction foretold the differential response of the four species.

Influences of Shade after Defoliation

Plants that were harvested at 8 cm and allowed to regrow until September showed yield responses to increasing shade similar to those of plants subjected to shading alone. Arizona cottontop showed the greatest response to the treatment; weight of herbage, stubble and roots declined significantly with increasing shade (Table 2). For bush muhly and plains bristlegrass, only weight of roots declined significantly. In the case of black grama, only weight of stubble declined with increasing shade. The shade-after-defoliation treatment did not affect significantly the total available carbohydrates in the roots of any species. However, there appeared to be a trend toward lower concentration of carbohydrates with increasing shade for bush muhly and black grama.

Shading vs. Shading after Defoliation

Compared with shade only, the shade-after-defoliation treatment had differential effects on yields of the four species. Mean herbage yield of Arizona cottontop for the shade-after-defoliation treatment was significantly above yield for the shade-only treatment (Tables 1 and 2) and the trend in yield of plains bristlegrass was higher, but not significantly so. In contrast, there was a significant reduction in mean herbage yield of black grama for the shade-after-defoliation treatment compared with shade only. Mean herbage yields of bush muhly tended to be lower for the shade-after-defoliation treatment, but not significantly so.

Average yield of stubble for Arizona cottontop was significantly higher under the shade-after-defoliation treatment than with shade alone (Tables 1 and 2). There was no change in yield of stubble of black grama, and nonsignificant increases in that for the other two species.

Although root weights of Arizona cottontop, bush muhly, and plains bristlegrass were significantly higher with the shade-after-defoliation treatment than the shade-only, the difference between treatments narrowed as shade increased (Tables 1 and 2). The response of black grama is in sharp contrast: there was essentially no difference in root weight between shade-only and shade-after-defoliation treatments regardless of the level of shade.

Mean total available carbohydrate concentrations in roots were the same between shade-only and shade-after-defoliation treatments.

Discussion and Conclusions

The adverse effect of shade on number of inflorescences, and weight of herbage, stubble, and roots indicates that all four species made their best growth in full sunlight. This concurs with Black's (1957) statement that "grasses as a group make the fastest growth at or about full daylight."

However, several responses indicate that there were differences among species in adaptation to shade. One of these was the differential response in length of leaf blades among species to increasing shade. According to Blackman and Wilson (1951a and 1951b), increased leaf length is an adaptive response of plants to reduced light intensity. The striking increase in leaf length with increasing shade displayed by Arizona cottontop, bush muhly, and plains bristlegrass suggests that the plants were adapting to shade. Based on this response, these three species can probably be classed as facultative skiophytes (plants which are heliophytes but are able to adapt to shaded conditions). Length of leaf blades of black grama were not affected by shade, suggesting that it did not adapt and is probably an obligate heliophyte.

Elongation of internodes with shading as manifested in Arizona cottontop and bush muhly has been associated with shade tolerance by McBee and Holt (1966), and may be an adaptive mechanism for shade avoidance as described by Grime and Jeffrey (1965).

The effect of shade on moisture content of Arizona cottontop and plains bristlegrass agrees with prior studies which have shown that moisture content of grasses generally increases with increasing shade (Pritchett and Nelson, 1951; Burton, Jackson, and Knox, 1959; and McGinnies, 1966). Lack of a response in moisture content in bush muhly and in black grama (except for the 80% shade treatment) is contrary to these findings. This differential response to shade suggests moisture content may be useful criterion to indicate shade adaptation by grasses.

Failure of total available carbohydrates in the roots to respond to increasing shade with both shade-only and shade-after-defoliation treatments is misleading unless considered in terms of the response of root weight to shade. Even though concentration of total available carbohydrates was unaffected by increasing shade, the total amount was reduced sharply since weight of roots declined. Lower levels of carbohydrates in turn would affect the ability of the plants to take up moisture and nutrients and to produce foliage regrowth after defoliation (Pritchett and Nelson, 1951). The level of carbohydrates in our plants subjected to shade after defoliation was in contrast with that of plants studied by Sullivan and Sprague (1943) and Ward and Blaser (1961), where combined treatments of defoliation and shading almost exhausted carbohydrate reserves. In our study, total available carbohydrates in roots of the plants increased under the shade-after-defoliation treatment for three of the four species.

Judging by yield data for herbage, stubble, and roots, black grama appeared to be more severely affected by the shade-after-defoliation treatment than the other three species. However, this is probably more of an indication of its sensitivity to defoliation than failure to adapt to shade. Also, the regrowth period for black grama and bush muhly was shorter because they were harvested for the shade-only treatment a month later than the other two species.

The fact that all species made their best growth in full sunlight but that Arizona cottontop, plains bristlegrass, and bush muhly were able to adapt to shade does not answer the basic question—why was production of these three grasses greater under mesquite trees than in the open? The results of this study alone, in fact, indicate that growth should have been best in the open. In companion studies, soil under mesquite trees was found to be more fertile than that in the open areas (Tiedemann, 1970). Nitrogen and sulfur in the mesquite soil are more abundant and more available to the native grasses than that in open soil. Phosphorus was no more abundant in the mesquite soil, but it was more readily available to plants than that in soil from open areas. This difference in soil fertility and nutrient availability is probably the main reason for the difference in production between the two locations.

The absence of black grama under mesquite trees and its failure to adapt to shade indicates that shade adaptation is an important factor. If Arizona cottontop, plains bristlegrass, and bush muhly were not facultative skiophytes, they would not likely grow under mesquite regardless of the nutrient regime.

Results of this study may give some clues to the reason cattle have been observed to graze closely under mesquite trees despite restricted accessibility created by low-hanging branches. Increasing moisture content with increased shade as observed in this study indicates that Arizona cottontop and plains bristlegrass plants growing under mesquite are probably more succulent than those growing in the open. This coupled with higher fertility of the mesquite soil suggests that plants growing under mesquite are more palatable to livestock than plants growing in adjacent open areas.

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