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RESPONSE OF ANDROPOGON GERARDII (POACEAE) TO FIRE-INDUCED HIGH VS. LOW IRRADIANCE ENVIRONMENTS IN TALLGRASS PRAIRIE: LEAF STRUCTURE AND PHOTOSYNTHETIC PIGMENTS¹

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ABSTRACT

Photosynthetic pigments and several structural characteristics were measured in leaves of *Andropogon gerardii* from tallgrass prairie populations in an unburned, low-irradiance site and a burned, high-irradiance site to determine if these species displayed sun/shade differences similar to those documented in forest species. Early in the growing season, leaves of *A. gerardii* in the low-irradiance, unburned site had significantly lower stomatal density, pore length, and conductance, as well as specific leaf mass and thickness than leaves from the high-irradiance, burned site. Moreover, the chlorophyll *a:b* ratio, carotenoid content, and bundle sheath-vascular complex area were significantly lower, but chlorophyll content (mass/mass) was greater in leaves in unburned vs. burned sites. These differences are consistent with sun/shade adaptations reported for forest understory plants and may contribute to the low productivity of *A. gerardii* in unburned tallgrass prairie.

EARLY SEASON growth of grasses in unburned, ungrazed tallgrass prairie occurs in a very low-irradiance environment due to the accumulation of a large amount of standing dead biomass (Old, 1969; Knapp, 1984). Indeed, incident photosynthetically active radiation available to shoots emerging in undisturbed prairie during the initial weeks of the growing season may be as much as 58% lower within the standing dead canopy when compared to above-canopy levels and only 1% at the soil surface (Knapp, 1984). In contrast, spring burning removes the dead canopy, allowing the resprouting grasses to emerge in a high-irradiance environment. The dominant species in many tallgrass prairies, *Andropogon gerardii*, has been reported to have a greater photosynthetic rate and increased stomatal conductance and leaf thickness in response to increased irradiance after fire (Knapp, 1985). These differences in response to irradiance are among the many sun/shade adaptations documented from comparisons of species in forest understory environments and those in gaps or open, high-irradiance sites (Boardman, 1977). Ad-

ditional sun/shade differences include decreased internal to surface leaf area ratios, chlorophyll *a:b* ratios, stomatal density, and increased chlorophyll content (mass/mass) in low vs. high irradiance populations (Young and Smith, 1980, and references therein). Modifications of leaf structure and pigment content in response to low irradiance are thought to be adaptive in a light-limited environment (Boardman, 1977), whereas the leaf structural characteristics that result from growth under high irradiance may increase growth and photosynthetic rates (Nobel and Longstreth, 1981). The purpose of this study was to examine several leaf structural and photosynthetic pigment characteristics in *A. gerardii* in an unburned (low-irradiance) and a burned (high-irradiance) site and to assess the possible contribution of these characteristics to the observed postfire increase in photosynthetic rates, production, and competitive ability of this grass in tallgrass prairie.

MATERIALS AND METHODS—Research was conducted on the Konza Prairie Research Natural Area in northeast Kansas (Riley County) in early June 1984. Study sites were located on lowland soils (Pachic Argiustolls) in two watersheds (>20 ha): one burned on 18 April 1984 (but not previously burned for 3 yr) and an unburned watershed (not previously burned for 5 yr). Fully expanded leaves of *A. gerardii* Vitman. were collected from populations in burned and unburned prairie and stored in humidified containers for transport back to the laboratory. Leaves from unburned prairie had

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TABLE 1. Comparison of leaf structural characteristics measured in sun (burned) and shade (unburned) populations of *A. gerardii* in tallgrass prairie. Values in () are standard errors of the mean, * denotes significant difference between means ($P < 0.05$), and ns denotes no significant difference

| Character | Burned | Unburned | |
|---|--------------|--------------|----|
| Stomatal density (#/mm ²) | | | |
| Abaxial | 108.5 (3.8) | 89.6 (4.6) | * |
| Adaxial | 6.1 (1.6) | 4.7 (2.7) | ns |
| Stomatal pore length (μm) | | | |
| Abaxial | 44.7 (0.8) | 34.8 (0.5) | * |
| Adaxial | 45.8 (2.0) | 35.5 (0.8) | * |
| Stomatal conductance (mm/s) | | | |
| Abaxial | 3.52 (0.20) | 1.84 (0.11) | * |
| Adaxial | 0.60 (0.07) | 0.58 (0.06) | ns |
| Total (calculated) | 4.12 | 2.42 | |
| Specific leaf mass (mg/cm ²) | 5.13 (0.15) | 3.37 (0.16) | * |
| Leaf thickness (μm) | 172.6 (2.8) | 140.9 (3.1) | * |
| Chlorophyllous/nonchlorophyllous tissue (area ratio) | 1.53 (0.12) | 2.01 (0.19) | * |
| Bundle sheath—primary vascular bundle complex area (μm ²) | 23,548 (809) | 18,099 (950) | * |

expanded in a relatively low-irradiance environment during the previous 4 wk and were just emerging above the dead canopy at the time of collection. In the field, midday stomatal conductance to water vapor diffusion was measured on both abaxial and adaxial surfaces of 10 leaves from each population with a diffusion porometer (LI-700, Li-Cor, Inc.) calibrated prior to the measurements made in each watershed. Total conductance was calculated as the sum of abaxial and adaxial values.

Stomatal density and pore length were measured on abaxial and adaxial surfaces of 15 leaves from each population with a light microscope equipped with a calibrated ocular grid. Microscopic examination of transverse sections of an additional 15 leaves (infiltrated with distilled water) were used to measure leaf thickness, the ratio of the area occupied by chlorophyllous to nonchlorophyllous tissues, and the area of the bundle sheath—primary vascular bundle complex. Specific leaf mass (dry mass/unit area) was determined from sections of 10 leaves per site by measuring the dimensions of a leaf section while fresh, followed by drying at 60 C for 48 hr and weighing. Chlorophyll *a* and *b* and carotenoid content were measured in leaves of eight tillers from each site using an acetone-water extract and a grating spectrophotometer (Beckmann DB-GT) at 663, 644, and 452 mμ wavelengths (Robbelen, 1957). Pigment content was expressed on both a mass/mass and mass/leaf area basis. Statistical comparisons of all sample means were made using Student's *t*-test at the $\alpha = 0.05$ level of significance (Zar, 1974).

RESULTS AND DISCUSSION—Sun/shade differences in leaf structure and pigment content in *A. gerardii* were evident in response to fire in tallgrass prairie. At the unburned, low-irradiance site, leaves showed a 17 and 22% decrease in stomatal density and pore length, respectively, which resulted in a 41% decrease in stomatal conductance compared to those in burned prairie (Table 1). Moreover, leaf thickness was 18% lower, specific leaf mass 34% lower, and the area of the bundle sheath—vascular complex 23% lower in leaves emerging in unburned vs. burned prairie. The ratio of chlorophyllous to nonchlorophyllous tissue within leaves was 31% greater in unburned

TABLE 2. Comparison of chlorophyll and carotenoid pigment content of leaves from sun (burned) and shade (unburned) populations of *A. gerardii* in tallgrass prairie. Values in () represent standard errors of the mean, * denotes significant difference between means ($P < 0.05$), and ns denotes no significant difference between means

| Character | Burned | Unburned | |
|-------------------------|--------------|--------------|----|
| Total chlorophyll | | | |
| (mg/g) | 3.49 (0.34) | 5.25 (0.59) | * |
| (mg/m ²) | 179.1 (17.3) | 179.2 (19.5) | ns |
| Chlorophyll <i>a:b</i> | | | |
| (Ratio) | 4.24 (0.07) | 3.68 (0.23) | * |
| Total carotenoids | | | |
| (mg/g) | 1.21 (0.04) | 1.31 (0.08) | ns |
| (mg/m ²) | 62.2 (2.2) | 44.7 (2.6) | * |
| Chlorophyll: carotenoid | | | |
| (Ratio) | 2.84 (0.21) | 3.97 (0.32) | * |

prairie. Total chlorophyll content of leaves in unburned prairie was 50% greater on a mass/mass basis but not significantly different on a mass/area basis (Table 2). The same relationship was evident when chlorophyll *a* or *b* was compared between sites, but the chlorophyll *a*:*b* ratio was 15% greater in leaves from the high-irradiance (burned) population. In contrast to chlorophyll content, total carotenoid content in leaves was not significantly different between sites on a mass/mass basis but was 28% lower on a mass/area basis in the unburned population. Finally, the ratio of chlorophyll to carotenoid pigment content was significantly greater in the unburned population (Table 2).

The response to fire (and consequently, irradiance) of the characters surveyed in *A. gerardii* was consistent with sun/shade differences reported for other species (Boardman, 1977). The greater size of the bundle sheath-vascular complex in the high irradiance (burned) environment was reflected in the increase in leaf thickness and specific leaf mass and may contribute to an increase in the ratio of mesophyll cell surface area to leaf surface area ($A^{\text{mes}}:A$). Increased $A^{\text{mes}}:A$ is reported to occur in high irradiance environments and may contribute to increased mesophyll conductance to CO_2 and photosynthetic rates (Nobel, Zaragoza and Smith, 1975). There was no significant increase in the number of bundle sheaths per unit leaf width between sites but the greater amount of nonchlorophyllous tissue in burned site leaves (mostly sclerophyllous support tissue) probably also contributed to increased leaf thickness and specific leaf mass in the burned population.

The lower chlorophyll *a*:*b* ratio in the unburned population is typical of shade plants and is thought to enable more efficient light absorption under shade conditions as a result of a relative increase in chlorophyll *b* (Boardman, 1977). Comparisons of pigment concentrations between burned and unburned populations were dependent on whether data were expressed on a mass/mass or mass/area basis (Table 2). The higher mass/mass chlorophyll concentrations in the unburned population, a characteristic of shade leaves, contrasts with the similar mass/area chlorophyll content between populations. This suggests that reduced leaf thickness (specific leaf mass) in unburned plants was primarily responsible for a higher mass/mass pigment concentration. In contrast, similar mass/mass carotenoid concentrations between populations resulted in a significantly greater mass/area carotenoid content in the thicker leaves of the burned population. This increase in carotenoid pigments under high irradiance (reflected in the lower chlorophyll:

carotenoid ratio; Table 2) may protect the chlorophyll from damage from photo-oxidation or ultraviolet radiation (Goodwin, 1980).

The presence of these "shade" characteristics in *A. gerardii* in unburned prairie may initially be adaptive much as they are in forest understory plants. However, two unique aspects of the low-irradiance environment in tallgrass prairie differ substantially from the forest understory. First, *A. gerardii* grows under low-irradiance conditions for a relatively short period of time (2–5 wk) as opposed to the entire season for understory plants. Thus, shoots of *A. gerardii* with shade characteristics soon emerge into a high-irradiance environment where these modifications may reduce their growth and competitive ability relative to "sun" leaves in burned prairie. Although biochemical acclimation of leaves can be relatively rapid when transferred from low to high irradiance (Hatch, Slack and Bull, 1969), potential structural changes are limited in mature leaves (Boardman, 1977). Knapp (1985) reported that 5 wk after growth of unburned *A. gerardii* shoots above the standing dead canopy, photosynthetic rates were still 45% lower in unburned than burned sites, but at the end of the season, photosynthetic rates were equal in burned and unburned prairie. Thus, during June and early July when, in most years, growth conditions in NE Kansas are optimal for C_4 grasses (Knapp, 1984), the growth potential of *A. gerardii* in unburned prairie may be restricted as a result of these shade-induced leaf characteristics.

A second difference in prairie vs. forest systems is that species in forested systems may, through selection acting on the propagules of sun- or shade-adapted genotypes, occupy only specific irradiance environments. For example, Young (1983) found that seeds from an understory herb growing in an open microhabitat were more likely to germinate in a high-irradiance site, whereas only seeds from plants in shaded environments were able to germinate in the dark. In contrast, *A. gerardii* in tallgrass prairie has been subjected to a stochastic fire and early season irradiance regime for thousands of years (Wells, 1970). Hence, plasticity of the sun/shade responses in this grass may be requisite for dominance in this ecosystem.

In conclusion, the response of *A. gerardii* to the ephemeral low-irradiance environment in tallgrass prairie may contribute substantially to the decrease in production and vigor of this grass compared to burned sites. Although the modifications in pigment content that occurred under low irradiance may be adaptive, the leaf structural changes may reflect the need of un-

burned shoots to invest a greater proportion of their synthetic capacity in upward growth toward a more optimal irradiance environment.

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