Vol. 17(1), pp. 147-155, January, 2021
DOI: 10.5897/AJAR2020.15223
Article Number: 1DC3E0165851
ISSN: 1991-637X

http://www.academicjournals.org/AJAR

African Journal of Agricultural Research

Full Length Research Paper

Effect of crop canopy manipulation on light interception, growth, and development of wild proso millet and giant foxtail in row-cropping systems

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Received 23 September, 2020; Accepted 9 December, 2020

Crop canopy architecture is known to affect weed performance. Field experiments were conducted to examine the effect of altered crop canopy architecture and light interception on growth and development of wild proso millet and giant foxtail, two problematic weed species. Crop canopy architecture was manipulated by planting two sweet corn varieties contrasting in canopy architecture (Bonus-has a dense leaf canopy and Sprint-has an open leaf canopy) at two row spacings (51-cm and 76-cm rows). Results showed that sweet corn variety, rather than row spacing, altered crop canopy architecture, which in turn altered photosynthetically active radiation (PAR) and red:far-red light ratio (R:FR) received by both weeds. The competitive Bonus canopy had a higher ($P<0.05$) PAR and R:FR than Sprint at anthesis and harvest. Bonus also more effectively suppressed weed growth and development than Sprint, and weeds growing on Bonus plots had reduced tiller numbers, reduced biomass, lower population densities, and reduced seed production ($P<0.05$). These responses were attributed to the Bonus canopy having a higher canopy area index, which intercepted more light resulting in lower PAR and R:FR received by both weeds. This study suggests that crop variety selection is an important consideration for weed suppression in row-cropping systems.

Key words: Crop canopy architecture, light interception, photosynthetically active radiation, red:far-red ratio, row spacing, sweet corn, wild proso millet, giant foxtail.

INTRODUCTION

Increasing crop competition is an effective and sustainable strategy for controlling weeds in cropping systems (Jha et al., 2017; Mhlanga et al., 2016; Sardana et al., 2016). Crop competition can be enhanced through crop canopy architecture manipulation by selecting competitive crop varieties, optimizing row spacing, and increasing seeding rates (Jha et al., 2017; Sardana et al., 2016; Swanton et al., 2015; Weiner et al., 2001). Crop

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canopy architecture is known to affect weed performance, and a denser or more closed crop canopy makes weeds less competitive by reducing light intercepted for weed growth and development (Jha et al., 2017; Drews et al., 2009), which ultimately reduces weed establishment. Cultivation of competitive varieties is an economical and sustainable approach in integrated weed management (Andrew et al., 2015), reducing the environmental risk of herbicide use to control weeds.

Wild proso millet (*Panicum miliaceum* L.) and giant foxtail (*Setaria faberi* Herrm.) are annual grass weeds that have spread rapidly throughout the majority of the corn and soybean producing regions in the United States, thus becoming serious weed problems (Cavers and Kane, 2016; Williams et al., 2009). The two weed species are vigorous competitors in row-cropping systems in the Midwest, and their rapid spread has been attributed to the ability to adapt to several environments, tremendous reproductive capabilities, and the ability to emerge throughout the growing season. The overall objective of this study was to examine the effect of sweet corn canopy architecture manipulation on the growth and development of wild proso millet and giant foxtail in row-cropping systems.

One major effect of crop canopy manipulation is the alteration of light interception, which has significant effects on the competitive ability of crops over weeds (Ballare and Casal, 2000; Borger et al., 2010; Ghersa et al., 1994; Holt, 1995). Important aspects of light affecting plant growth and development are the quantity of total energy (photosynthetically active radiation-PAR), spectral quality (red:far-red ratio-R:FR), duration, and photoperiod (Schmitt and Wulff, 1993). An increase in crop canopy density causes a reduction in PAR received per plant and marked changes to occur in R:FR (Casal and Smith, 1989; Fiorucci and Fankhauser, 2017). Alteration of light quality can affect the development of shaded plants by influencing physiological processes mediated by phytochrome (Keuskamp et al., 2010; Martínez-García et al., 2010; Smith and Whitelam, 1990). Developmental responses mediated by phytochrome provide mechanisms for the shade avoidance, which is accompanied by changes in plant phenotypes (Carriedo et al., 2016; Fiorucci and Fankhauser, 2017; Pierik and Wit, 2014; Smith et al., 1990; Smith and Whitelam, 1990). Many crop species exhibit altered growth response (shade avoidance syndrome) due to reduced light availability by growth patterns such as taller stature, reduced branching or tillering, and lower biomass (Carriedo et al., 2016; Franklin and Whitelam, 2005; Pierik and Wit, 2014). A differential response to light quality under crop canopies could be responsible, at least in part, for the displacement of giant foxtail by wild proso millet in midwestern sweet corn production fields. In this study, the effect of sweet corn canopy architecture manipulation on light interception, growth, and development of wild proso millet and giant foxtail was examined in field experiments.

MATERIALS AND METHODS

Experimental site

Field experiments were conducted for two years (1999 and 2000) at the Southern Research and Outreach Center in Waseca, University of Minnesota. The experimental site's soil was a Webster clay loam (fine-loamy, mixed, mesic, Typic Haplaquoll) with organic matter ranging from 6.3 to 7.4% and pH ranging from 7.4 to 7.5. The study area, on which field corn (*Zea mays*) had been grown the previous season was chisel plowed each fall and tilled with a field cultivator in the spring of each year to prepare the seed bed. Before planting, nitrogen fertilizer was applied at a rate of 134 kg N ha^{-1} in the form of urea. After ploughing, two sweet corn varieties contrasting in canopy architecture (Bonus-has a dense leaf canopy and Sprint-has an open leaf canopy) were planted in separate designated fields at 74,130 plants ha^{-1} using a six-row planter, and hand-thinned to 56,833 plants ha^{-1} after germination to achieve a uniform plant population. Plots were cultivated between rows for four weeks after planting. Broadleaf weeds in the plots were controlled using bentazon applied post-emergence at 0.56 kg ha^{-1} and escaped broadleaf weeds and undesired grass weeds removed by hand weeding. When plots were weed-free, wild proso millet and giant foxtail seeds was hand-seeded using a broadcast spreader after chisel plowing the fall preceding trial establishment to augment the existing seed banks. A low seeding rate of 30 seeds m^{-2} was used to obtain low population density stands to avoid intraspecific and interspecific weed competition. To reduce seed desiccation, decay, and predation, weed seed was incorporated using a field cultivator operating at a depth of 5 cm immediately following seeding.

Experimental design

The experiment was laid out in a randomized complete block design with four replications. To manipulate crop canopy density, four treatments were used: combinations of two row spacings (51-cm and 76-cm), and the two sweet corn varieties. The resulting four combinations of crop canopy architectures labeled Bonus51, Bonus76, Sprint51, and Sprint76 were seeded into 15.2 x 9.1 m plot area. Each plot area was subdivided into weed-crop plot (9.1 x 10.7 m), and two 4.6 x 4.6 m control plots, one crop-free and one weed-free established side by side for comparison. The following weed population densities were achieved outside the monitored six rows: 0 in weed-free plots; 4 to 9 weeds m^{-2} in weed-crop plots; and 13 to 20 weeds m^{-2} in crop-free plots. Weeds were hand-thinned within the six-row area monitored for light competition to leave 20 target plants of wild proso millet and giant foxtail, which were monitored throughout the season.

Data collection

Twenty sweet corn, 20 wild proso millet, and 20 giant foxtail plants were tagged for observation throughout the growing season in the center area of the weed-crop plots. Twenty sweet corn plants were also tagged in the weed-free plots. To examine the growth and development of wild proso millet and giant foxtail in pure stands without interspecific competition, 20 plants of each species were also tagged in the crop-free plots. The weeds that were tagged emerged at the same time as the sweet corn and were within the sweet corn rows, not between the rows. An approximate 12-m length of the six center rows of each plot was used for plant data collection.

Data on the number of tillers per plant and shoot height were collected weekly for each tagged plant starting from three weeks after planting. In addition, the following data were collected at sweet corn anthesis (tassel emergence) and harvest: weed population

density, above ground crop and weed biomass, R:FR, PAR, and crop canopy area index (CAI). Sweet corn and weed shoot heights were measured from the base of the plant to the furthest natural extension of the uppermost part of the plant (leaves were not extended by hand). Weed population densities were collected from three 0.26 m^2 quadrats randomly placed in the six-monitored center rows. Also, at anthesis and harvest, sweet corn plants and weed biomass samples were harvested from a 1.5-m length of row area (0.15 m^2 area) located outside the 6-center rows under weekly observation. Biomass samples were harvested from crop-free, weed-free, and weed-crop plots and separated by species before drying. The samples were dried at 70°C for three days, and then above ground dry weight (biomass) of each species measured. At harvest, fresh ear weight for the same sweet corn plants used for dry weight determination was weighed to verify that sweet corn yield was not affected by weed competition.

Photosynthetically, active radiation ($\mu mols^{-1}m^{-2}$) was measured in weed-free plots using an LI-COR Model LI-191SA line quantum sensor to monitor canopy development at anthesis and again at harvest. The 1-m line quantum sensor was placed above and then parallel to the length of the sweet corn row at the soil surface to measure PAR. The R:FR was recorded in weed-free plots using an LI-COR Model 1800 spectroradiometer at anthesis and harvest. The R:FR readings were taken both above (direct sunlight) and below the sweet corn canopy at the soil surface. To measure the R:FR from direct sunlight (reference spectrum), the spectroradiometer's optical sensor was placed on a tripod stand away from vegetation in an open area of the field and programmed to automatically record the reading. The below canopy R:FR reading was determined by placing the spectroradiometer optical sensor parallel and adjacent to a sweet corn row. All light measurements were made on clear days between 1100 and 1300 solar time, and for each sampling, four locations per plot were used. Sweet corn canopy area index as an estimate of leaf area index (LAI) was estimated using an LI-COR Model 2000 plant canopy analyzer. Weed seed rain was collected following the method designed by Forcella et al. (1996). Four 10-cm diameter styrofoam cups (seed traps) was placed 0.7 m apart, one per row in a diagonal transect across four monitored rows in the weed-crop and crop-free plots six weeks after planting. Seed collection continued after crop harvest until October since some weed seeds had not reached physiological maturity until later in the growing season.

Statistical analysis

All data were tested for normality and found to be homogenous, and thus data transformation was not necessary. Data were analyzed using one-way Analysis of Variance. Since there was no significant year by treatment interactions for all traits (Supplementary File), data for the two growing seasons were combined for each treatment-variety combination. For each measured phenotypic trait, the Fisher's Protected Least Significant Difference (LSD) test was used to determine differences between means and differences larger than the LSD considered significant at the 5% significance level.

RESULTS AND DISCUSSION

Effect of sweet corn canopy architecture on CAI, PAR, and R:FR

The CAI, PAR, and R:FR were measured to examine light interception for the two sweet corn varieties under weed-free conditions. Bonus had a lower ($P<0.05$) CAI than Sprint (Figure 1A). The higher Bonus CAI resulted in greater light interception compared to Sprint. Row spacing did not significantly alter PAR and R:FR transmitted through sweet corn canopies, but sweet corn variety did. The effects of row spacing may not have been significant because PAR and R:FR were measured within the row rather than between rows. Bonus had a higher PAR ($P<0.05$) than Sprint both at anthesis and at harvest (Figure 1B). Additionally, more red light was absorbed by the competitive Bonus canopy, lowering the R:FR compared to Sprint below the canopy at the soil surface (Figure 1C). Consistent with our observations, Casal et al. (1986) reported that density reduced the proportion of incident radiation intercepted per plant and the R:FR ratio of the light received below the plant. Additionally, Drews et al. (2009) reported that more competitive wheat cultivars were taller, had higher ground cover and light interception compared to the less competitive wheat cultivars.

Weed tiller number and shoot height

Sweet corn variety significantly affected the number of tillers of wild proso millet and giant foxtail, and both weeds had higher ($P<0.05$) tiller numbers in plots with the Sprint sweet corn variety compared to Bonus (Figure 2A). Therefore, Bonus was more effective in suppressing both weeds than Sprint. This result could be due to Bonus' denser canopy and higher CAI (1.7) compared to that of Sprint (1.3), which led to more PAR interception in Bonus (Bonus-250 $\mu mol\ s^{-1}m^{-2}$; Sprint-550 $\mu mol\ s^{-1}m^{-2}$). Additionally, Bonus had a lower R:FR that reached the canopy compared to Sprint (Bonus-0.25 and Sprint-4.0). Similarly, reduced tiller production of *Paspalum dilatatum* and *Lolium multiflorum* under a denser canopy has been reported by Casal et al. (1986). In our study, wild proso millet produced twice as many tillers as giant foxtail regardless of sweet corn variety (Figure 2A), indicating that weed tiller production is also variable with weed species. As expected, tiller production was highest in crop-free plots (20-30 tillers per wild proso millet plant and 10-5 tillers per giant foxtail plant), where weeds experienced minimum competition with no crop canopy and thus received more PAR. In weed-crop plots, tiller numbers averaged five tillers per plant for wild proso millet and two tillers per giant foxtail plant. Although only a few studies have examined tillering patterns for specific weed species underneath crop canopies, changes in tillering for crop species in the presence of weeds competition or under low light conditions have been reported. Wheat tiller numbers reduced under downy brome or wild oat competition (Balyan et al., 1991; Challaiah et al., 1986; Meulen and Chauhan, 2017). Interference by weeds also reduced rice tillering mainly due to competition and light quality interference (Merotto Jr and Fischer, 2002; Tabot, 2015). Interestingly, row spacing had no effect on tiller production for both wild

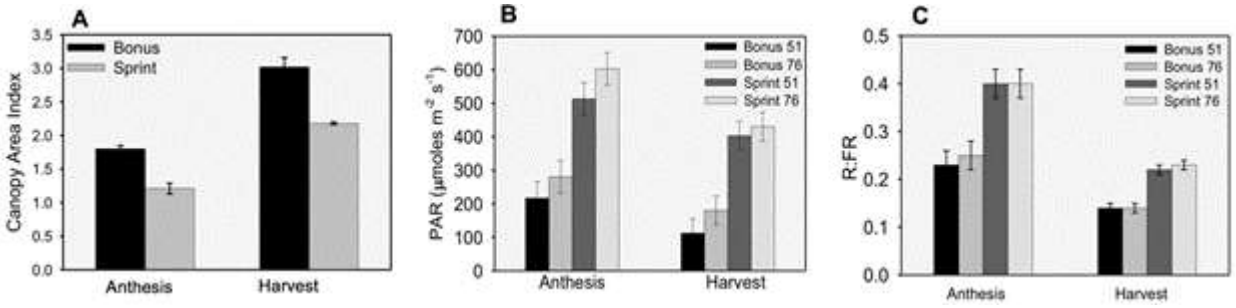

Figure 1. A) Crop canopy index for the two sweet corn varieties at anthesis and harvest. Crop canopy index was under weed-free conditions and differed (P<0.05) by variety but not by row spacing. **B)** Photosynthetically active radiation at the soil surface at anthesis and harvest under weed-free conditions. **C)** R:FR at the soil surface at anthesis and harvest under weed-free conditions.

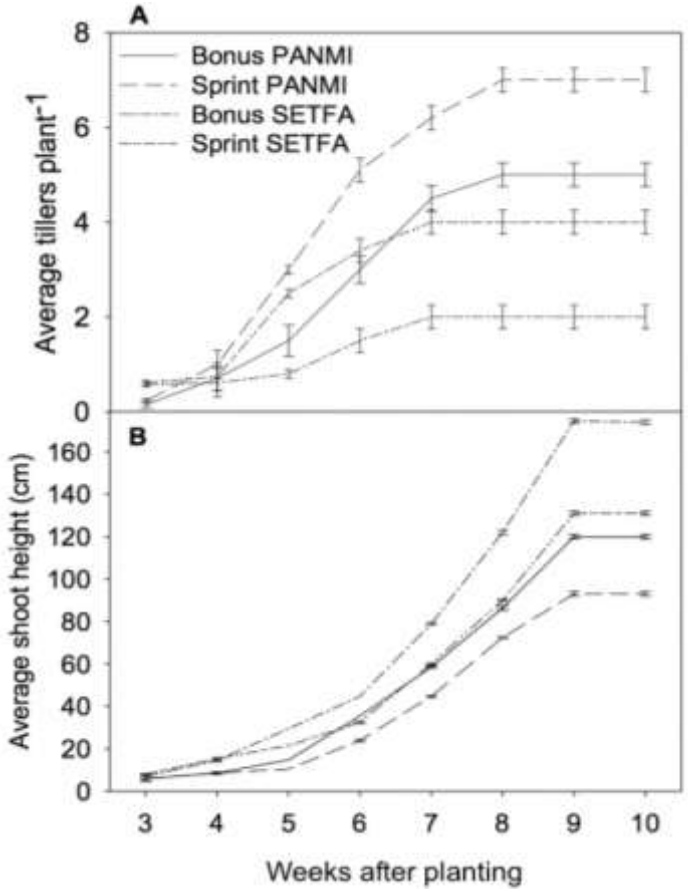

Figure 2. Average tillers per plant (A) and average shoot height (B) for both weeds (wild proso millet-PANMI, and giant foxtail-SETFA) when grown with respective sweet corn varieties. Row spacing was not significant (P>0.05), and data is combined across row spacing. Error bars represent the standard error.

proso millet and giant foxtail in our study (Supplementary File).

Sweet corn variety significantly (P<0.05) increased shoot height for both weed species, and plants were etiolated when growing under the more competitive Bonus canopy than when growing under the Sprint canopy (Figure 2B). Similar observations were reported for three grass species (*L. multiflorum*, *Sporobolus indicus*, and *P. dilatatum*) tested under variable light conditions (Casal et al., 1987a). The percent change in weed shoot height

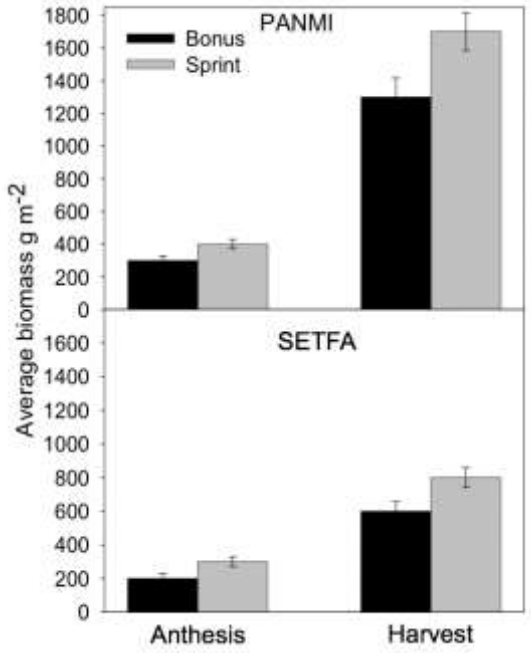

Figure 3. Average above ground biomass of wild proso millet-PANMI (top panel), and giant foxtail-SETFA (bottom panel) at sweet corn anthesis and harvest. Row spacing was not significant (P>0.05), and data is combined across row spacings. Error bars represent the standard error.

and above ground biomass within each species in response to altered crop canopy architecture was similar (P>0.05) for giant foxtail compared to wild proso millet. Shoot height increased by 31% for giant foxtail and by 29% for wild proso millet when growing under the competitive Bonus canopy compared to the more open Sprint canopy.

Above ground weed biomass

Sweet corn variety also significantly affected the above ground biomass for both weeds, and weeds grown in the Sprint plots had higher biomass at both sweet corn anthesis and harvest compared to weeds in the Bonus plots (Figure 3). Our results suggest that the denser Bonus canopy was more competitive than both weeds and effectively suppressed wild proso millet and giant foxtail compared to Sprint. The above ground weed biomass accumulated by sweet corn at anthesis was 36% lower for giant foxtail and 34% lower for wild proso millet, when grown under Bonus compared to Sprint, respectively. Because the growth of wild proso millet and giant foxtail was similar within each crop canopy density, it seems unlikely that differential response to crop canopy density is responsible for wild proso millet dominance over preexisting stands of giant foxtail in sweet corn. The sweet corn row spacing tested in our study did not affect (P>0.05) above ground biomass for both wild proso millet and giant foxtail (Supplementary File). Although row spacing results from our study were not significant, previous studies have shown that a more dense crop canopy resulting from narrower plant spacing reduced weed biomass in maize (Abouziena et al., 2008; Fanadzo et al., 2010; Mhlanga et al., 2016; Murphy et al., 1996), wheat (Weiner et al., 2001; Olsen et al., 2005; Kristensen et al., 2008; Olsen et al., 2012), rice (Tabot, 2015), sorghum (reviewed by Peerzada et al., 2017), soybean (reviewed by Bradley, 2006) and sunflower (Mouillon et al., 2020), although the magnitude of biomass reduction varied with crop or weed species.

Weed population density

In our study, reducing row spacing from 76 to 51 cm did not affect weed population density, nor was there any significant interaction of row spacing with sweet corn variety. Weed population density of both weed species was similar (P>0.05) for Bonus and Sprint at anthesis. However, at harvest, weed population density of wild proso millet and giant foxtail was higher when growing

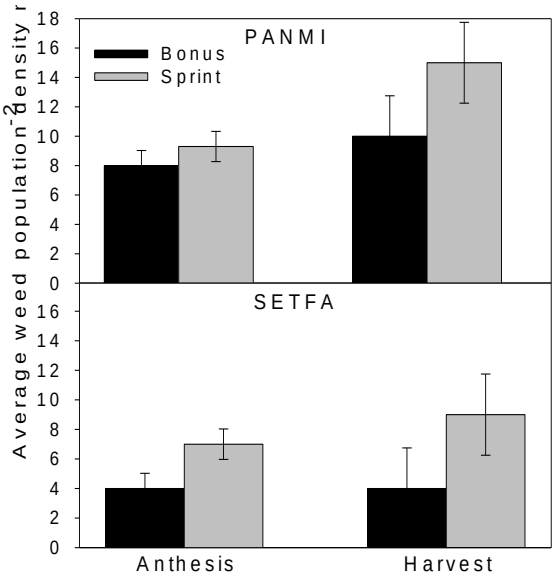

Figure 4. Average weed population density of wild proso millet-PANMI (top panel), and giant foxtail-SETFA (bottom panel) at sweet corn anthesis and harvest. Row spacing was not significant (P>0.05), and data is combined across row spacings. Error bars represent the standard error.

with Sprint than with Bonus (Figure 4). Therefore, sweet corn variety, but not row spacing, altered weed population density. This could have been because weeds within sweet corn rows rather than between rows were monitored. Bonus resulted in a lower weed population than Sprint partly because Bonus had a denser canopy area index (higher CAI) that intercepted more light, thereby reducing the amount of light reaching the soil surface. Westgate et al. (1997) reported that canopies with greater LAI intercepted more incident light earlier in the season, regardless of row spacing. Observations from our study agree with Johnson et al. (1998), who reported that field corn row spacing had little impact on visual control of weeds, weed density, weed biomass, and height. These findings are contrary to studies that reported that manipulating field corn row spacing could make crops more competitive with weeds (Acciares and Zuluaga, 2006; Fanadzo et al., 2010; Mhlanga et al., 2016; Murphy et al., 1996; Teasdale, 1995). Manipulating row spacing is reported to play a role in reducing the potential for weed interference by increasing the amount of light that is intercepted by the crop canopy (Fanadzo et al., 2010; Teasdale 1995).

Weed seed production

Row spacing did not affect (P>0.05) the amounts of seed produced by either weed species (Supplementary File). However, weeds growing in Sprint sweet corn plots had higher (P<0.05) seed production for wild proso millet and giant foxtail, especially at harvest for wild proso millet and postharvest for both wild proso millet and giant foxtail (Figure 5). Therefore, compared to Sprint, weeds growing in the more competitive Bonus canopy produced fewer seeds. Wild proso millet averaged four times total production for the season, but 10% production occurred at or before harvest, while giant foxtail total season seed rain was approximately twice that of wild proso millet, all of it (100%) occurred after harvest. Thus, the impact of giant foxtail seed rain can be lessened through postharvest management. Seed rain of wild proso millet and giant foxtail increased by 12% and 31%, respectively in the absence of crop canopy when free of crop competition. Notably, wild proso millet seed rain increased disproportionately more than giant foxtail when grown without competition, indicating that altogether the early seed rain of wild proso millet gives it a competitive edge compared to giant foxtail. Giant foxtail has a potential competitive edge over wild proso millet if postharvest management is not done.

Sweet corn production parameters

Averaged across row spacing, the two sweet corn varieties differed in the above ground biomass (Figure 6A) and fresh ear weight (Figure 6B). Compared to Sprint, Bonus variety had higher (P<0.05) above ground biomass (Figure 6A) and higher (P<0.05) fresh ear weight

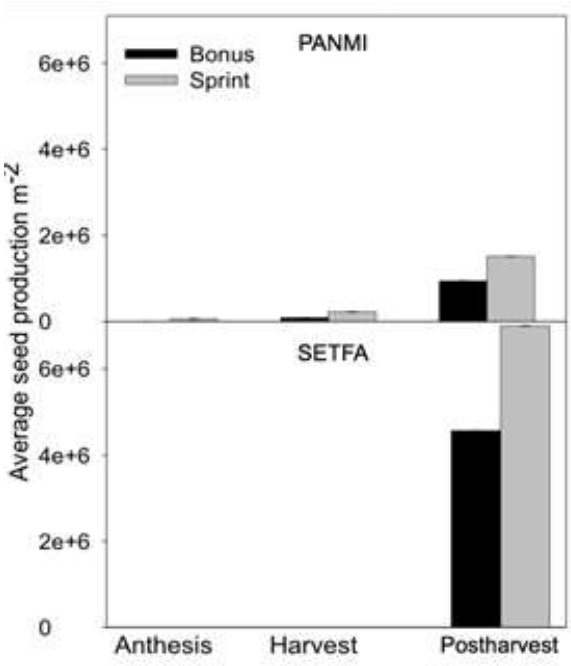

Figure 5. Average seed production of wild proso millet-PANMI (top panel) and giant foxtail-SETFA (bottom panel) at sweet corn anthesis, harvest, and postharvest. Row spacing was not significant (P>0.05), and data is combined across row spacing. Error bars represent the standard error.

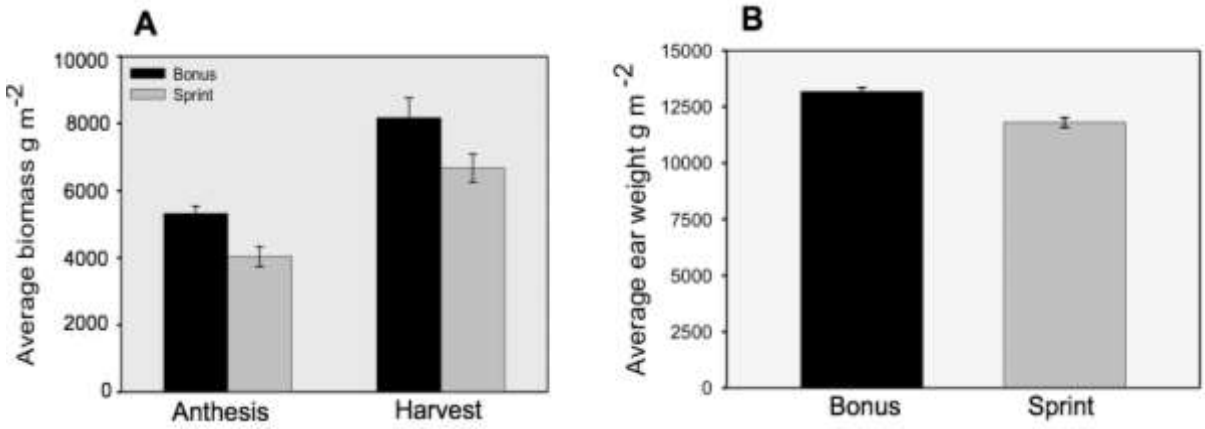

Figure 6. A) Average above ground biomass for the two sweet corn varieties at anthesis and harvest. B) Average fresh ear weight for each sweet corn variety. Error bars represent the standard error.

(Figure 6B). Sweet corn above ground biomass and fresh ear weight did not differ between experimental plots with weeds and weed-free plots, suggesting that observed production parameters are due to sweet corn variety and not weed competition. This could be because the weed population densities of both weed species were maintained at low levels during the experiment.

Conclusions

This study showed that sweet corn variety was the single most important variable affecting weed growth and development of wild proso millet and giant foxtail. Therefore, crop variety is a major factor for consideration when growing crops in environments where wild proso

millet and giant foxtail and other problematic weeds are predominant. Similar to our observed Bonus variety's competitiveness against wild proso millet, So et al. (2009) reported that longer maturity sweet corn hybrids were more competitive against wild proso millet compared to early maturing hybrids. The relationship between crop cultivar and weed suppression has also been studied for other cereals of economic importance, and traits such as canopy architecture, plant height, speed of development, and partitioning of resources reported to affect the competitiveness of crop cultivars (reviewed by Andrew et al., 2015).

Row spacing did not alter any of the weed phenotypic traits measured in our study, possibly due to the low seeding rates used to optimize marketable sweet corn yield. Therefore, our study found minimal light competition-related benefits of reducing sweet corn row spacing from 76 to 51 cm as a method of suppressing growth and development of wild proso millet and giant foxtail. Because several other studies, as mentioned earlier, have reported a reduction in weed performance with narrower row spacing, this is a sustainable method for weed suppression in integrated weed management, however, optimal row spacing should be carefully selected for each crop. Observed differences in crop and weed growth responses between published studies could be due to crop variety and environment. Future studies should examine other problematic weed species' phenotypic response to alteration of light interception and further study the potential of using crop suppression for designing optimal integrated weed management strategies.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

ACKNOWLEDGEMENTS

The authors thank the Agricultural Utilization Research Institute (AURI) Project, PRO 501, for funding this research work. Special recognition goes to Drs F. Forcella and A.G. Johnson for their technical guidance during the study period. Our gratitude also goes to the following: Project AgGrad for financial support, Jim Hebel, Brad Kinkaid, and various student workers for field and technical assistance.

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