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Comparative Ecophysiology of Grain Sorghum and *Abutilon theophrasti* in Monoculture and in Mixture

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Abstract

Selection of crop genotypes that are more competitive with weeds for light interception may improve crop yield stability in the presence of weeds. The effects of interference on ecophysiological characteristics of *Abutilon theophrasti* Medic. and three morphologically diverse grain sorghum hybrids was evaluated to determine the relative tolerance and suppressive ability of the three hybrids and specific traits that may contribute to those differences. A tall hybrid was more tolerant to *A. theophrasti* interference than two medium stature hybrids. Early leaf area growth of two medium-stature sorghum hybrids was reduced by *A. theophrasti* interference, whereas early growth of a tall hybrid was unaffected. The height of *A. theophrasti* was greater than two moderate-stature hybrids but lower than the tall hybrid. Greatest leaf area density (L_D) of the tall sorghum hybrid was above that of *A. theophrasti*, whereas greatest L_D of medium-stature hybrids was below that of the weed. In monoculture, the partitioning of new biomass to various plant organs was similar among sorghum hybrids, whereas the tall sorghum hybrid partitioned less biomass to leaves and more to stems than medium hybrids in mixture. The results indicate that the three hybrids differ in their susceptibility to *A. theophrasti* competition. Crop traits that may contribute to greater crop competitiveness include greater maximum height and its growth rate and greater height of maximum leaf area distribution.

Keywords: *Abutilon theophrasti*, competition, velvetleaf, growth analysis, leaf area distribution

Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is the fifth most important cereal crop worldwide and a major staple food of people in the semi-arid tropics (ICRISAT, 1990). Sorghum yield loss resulting from grassy weeds and *Striga* spp. could reach 80–100% depending on rainfall and soil fertility (Lagoke et al., 1991). Chandler (1981) estimated that weed competition costs sorghum producers almost $250 million per year in yield reductions in the USA. *Abutilon theophrasti* Medic. (velvetleaf) is an important weed throughout the region in which maize (*Zea mays* L.) and soyabean (*Glycine max* [L.] Merr.) are grown in the USA, and its geographical range is still expanding (Spencer, 1984). Roeth et al. (1983) reported that *A. theophrasti* has increased dramatically in Nebraska and is now considered one of the most troublesome weeds in sorghum.

Concerns over herbicide resistance and non-target effects of herbicide use in many developed countries, as well as their low accessibility in developing countries, have resulted in a need to develop integrated approaches to weed management in many agricultural systems. Improved cultivar competitiveness and tolerance to weeds were suggested as methods of reducing the negative effects of weeds on crop yield (Jordan, 1993). Under adequate soil nitrogen and water, competition for light is the primary cause of yield loss from weeds (Munger et al., 1987). Competition for light is an instantaneous process that depends on the relative share of available light absorbed by a species in a mixed canopy and the efficiency of energy use in dry matter production (Lawlor, 1995). Light absorption in mixed canopies is determined by the leaf area index (LAI) of the species, plant height, vertical leaf area distribution and leaf angle distribution (Lindquist & Mortensen, 1999). Lindquist & Mortensen (1998) showed that morphologically different maize hybrids differed in their tolerance to and ability to suppress *A. theophrasti* seed production. Weed interference studies in sorghum are limited in number, and little is known about the interference between *A. theophrasti* and sorghum.

The first objective of this research was to compare the tolerance and relative suppressive ability of three sorghum hybrids grown in mixture with *A. theophrasti*. The second objective was to compare sorghum and *A. theophrasti* growth and canopy characteristics to evaluate which may contribute to differences in tolerance and weed suppressive ability.

Materials and methods

Experiments were conducted during two growing seasons in 1996 and 1997 at the University of Nebraska Agronomy Farm at Havelock, Nebraska (40° 50′N, 96° 36′W; 347 m a.s.l.), and at the Agricultural Research and Development Center near Mead, Nebraska (41° 14′N, 96° 29′W; 370 m a.s.l). Soils at both sites are a Sharpsburg silty clay loam (fine, smectitic, mesic, Typic Argiudoll) with 3.2% and 2.6% soil organic matter respectively. Treatments consisted of a factorial combination of three grain sorghum hybrids and three weed infestation levels arranged in a split-plot treatment design with four replicates. Sorghum hybrids were treated as whole plots and weed infestation levels as subplots. Sorghum hybrids were selected on the basis of their variation in height, leaf area and leaf display (Dekalb FS2 tall ≥ 1.8 m; Dekalb DK54 and Dekalb X260 medium tall ≤ 1.5 m; Dekalb; Monsanto, St Louis, MO, USA). Similarity in time to maturity among sorghum hybrids was intentionally selected to avoid any confounding between the effect of hybrid morphology and differential crop growth stage. Weed infestation treatments included monoculture crop (completely weed-free), low weed infestation level (*A. theophrasti* emerged after herbicide application 2 weeks after crop emergence) and high weed infestation level (*A. theophrasti* present during the entire growth cycle of sorghum). An experimental unit was a six row (0.76 m apart) by 15 m plot. Maize and sorghum were grown 1 year before the establishment of these experiments at Mead and Havelock respectively. Fields were disked in spring for seedbed preparation, and phosphorus and nitrogen fertilizers were applied at 20 kg P ha^{-1} and 36 kg N ha^{-1}. Sorghum was seeded at 180,000 seeds ha^{-1} with a John Deere max-emerge planter (Deere & Co., Moline, IL, USA) containing Kinze D8524 (Williamsburg, IA, USA) plates to allow precise seed spacing. *Abutilon theophrasti* seeds were broadcast at 25 kg ha^{-1} over the entire area at planting using a PTO-driven fertilizer spreader at both locations in 1996 and at Havelock in 1997. A hand spreader was used at Mead in 1997. Weed seeds were presoaked in a 70 °C hot water bath for 4–5 min, then dried at room temperature to increase germination rate (Khedir & Roeth, 1981). Planting dates were June 6 and 7, 1996, and June 2 and 4, 1997, for Havelock and Mead respectively. Timing of weed removal reflected common practice in the area. Propachlor (Ramrod, 480 g a.i. L^{-1}; Monsanto) was applied at 6.5 kg a.i. ha^{-1} at planting to control common grasses. Bentazon (Basagran, 480 g a.i. L^{-1}; BASF, Research Triangle Park, NC, USA) was applied at 0.84 kg a.i. ha^{-1} with 28% urea ammonium nitrate (UAN) solution to control *A. theophrasti* at the three-leaf stage in weed-free and low weed infestation level treatments. *Abutilon theophrasti* plants emerging after treatment were removed by hand in the weed-free treatment, but allowed to compete with the crop in the low weed infestation treatment. No post-emergence herbicide was applied to the high infestation level treatments, but weeds other than *A. theophrasti* were removed by hand as needed.

Two plants of both sorghum and *A. theophrasti* were destructively harvested weekly in each plot to assess dry matter accumulation beginning 2 weeks after emergence and ending at physiological maturity. One plant was randomly identified in each of rows 2 and 5 of each experimental unit, ensuring that at least 1 m separated it from a previously harvested plant. Plant height was measured before clipping plants at the soil surface. Height was measured to the extended tip of the tallest leaf before sorghum anthesis and to the top of the panicle after anthesis. *Abutilon theophrasti* height was measured to the highest point on the main stem. Harvested plants were separated into green leaves, stems and reproductive tissue. Green leaves were separated by cutting the lamina at the collar for sorghum or at the attachment of the petiole to the lamina for *A. theophrasti*. The panicle was separated from the stem at the last node. Leaf area was measured with an area meter (LI-3100, LiCor, Lincoln, NE, USA) and oven dried at 60 °C to constant mass. At early boot stage, 10 plants were randomly selected from each treatment in two replicates and clipped at the soil surface. Plants were separated as described above into different plant organs. The leaf area was determined and oven dried to determine the specific leaf area (SLA; m^2 g^{-1}), which was used to calculate leaf area from leaf biomass at subsequent harvests. To determine the extinction coefficient for diffuse radiation, photosynthetic photon flux density (PPFD) was measured at sorghum anthesis under uniform overcast sky conditions in monoculture treatments at both locations in 1997. Attenuation of only diffuse radiation was measured because extinction coefficients for the direct components of radiation can be derived from that for diffuse radiation (Spitters, 1986). A line quantum sensor (LI-191SA; LiCor) and a point sensor (LI-190SA; LiCor) were used simultaneously to measure incident PPFD at 0.2 m intervals within and above the canopy respectively. Two plants were harvested where PPFD measurements were taken and separated into leaves, stems and reproductive organs using a stratified clip at 0.2-m height intervals. Leaf area was determined for each height interval, and tissues were dried to constant weight.

Data analyses

Phenological development was quantified using a dimensionless scale where 0 represents emergence, 1 is sorghum anthesis or *A. theophrasti* flower initiation, and 2 is sorghum physiological maturity or complete loss of *A. theophrasti* leaves. Development stage is calculated from thermal units (TU) accumulated after plant emergence using a base temperature of 10 °C for *A. theophrasti* (Lindquist et al., 1998) and 15 °C for sorghum (Eastin, 1972). Estimates of canopy characteristics were obtained for each experimental unit using methods outlined by Lindquist et al. (1998) and Lindquist & Mortensen (1999). Characteristics measured included: apparent leaf area index at emergence [$\ln(LAI_o)$] and early leaf area growth rate (RGRL), which were obtained from a regression of ln(LAI) on thermal time from emergence until LAI approaches 1.0; thermal time from emergence to 50% maximum height (H_a/H_b) and maximum height (H_m), obtained by fitting measured height on thermal time (TU) using the logistic function ($\text{height}=H_m/[1 + \exp(H_a - H_b TU)]$; leaf area distribution, quantified using $LAI_r=1 - \exp\{-[((1 - HT_r)/LD_a)LD_b]\}$, where LAI_r is relative LAI at relative height HT_r, LD_a is relative height of maximum leaf area density (from the top of the canopy), and LD_b defines the slope of the leaf area density relationship; specific leaf area (SLA); biomass partitioning coefficients ($P_C=\Delta W_c/\Delta W_T$, where ΔW_c is the change in biomass of organ group c, and ΔW_T is the change in total above-ground biomass). Extinction coefficient estimates were obtained for each experimental unit of the monoculture treatments in 1997. Least squares linear and non-linear regression analyses were used to obtain estimates of canopy characteristics for each experimental unit. After testing parameter estimates for homogeneity of variance, differences among hybrids were tested using analysis of variance (SAS, 1996). Simple effects (i.e. hybrid × weed infestation at a given level of weed infestation) were evaluated when hybrid × weed infestation level interaction was present. In the absence of a hybrid × weed infestation level interaction, single degree of freedom contrasts were used to compare estimates among sorghum hybrids or among weed infestation levels. Data were not combined because weed infestation levels differed among sites and years.

Results and discussion

Weather, phenology and plant population

Rainfall was greater and more evenly distributed in 1996 than in 1997 at Havelock and was above the long-term average during the maximum growth stage in 1996. Rainfall in both years at Mead was similar to that for Havelock in 1996. Cooler minimum and maximum temperatures were recorded in 1996 than in 1997 at both locations (Traoré, 1999).

Monoculture-grown DK54 reached physiological maturity 5 days later than the other two hybrids at Havelock in 1996. Anthesis and physiological maturity of medium-stature hybrids were delayed 5–9 days when grown in mixture with *A. theophrasti* (Traoré, 1999). *Abutilon theophrasti* flower initiation did not differ in mixture compared with monoculture, probably because it is more sensitive to photoperiod than to interspecific competition.

Sorghum population averaged 14 and 15 plants m^{-2} at Havelock and Mead, respectively, in 1996, and 15 plants m^{-2} at both locations in 1997. Weed monoculture densities averaged 27.7 and 12.8 plants m^{-2} in 1996 and 1997 at Havelock, and 29.2 and 26.6 plants m^{-2} at Mead. Insufficient *A. theophrasti* plants emerged after herbicide application in the low *A. theophrasti* infestation treatment to allow measurements to be taken on the weed. However, the effects of these few weeds on sorghum were evaluated. The high *A. theophrasti* infestation treatments averaged 32.6 plants m^{-2} in mixture with sorghum hybrids at Havelock in 1996 and only 2.6 plants m^{-2} in 1997, mainly because of insufficient moisture during early growth. At Mead, *A. theophrasti* in mixture averaged 28.2 and 20.5 plants m^{-2} in 1996 and 1997 respectively. Weed populations did not differ in mixture except at Mead in 1996, where *A. theophrasti* in mixture with the tall sorghum was greater (35 plants m^{-2}) than in mixture with the medium hybrids (25 plants m^{-2}).

Sorghum tolerance and A. theophrasti suppressive ability

Tolerance of the three sorghum hybrids to *A. theophrasti* interference was evaluated by comparing the per plant biomass (w) of sorghum in mixture relative to its biomass in monoculture (w_{mix}/w_{mono}) at the sample taken near physiological maturity. This allows for a clear comparison among hybrids, even though their biomass in monoculture may have differed. Relative yield of sorghum in the low infestation treatments did not differ from that in monoculture treatments, so only high infestation treatments will be discussed. Compared with the two medium hybrids, the tall hybrid had greater biomass in mixture relative to monoculture at both locations in 1996 (Table 1). Although the same trend was true in 1997, differences were not statistically different. These results indicate that the tall hybrid is more tolerant of *A. theophrasti* interference than the two medium hybrids.

Table 1. Mean sorghum relative per plant biomass (w_{mix}/w_{mono}) near physiological maturity and *A. theophrasti* per plant biomass in mixture as influenced by sorghum hybrid.

Year	Site	Hybrid	Sorghum relative yield	*A. theophrasti* biomass in mixture (g plant^{-1})
1996	Havelock	FS2	0.930	28.92
		DK54	0.459	28.44
		X260	0.513	24.17
		SE	0.0626	5.900
1996	Mead	FS2	0.946	18.43
		DK54	0.728	26.40
		X260	0.794	23.37
		SE	0.0750	1.825
1997	Havelock	FS2	0.841	20.06
		DK54	0.770	33.64
		X260	0.791	21.69
		SE	0.1186	5.543
1997	Mead	FS2	0.924	3.93
		DK54	0.807	6.00
		X260	0.846	2.90
		SE	0.0572	1.184

The relative ability of the three sorghum hybrids to suppress *A. theophrasti* growth was evaluated by comparing *A. theophrasti* per plant biomass at the final sampling time of the season. Weed biomass was lower in the presence of the tall hybrid compared with the two medium hybrids at Mead in 1996 (Table 1), indicating that the tall hybrid suppressed its growth more than the medium hybrids did. At Mead in 1997, *A. theophrasti* biomass per plant was greatest in the presence of DK54, indicating that this hybrid was less suppressive than either X260 or FS2. No differences in *A. theophrasti* per plant biomass were observed at Havelock.

Canopy characteristics

Early leaf area growth rate

A hybrid × *A. theophrasti* infestation level interaction was observed at Havelock in 1996 and at Mead in 1997 for early leaf area growth rate (RGRL, Table 2). In monoculture treatments, the tall sorghum hybrid (FS2) generally had smaller RGRL than the medium hybrids, whereas RGRL did not differ among sorghum hybrids in mixture (Tables 3 and 4). Thus, early leaf area growth of the two medium hybrids was reduced by *A. theophrasti* interference, whereas early growth of the tall hybrid was not affected. Apparent leaf area index at emergence [$\ln(LAI_o)$] was smaller for DK54 than for the other hybrids across all weed treatments at Mead (Tables 3 and 4). Although DK54 had an apparent disadvantage at emergence, its growth rate was not reduced by *A. theophrasti* interference.

Table 2. Analysis of variance showing probabilities (P-values) of the main effects of sorghum hybrid (H), weed pressure (W) and their interactions on sorghum mean estimated regression coefficients for apparent leaf area at emergence [$\ln(LAI_o)$], early leaf area growth rate [RGRL $(d°C)^{-1}$], thermal time to 50% maximum height (H_a/H_b, d°C), maximum height (H_m, cm), relative height of maximum leaf area density ($1–LD_a$), leaf area distribution shape coefficient (LD_b) and extinction coefficients for diffuse radiation (K_{df})

Year	Site	Eff.	$\ln(LAI_o)$	RGRL	H_a/H_b	H_m	$1–LD_a$	LD_b	K_{df}
1996	Havelock	H	0.338	0.379	<0.001	<0.001	–	–	–
		W	0.199	0.104	<0.001	<0.001	–	–	–
		H×W	0.350	0.038	<0.001	0.005	–	–	–
	Mead	H	0.039	0.073	<0.001	<0.001	–	–	–
		W	0.392	0.500	0.064	0.001	–	–	–
		H×W	0.681	0.723	<0.001	<0.001	–	–	–
1997	Havelock	H	0.241	0.250	0.004	<0.001	0.035	0.644	<0.001
		W	0.436	0.356	0.003	0.001	0.986	0.991	–
		H×W	0.167	0.215	<0.001	0.010	0.020	0.440	–
	Mead	H	0.001	0.031	<0.001	<0.001	0.004	0.001	<0.001
		W	0.879	0.994	0.007	0.007	0.172	0.972	–
		H×W	0.576	0.020	<0.001	<0.001	0.027	0.042	–

Table 3. Mean sorghum apparent leaf area at emergence [$\ln(\mathrm{LAI}_o)$], early leaf area growth rate [RGRL $(\mathrm{d°C})^{-1}$], thermal time to 50% maximum height (H_a/H_b, d°C) and maximum height (H_m, cm) at Havelock and Mead in 1996

	Havelock				Mead			
Treatments	$\ln(\mathrm{LAI}_o)$	RGRL	H_a/H_b	H_m	$\ln(\mathrm{LAI}_o)$	RGRL	H_a/H_b	H_m
FS2 no weed	–4.89	0.018	377	240	–5.54	0.023	380	221
FS2 low weed	–4.89	0.021	360	231	–5.54	0.023	362	214
FS2 high weed	–4.89	0.019	356	234	–5.54	0.023	338	198
DK54 no weed	–4.89	0.022	242	145	–6.02	0.025	251	133
DK54 low weed	–4.89	0.020	253	149	–6.02	0.025	251	131
DK54 high weed	–4.89	0.020	212	125	–6.02	0.025	240	127
X260 no weed	–4.89	0.021	242	143	–5.96	0.025	246	128
X260 low weed	–4.89	0.021	235	141	–5.96	0.025	244	127
X260 high weed	–4.89	0.018	214	118	–5.96	0.025	242	121
SE	0.089	0.0005	6.0	3.6	0.150	0.0007	8.4	4.9

Abutilon theophrasti has been reported to have a low growth rate early in its development, with greatest growth occurring about 6–8 weeks after emergence (Roeth et al., 1983). Weed $\ln(\mathrm{LAI}_o)$ and RGRL were always lower than that of sorghum (Table 5, statistics not shown) and similar to those reported by Lindquist & Mortensen (1999). Weed RGRL was reduced equally by the three sorghum hybrids (Table 5).

Height growth rate and maximum height

A hybrid–infestation level interaction was observed for maximum height in all site–years (Table 2). In monoculture treatments, the tall hybrid (FS2) reached a greater maximum height (H_m) than the other hybrids (Tables 3 and 4). Maximum height of all hybrids was reduced by about 10% in mixture with *A. theophrasti*. Monoculture-grown *A. theophrasti* reached a higher H_m than in mixture (Table 5). Maximum height of *A. theophrasti* was reduced equally in the presence of all hybrids in all site–years (Table 5). Height reduction ranged from 22% to 60% depending on location and year. The weed grew taller than the two medium hybrids in all site–years except Mead in 1997, giving *A. theophrasti* a net competitive advantage in mixture with the short or medium sorghum hybrids in those site–years. Similar height differences have been reported for *A. theophrasti* competing with other crops (Roeth et al., 1983). Akey et al. (1990) attributed greater light interception to a greater *A. theophrasti* height and dry matter allocation to branches in the upper layers of the canopy when competing with *Glycine max* L.

Differences in height can contribute to differences in competitiveness between hybrids by increasing the ability of the crop to shade weeds. A strong correlation between maximum plant height and competitive ability has been demonstrated for many crop species (Berkowitz, 1988). Our results indicate that, because the tall sorghum hybrid was taller than *A. theophrasti*, it may be more competitive for light than the medium-stature hybrids, which were typically shorter than *A. theophrasti* late in the season. Variation in time course of height growth among hybrids may also contribute to differences in time to canopy closure, the time course of radiation interception and, ultimately, differences in rela-

Table 4. Mean sorghum apparent leaf area at emergence [$\ln(\mathrm{LAI}_o)$], early leaf area growth rate [RGRL $(\mathrm{d°C})^{-1}$], thermal time to 50% maximum height (H_a/H_b, d°C), maximum height (H_m, cm), relative height of maximum leaf area density ($1-\mathrm{LD}_a$) and leaf area distribution shape coefficient (LD_b) at Havelock and Mead in 1997

	Havelock						Mead					
Treatments	$\ln(\mathrm{LAI}_o)$	RGRL	H_a/H_b	H_m	$1-\mathrm{LD}_a$	LD_b	$\ln(\mathrm{LAI}_o)$	RGRL	H_a/H_b	H_m	$1-\mathrm{LD}_a$	LD_b
FS2 no weed	–4.36	0.018	275	176	0.637	3.05	–6.60	0.028	239	141	0.534	3.50
FS2 low weed	–4.36	0.018	265	166	0.635	3.05	–6.60	0.030	242	147	0.527	3.17
FS2 high weed	–4.36	0.018	256	158	0.606	3.05	–6.60	0.029	239	146	0.572	3.22
DK54 no weed	–4.36	0.018	228	126	0.626	3.05	–7.51	0.032	246	159	0.559	3.43
DK54 low weed	–4.36	0.018	228	130	0.653	3.05	–7.51	0.032	243	156	0.541	3.54
DK54 high weed	–4.36	0.018	220	121	0.655	3.05	–7.51	0.032	243	156	0.556	3.43
X260 no weed	–4.36	0.018	216	118	0.686	3.05	–6.90	0.032	240	145	0.621	2.46
X260 low weed	–4.36	0.018	215	118	0.667	3.05	–6.90	0.029	240	147	0.614	2.52
X260 high weed	–4.36	0.018	211	116	0.688	3.05	–6.90	0.030	232	141	0.612	2.66
SE	0.175	0.0009	8.8	4.7	0.0188	0.153	0.322	0.0014	7.3	2.2	0.0104	0.159

Table 5. Mean *A. theophrasti* apparent leaf area at emergence [$\ln(\mathrm{LAI}_o)$], leaf area growth rate [RGRL $(\mathrm{d}°\mathrm{C})^{-1}$], thermal time to 50% maximum height (H_a/H_b, d°C), maximum height (H_m, cm), relative height of maximum leaf area density ($1 - \mathrm{LD}_a$) and the leaf area distribution shape coefficient (LD_b)

Year	Site	Treatment	$\ln(\mathrm{LAI}_o)$	RGRL	H_a/H_b	H_m	$1 - \mathrm{LD}_a$	LD_b
1996	Havelock	Vel* mono	–5.92	0.015	685	207	–	–
		Vel-FS2mix	–5.79	0.015	624	176	–	–
		Vel-DK54mix	–5.41	0.014	615	157	–	–
		Vel-X260mix	–5.14	0.013	611	152	–	–
		SE	0.203	0.0008	24.3	12.8	–	–
	Mead	Vel mono	–6.70	0.018	685	239	–	–
		Vel-FS2mix	–6.16	0.015	624	153	–	–
		Vel-DK54mix	–6.84	0.016	615	151	–	–
		Vel-X260mix	–6.68	0.016	611	153	–	–
		SE	0.173	0.0011	24.3	8.89	–	–
1997	Havelock	Vel mono	–6.05	0.018	762	236	0.805	1.13
		Vel-FS2mix	–7.58	0.012	530	139	0.872	1.90
		Vel-DK54mix	–5.98	0.014	485	134	0.867	1.76
		Vel-X260mix	–7.29	0.012	521	131	0.856	1.76
		SE	0.752	0.0018	54.7	15.0	0.0243	0.257
	Mead	Vel mono	–4.76	0.010	758	234	0.805	1.13
		Vel-FS2mix	–2.17	0.002	694	99	0.872	1.90
		Vel-DK54mix	–2.83	0.003	532	90	0.867	1.76
		Vel-X260mix	–2.44	0.001	623	85	0.856	1.76
		SE	0.422	0.0009	93.8	13.5	0.0243	0.257

*Vel = *A. theophrasti* in monoculture or mixture.

tive competitive ability (Lindquist et al., 1998). Because height parameters differed among years and locations, our results indicate that height growth and its response to interference is dependent in part upon environmental conditions. Further research directed at understanding crop and weed height growth response to edaphic and micrometeorological conditions is needed.

Leaf area distribution

Vertical leaf area distribution was measured only in 1997. There was a sorghum hybrid–weed infestation interaction for both leaf area distribution parameters at Havelock and Mead (Table 2). Relative height at which maximum leaf area density occurs ($1 - \mathrm{LD}_a$) was higher for the medium hybrid X260 than for the other hybrids grown in monoculture at both sites (Table 4). However, actual height at which maximum leaf area density occurs [$H_m(1 - \mathrm{LD}_a)$] was higher for the tall sorghum hybrid than for the two medium hybrids grown in monoculture (Figure 1). The relative height of maximum leaf area density of *A. theophrasti* grown in monoculture was much higher than for all sorghum hybrids (Table 5), suggesting that, if all plants were the same height in mixture, *A. theophrasti* would have a large proportion of its leaf area above the sorghum canopy. However, because FS2 was taller than *A. theophrasti* in mixture, whereas *A. theophrasti* was taller than X260 and DK54, FS2 was not as severely shaded by *A. theophrasti* late in the growing season. Height of maximum leaf area density of FS2 decreased in mixture at Havelock, whereas that of DK54 increased and that of X260 did not vary. In contrast, height of maximum leaf area density of FS2 increased in mixture at Mead, whereas that of DK54 and X260 did not vary from monoculture. The differential response of vertical leaf area distribution of sorghum hybrids to *A. theophrasti* infestation among sites was probably caused by differences in the intensity of competition between sorghum and *A. theophrasti* resulting from different soil moisture conditions. Medium-stature sorghum hybrids were shaded by *A. theophrasti* late in the growing season, suggesting that *A. theophrasti* will intercept a greater proportion of the incident PPFD at the expense of medium sorghum hybrids. Maximum *A. theophrasti* leaf area density was closer to the top of the *A. theophrasti* plant when grown in mixture, probably because of the senescence of leaves low in the canopy. However, because *A. theophrasti* H_m was reduced in mixture, leaf area was distributed lower in the canopy when grown in mixture with sorghum hybrids compared with *A. theophrasti* in monoculture (Table 5, Figure 1E and F). Both sorghum and *A. theophrasti* varied their vertical leaf area distribution as a result of interspecific competition. Any factor that differentially alters a plant's ability to intercept light in relation to that of neighboring plants should influence its ability to compete for light (Rhodes & Stern, 1978).

Specific leaf area

Mean specific leaf area ($m^2\ g^{-1}$, SLA) of both *A. theophrasti* and sorghum was similar to values reported by others (McCree, 1983; Bazzaz et al., 1989; Lindquist & Mortensen, 1999). Sorghum SLA differed among hybrids in monoculture (Figure 2). Early in the season (developmental stage, DVS=0.2), the medium hybrids had greater SLA than the tall sorghum hybrid. Between the medium sorghum hybrids, DK54 had a greater SLA than X260. At early boot stage (DVS=0.6), the tall sorghum hybrid and DK54 had greater SLA than X260. McCree (1983) showed that sorghum SLA decreased with increasing plant size under both controlled environment and field conditions. In mixture with *A. theophrasti*, sorghum SLA showed a similar trend to that observed in monoculture (Figure 2). However, the tall sorghum hybrid and DK54 had greater SLA than X260 early in the season, whereas DK54 had a greater SLA than the other sorghum hybrids late in the season. *Abutilon theophrasti* in monoculture had lower SLA than sorghum during early development, whereas *A. theophrasti* in mixture

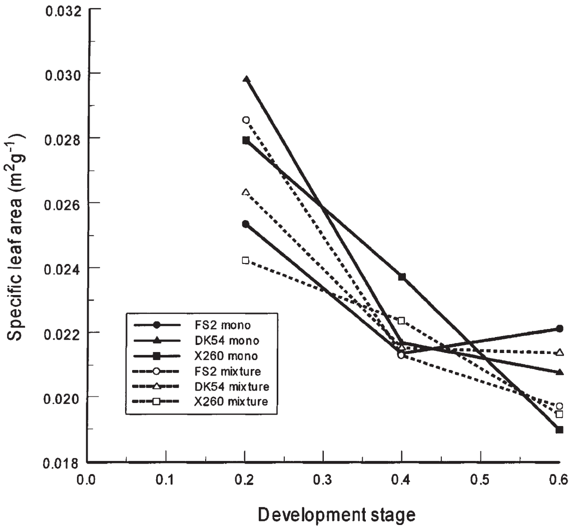

Figure 2. Mean specific leaf area ($m^2\ g^{-1}$) as a function of development stage for three sorghum hybrids (FS2, DK54 and X260) grown in monoculture and in mixture with *A. theophrasti* at Havelock in 1996.

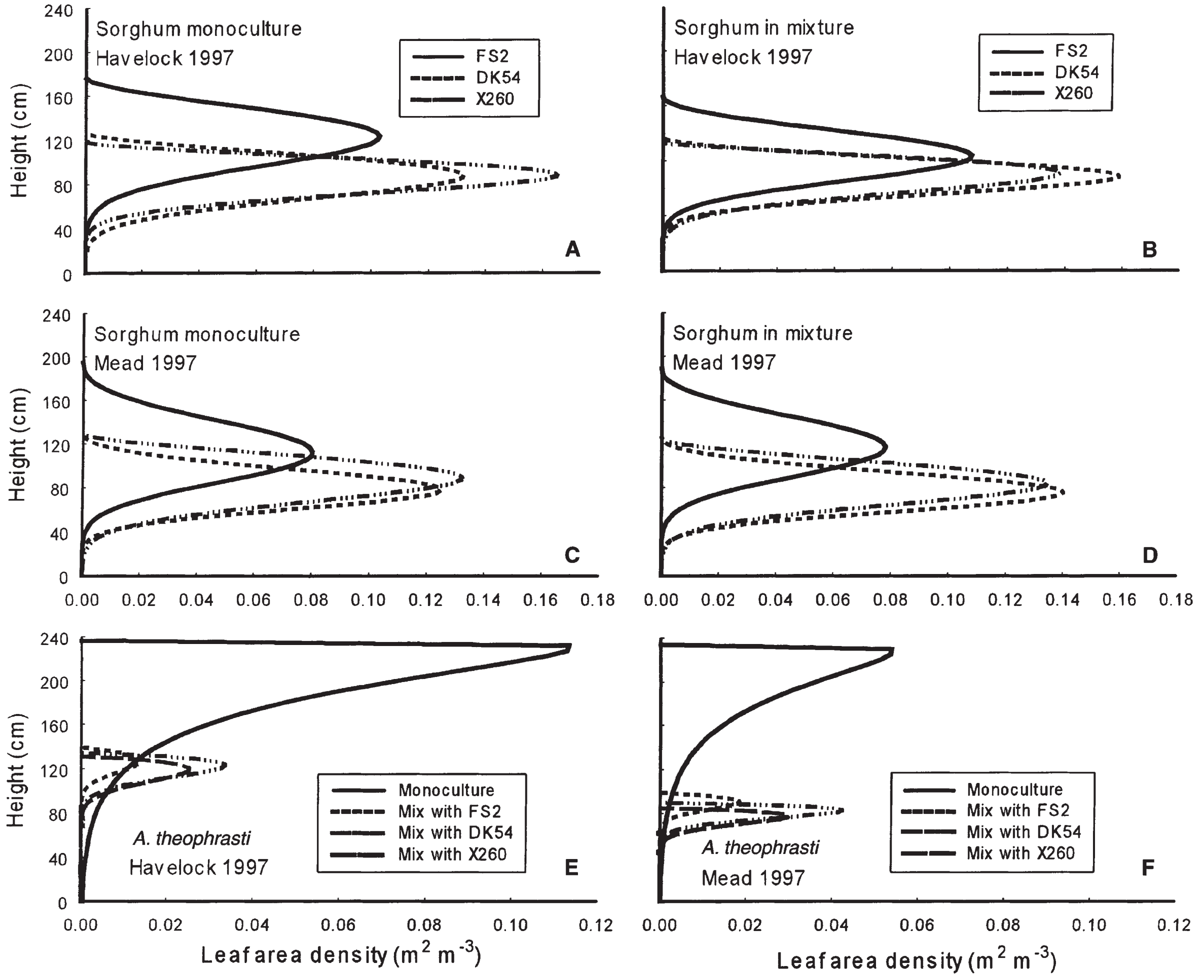

Figure 1. Leaf area density ($m^2\ m^{-3}$) over height of sorghum (A–D) and *A. theophrasti* (E and F) in monoculture and in mixture at Havelock and Mead in 1997.

had higher SLA than in monoculture (data not shown). Assuming equivalent partitioning of biomass to leaf, a hybrid with a greater SLA will produce the larger LAI (Lindquist & Mortensen, 1999).

Biomass partitioning

Partitioning of new biomass to leaf and stem was similar among sorghum hybrids grown in monoculture and in mixture except at Havelock in 1996, where a hybrid × weed infestation × sample date interaction was observed for the leaf partitioning coefficients (Table 6). This interaction indicates that the response of sorghum hybrids to *A. theophrasti* interference varied with development stage (DVS) of the crop. In monoculture, the partitioning of new biomass to leaf and stem was similar among sorghum hybrids and decreased with development stage (Figures 3A and C). In mixtures, partitioning of new biomass to leaf and stem was similar among sorghum hybrids during the early stages of development. However, the tall hybrid partitioned less new biomass to leaf and more biomass to stem compared with the medium hybrids at DVS=0.6 (Figure 3B). The increase in biomass partitioned to stem contributed to the lack of height response of FS2 to *A. theophrasti* competition in that site–year. Partitioning of new biomass to panicle was similar among hybrids at Mead, whereas the medium sorghum hybrids partitioned more new biomass to panicle than the tall hybrid at Havelock. The partitioning of new biomass to leaf and stem in *A. theophrasti* was similar in mixture with the three hybrids (Table 7). Weed stem and reproductive organs were combined late in the season, and no partitioning coefficient was assessed for reproductive organs (data not shown).

Radiation attenuation into the canopy

Estimates of extinction coefficients for diffuse radiation differed among sorghum hybrids in monoculture (Table 2). Extinction coefficients were greater (K_{df}= 0.62 ± 0.034) for medium sorghum hybrids than for the tall hybrid (K_{df}=0.54 ± 0.034). The extinction coefficient for monoculture-grown *A. theophrasti* was smaller (K_{df}=0.45 ± 0.034) than that of sorghum. The smaller value of K_{df} for *A. theophrasti* is contrary to theoretical predictions, as *A. theophrasti* leaf angle distribution appears more planophile than that of sorghum. However, Lindquist & Mortensen (1999) also showed that *A. theophrasti* K_{df} was smaller than that of maize. The smaller K_{df} may be the result of greater transmission of PPFD through leaves. Estimates of K_{df} for sorghum and *A. theophrasti* were within the range of those reported by others (Flenet et al., 1996; Lindquist & Mortensen, 1999). Greater extinction coefficients indicate that more radiation is intercepted per unit leaf area and may confer greater competitive advantage to the hybrid by providing more shade.

Conclusions

Tolerance to and suppression of *A. theophrasti* growth differed among sorghum hybrids. In general, the tall hybrid FS2 was more tolerant to *A. theophrasti* interference at all site–years. The tall hybrid also suppressed *A. theophrasti* growth more than the other hybrids, but only in one site–year. Ecophysiological characteristics and their response to *A. theophrasti* competition varied among sorghum hybrids, indicating that certain canopy characteristics may contribute to differences in hybrid toler-

Table 6. Analysis of variance showing probabilities (P-values) of the main effects of sorghum hybrid (H), weed infestation (W) and interactions on sorghum mean estimated partitioning coefficients for leaf and stem at Havelock and Mead in 1996 and 1997.

	Havelock		Mead	
Year/treatment	Pcleaf	Pcstem	Pcleaf	Pcstem
1996				
H	0.881	0.046	0.868	0.798
W	0.860	0.105	0.271	0.869
H×W	0.412	0.430	0.957	0.122
Sample time (samp)	<0.001	<0.001	<0.001	<0.001
H×samp	0.123	0.047	0.839	0.553
W×samp	0.821	0.873	0.037	0.047
H×W×samp	0.014	0.442	0.749	0.934
1997				
H	0.151	0.081	0.067	0.037
W	0.157	0.400	0.631	0.118
H×W	0.415	0.531	0.729	0.273
Sample time (samp)	<0.001	<0.001	<0.001	<0.001
H×samp	0.165	0.253	0.128	0.362
W×samp	0.215	0.228	0.192	0.037
H×W×samp	0.616	0.280	0.358	0.406

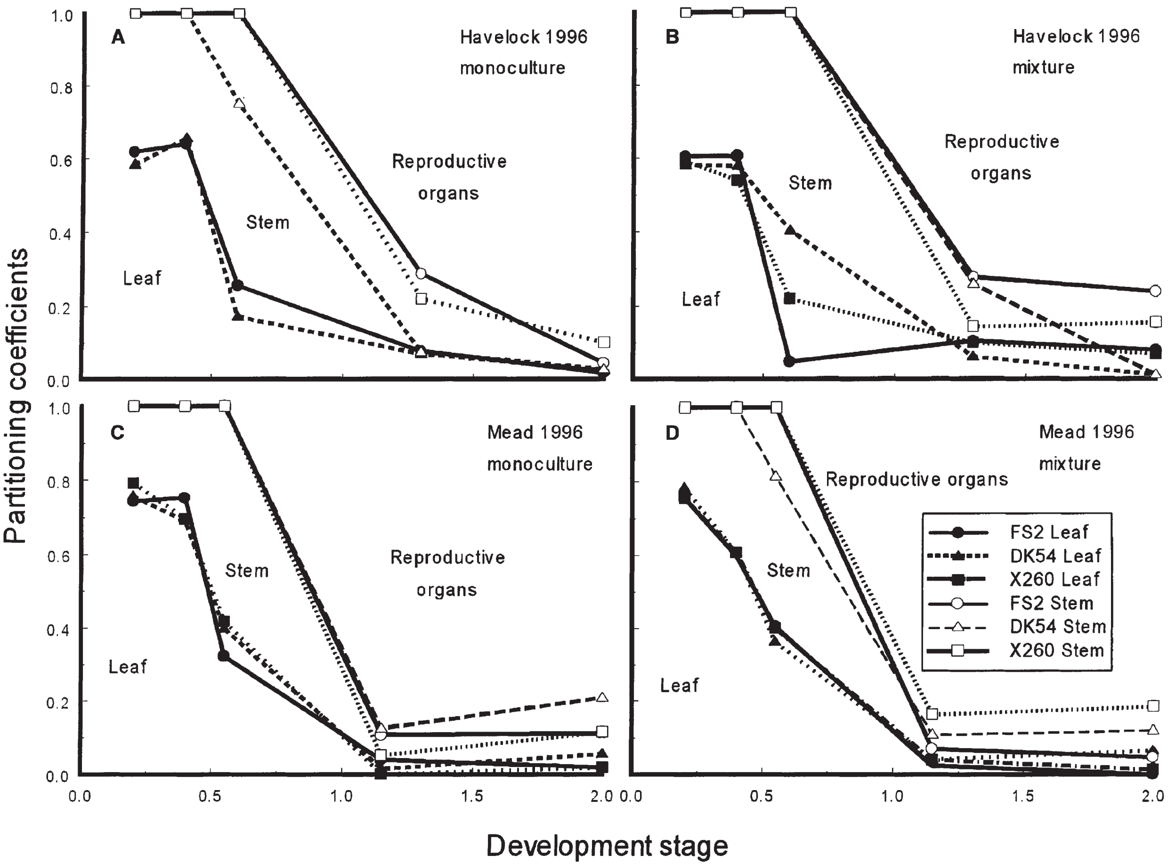

Figure 3. Partitioning of new biomass to leaf, stem and reproductive organs of three sorghum hybrids grown in monoculture (A and C) and in mixture (B and D) at Havelock and Mead in 1996.

ance and *A. theophrasti* suppression. Sorghum hybrids suppressed *A. theophrasti* early season leaf area growth equally. Maximum height was greater for the tall sorghum hybrid than for the medium hybrids in monoculture. Although thermal time to 50% maximum height was also greater, FS2 height exceeded that of the medium-stature hybrids at an early growth stage. Greater height early in the season can contribute to differences in tolerance and suppressive ability among hybrids. The tall hybrid had its leaf area distributed higher in the canopy than the medium hybrids, which may contribute to greater light interception by the tall hybrid late in the season compared with medium hybrids, especially in mixture. Monoculture *A. theophrasti* leaf area was distributed higher in the canopy than that of sorghum, but both height and vertical leaf area distribution were strongly reduced in mixture. Despite a substantial reduction in height, *A. theophrasti* was able to overtop medium-stature hybrids. The greater height combined with greater leaf area density high in the *A. theophrasti*

Table 7. Analysis of variance showing probabilities (P-values) for the main effects of sorghum hybrid (H), sample time and interactions on *A. theophrasti* mean estimated partitioning coefficients for leaf and stem at Havelock and Mead in 1996 and 1997.

	Havelock		Mead	
	Pcleaf	Pcstem	Pcleaf	Pcstem
1996				
H	0.136	0.136	0.856	0.856
Sample time	<0.001	<0.001	<0.001	<0.001
H×sample time	0.060	0.060	0.157	0.157
1997				
H	0.252	0.252	0.067	0.067
Sample time	0.003	0.003	<0.001	<0.001
H×sample time	0.264	0.264	0.128	0.128

canopy contributed to greater light interception by the weed at the expense of the medium-stature hybrids. The ability to modify the height of maximum leaf area density in the presence of *A. theophrasti* may be an important mechanism for improved tolerance and weed suppression. Greater extinction coefficients for diffuse radiation for the medium hybrids indicate greater efficiency of radiation interception per unit leaf area. In a sensitivity analysis of the model INTERCOM, Lindquist & Mortensen (1997) showed that an increase in K_{df} may improve crop tolerance to weed interference, but yield in monoculture was reduced because of the reduced penetration of high-intensity radiation to lower canopy layers. Therefore, the lower K_{df} for the tall sorghum hybrid may reduce its competitive ability, but increase its weed-free crop yield. Specific leaf area of sorghum hybrids is generally reduced in mixture with *A. theophrasti* during early season growth. However, SLA of the medium hybrids increased in mixture later in the season, whereas the tall sorghum SLA was reduced in mixture. Specific leaf area reflects leaf thickness and the relative proportion of assimilatory and conductive or mechanical tissues in leaves (Kvet et al., 1971). The increase in SLA of the medium hybrids in mixture may have been the result of acclimation to optimize CO_2 assimilation in a light-limiting environment (below the *A. theophrasti* canopy). Because leaves of the tall sorghum hybrid were above that of *A. theophrasti* (and therefore not light limited), acclimation to reduced radiation was not necessary for FS2. Greater partitioning of new biomass to leaf during vegetative development may reduce the time to canopy closure and lead to greater tolerance and weed suppressive ability. Selection of hybrids with greater competitiveness with weeds through improved light utilization remains one approach to improving crop productivity in the presence of weeds. The results of this study indicate that careful selection of sorghum hybrid may improve sorghum productivity in the presence of *A. theophrasti*.

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