Light absorption and competition in mixed communities of *Hordeum leporinum-Euphorbia scordifolia*

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Abstract

The effect of *Euphorbia scordifolia* and *Hordeum leporinum* competition on leaf area development, radiant energy absorption, and dry matter production was evaluated in a field experiment. Profile measurements (0-0.3, 0.3-0.6, 0.6-0.9, and >0.9 m above ground) of absorbed photosynthetically active radiation (APAR) and leaf area index (LAI) by species were taken at four densities of *E. scordifolia* (0, 1, 4, and 12 plants per m^2). APAR calculated for *H. leporinum* in mixed communities was 79, 77, and 49 % of the APAR in *H. leporinum* and LAI was reduced to 81, 65, and 37 %. LAI of *H. leporinum* was concentrated in the 0.3-0.6 m layer, while the taller *E. scordifolia* plants had the greatest LAI above 0.6 m. By absorbing radiant energy in the upper canopy, *E. scordifolia* reduced APAR penetrating to *H. leporinum*. Measurements of net photosynthetic and transpiration rates, leaf temperature, and stomatal conductance confirmed the importance of competition for PAR for plant growth and metabolism.

Additional key words: dry mass; leaf area index; leaf temperature; net photosynthetic rate; plant density; stomatal conductance; transpiration.

Introduction

The productivity of plant communities is governed in part by their ability to absorb and utilize photosynthetically active radiation (PAR). Numerous studies have shown an exponential relationship between leaf area index (LAI) and transmitted light in a canopy. Steiner (1987) reports that planting geometry can affect the transmission of radiant energy to the soil surface at a given LAI. In mixed plant-weed communities, competition for PAR is a major factor affecting plant yield. Weed density and morphology affect distribution of PAR in the canopy and absorption of PAR by the crop. Models have been developed recently to describe competition for PAR in mixed communities based on the vertical distribution of leaf area of each species in layers. Rimmington (1984) predicted growth of mixed populations using a layered

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canopy and utilizing the optical properties of each species when grown in monoculture. Spitters and Aerts (1983) simulated competition between species based on the shares of PAR and water absorbed by each species, again based on a vertically layered plant canopy.

E. scordifolia is the most common broadleaf weed in *H. leporinum* fields in the Great Plains in Egypt. The purpose of this study was to describe the distribution of leaves in a *H. leporinum-E. scordifolia* mixed canopy, and to quantify the effects of *E. scordifolia* competition on the absorption of PAR in a fully developed grain *H. leporinum* canopy.

Materials and methods

The study was conducted in 1996 at the Ismailiya research station on a Pullman clay, 12 plants per m^2 with 1-m row spacing. The area was heavily infested with *E. scordifolia* seed. A natural stand of *E. scordifolia* emerged at the same time as the *H. leporinum* and was thinned on 6 and 7 July to 0, 1, 4, and 12 plants per m^2 intrarow with *H. leporinum*. Plots were checked weekly to maintain the desired density of *E. scordifolia*. Soil water was maintained at more than 50 % of plant available water through the season. Fertilizer was applied at a rate of 13 g(N) m^{-2} and 15 g(P) m^{-2}.

Transmission and reflection of PAR within the canopy was measured at 0, 0.3, 0.6, and 0.9 m above the soil surface using *Li-Cor* (*LiCor,* Lincoln, USA) *191SB* line quantum sensors placed perpendicular to the rows at each of four levels. One bar faced upright for reception of transmitted PAR, the other was inverted for reception of reflected PAR. Instruments were staggered to avoid mutual shading. Two *Li-Cor 190SB* quantum sensors (sensing surface 100 mm^2) were placed above the canopy to monitor incoming and reflected PAR. Readings were taken from the field plots in succession. The 10 sensors were connected to a *Polycorder* data logger (*Omnidata International*, Logan, USA), and a set of 10 scans was initiated. For each scan, each sensor was sequentially read for 100 ms. A plot reading took about 25 s, after which the quantum sensors were moved to the next field plot. APAR for each layer and for the entire profile was calculated as follows:

$$APAR_n = [(I_u - Refl_u) - (Trans_l - Refl_l)]/10 \times 100,$$

where APAR = absorbed PAR [%] for layer n, I_u = incoming PAR at the top of layer n, $Refl_u$ = reflected PAR at the top of layer n, $Trans_l$ = transmitted PAR at the bottom of layer n, $Refl_l$ = reflected PAR at the bottom of layer n. Five sets of readings were taken between 15 and 20 August (*H. leporinum* growth stage 6 - Vanderlip and Reeves 1972) during cloudless periods near solar noon. All quantum sensors were intercalibrated prior to the experiment.

Leaf net photosynthetic (P_N) and transpiration rates (E), stomatal conductance (g_s), and leaf temperature (T_l) were measured using a *Li-Cor LI-6000* photosynthesis system. Three fully expanded, sunlit leaves (1520 mm^2 of leaf area) were exposed within the chamber.

At the end of experiments, plants were cut by layer from within the profile stands on 21 August. LAI, dry matter, and head means (when present) were determined for each species by layer and for the entire profile.

The experimental design was a randomized block with three replications. Values were analyzed by analysis of variance, and means compared by the Student-Newman-Keuls test at a significance level of 5 %.

Results and discussion

Three main sources of competition among plants are those for nutrients, water, and PAR. Allelopathic effects of *E. scordifolia* residues have been reported by Connick and Brandon (1986), however, all plots were exposed to uniform weed levels during

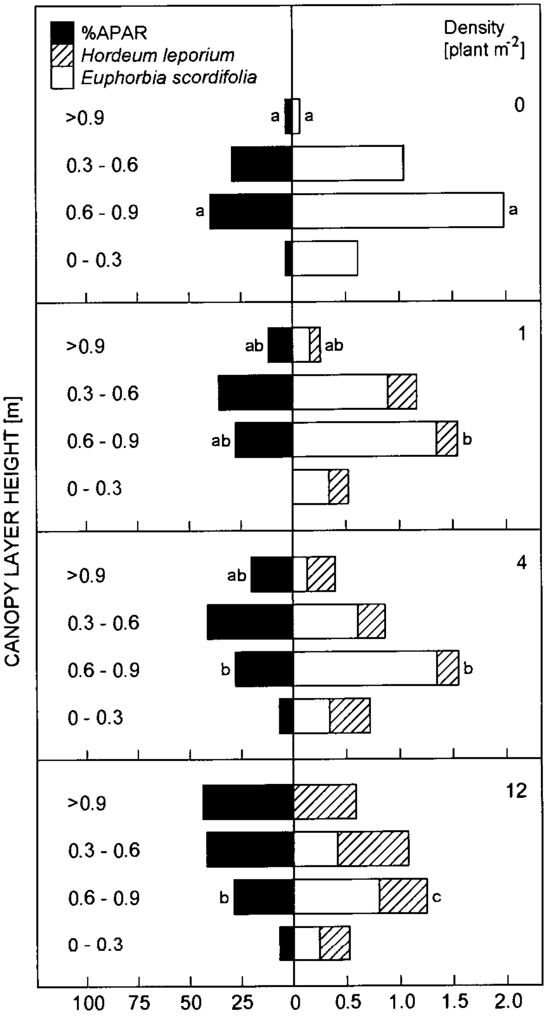

Fig. 1. Radiant energy absorption and leaf area index (LAI) as affected by height within the canopy of mixed *Hordeum leporinum* and *Euphorbia scordifolia* stands. Letters following bars indicate significant differences ($p<0.05$) between treatments by layer for combined total leaf area index, CLAI (*H. leporinum* LAI + *E. scordifolia* LAI, *right*) and absorbed photosynthetically active radiation (APAR, *left*) determined by Student Neuman Keuls multiple range test.

the germination and establishment of *H. leporinum*, at which period most plants show the greatest sensitivity to allelopathic effects. Partitioning of yield reduction due to water, nutrient, and PAR competition is not possible in our study; however, both nutrients and water were managed so as not to be limiting to *H. leporinum* plants. Spitters and Aerts (1983) suggested that these conditions would result in the greatest competition for PAR in mixed species canopies. No significant difference in seasonal water use from thinning to maturity was observed among treatments (230, 255, 230, and 195 mm for 0, 1, 4, and 12 *E. scordifolia* plants per m^2, respectively), indicating that each *H. leporinum* and *E. scordifolia* plant in the weedy plots would not have utilized less water than plants in the weed-free plots.

Total APAR was 12 and 16 % higher with *E. scordifolia* populations of 4 and 12 plants per m^2, respectively, compared to weed-free *H. leporinum* (Fig. 1). In weed-*H. leporinum* stand over 50 % of the total leaf area occurred in the 0.3-0.6 m layer, with high PAR penetration into that region. In mixed populations, *E. scordifolia* was generally taller than *H. leporinum*, plant heights over 1.4 m were observed. In such canopies, PAR absorption relative to *H. leporinum* was decreased between 0.3 and 0.6 m, which was a region dominated by *H. leporinum*, and increased significantly above 0.9 m where leaf area of *E. scordifolia* dominated.

As weed populations increased, the distribution of leaf area became more uniform by height throughout the profile, and PAR was increasingly absorbed in the upper layers of the profile by *E. scordifolia* leaves. Combined total LAI of both species (CLAI) did not differ significantly among treatments (Fig. 1). An approximation of PAR absorbed by each species was obtained by multiplying the percent of CLAI within a layer represented by each species by the APAR for that layer. Above 0.9 m, 13 and 41 % of total incoming PAR was absorbed by *E. scordifolia* populations of 4 and 12 plants per m^2, respectively. Estimated total APAR by *H. leporinum* in mixed populations was 79, 77, and 49 % of total APAR in *H. leporinum* for weed populations of 1, 4, and 12 plants m^{-2}, respectively. These results are consistent with those of studies by Loomis *et al.* (1968) and Clegg *et al.* (1974), who found that the structure of upper canopy affected PAR penetration into the canopy. Total LAI of *H. leporinum* decreased with increasing number of *E. scordifolia* (Table 1).

Maximum leaf area of *H. leporinum* was found between 0.3 and 0.6 m above the ground for all treatments. The greatest reductions in *H. leporinum* LAI also occurred between 0.3 and 0.6 m, being 26, 43, and 62 % for populations of 1, 4, and 12 *E. scordifolia* plants per m^2, respectively.

H. leporinum P_N decreased significantly in weed treatments, compared to weed-free treatments (Table 2). There was no significant difference in initial CO_2 levels among treatments, indicating that CO_2 in the ambient canopy had not been depleted by increasing *E. scordifolia* numbers or by reduced mixing within the canopy. Leaf temperatures increased slightly with *E. scordifolia* number, and the highest g_s of *H. leporinum* was measured in *E. scordifolia* populations of 12 plants per m^2, which also had the lowest *E*. The P_N/E ratio was significantly reduced by all concentrations of *E. scordifolia*, indicating that *E. scordifolia* competition reduced the photosynthetic efficiency (CO_2 assimilated/H_2O lost) of *H. leporinum*.

Table 1. *Hordeum leporinum* and *Euphorbia scordifolia* leaf area index (LAI) and dry matter (DM), and *H. leporinum* head matter (HM) [g m^{-2}]. Means within each layer followed by the same letter are not significantly different ($p<0.05$) as determined by the Student-Newman-Keuls Multiple Range Test.

Canopy height [m]	*Euphorbia* density [plant m^{-2}]	*H. leporinum* LAI	DM	HM	*E. scordifolia* LAI	DM
0 - 0.3	0	0.55ᵃ	188ᵃ	-	-	-
	1	0.39ᵃ	142ᵇ	-	0.14ᵃ	52ᵃ
	4	0.33ᵃ	99ᶜ	-	0.34ᵇ	110ᵇ
	12	0.20ᵃ	57ᵈ	-	0.25ᵃᵇ	124ᵇ
0.3 - 0.6	0	1.94ᵃ	189ᵃ	3ᵃ	-	-
	1	1.43ᵇ	137ᵇ	0ᵃ	0.17ᵃ	38ᵃ
	4	1.10ᶜ	111ᶜ	1ᵃ	0.29ᵇ	64ᵇ
	12	0.73ᵈ	58ᵈ	1ᵃ	0.42ᶜ	100ᶜ
0.6 - 0.9	0	1.01ᵃ	116ᵃ	51ᵃ	-	-
	1	0.94ᵃ	99ᵃ	38ᵃ	0.24ᵃ	42ᵃ
	4	0.83ᵃ	67ᵇ	20ᵃ	0.26ᵇ	68ᵃ
	12	0.39ᵇ	30ᶜ	9ᵇ	0.63ᵇ	114ᵇ
>0.9	0	0.07ᵃ	20ᵃ	17ᵃ	-	-
	1	0.12ᵃ	23ᵃ	14ᵃ	0.13ᵃ	40ᵃ
	4	0.06	10ᵇ	3ᵇ	0.25ᵃᵇ	74ᵇ
	12	0.01ᵃ	1ᵇ	10ᵃ	0.61ᵃ	159ᵇ
Total	0	3.55ᵃ	513ᵃ	72ᵃ	-	-
	1	2.87ᵇ	401ᵇ	52ᵇ	0.68ᵃ	173ᵃ
	4	2.31ᶜ	287ᶜ	25ᶜ	1.14ᵃ	322ᵇ
	12	1.30ᵈ	147ᵈ	12ᶜ	1.90ᵇ	296ᶜ

Generally, the leaf P_N/E ratio measurements indicated a slight water stress under full canopy midday conditions in the *H. leporinum* plants subjected to *E. scordifolia* competition. Because the measurements were made under conditions when the evapotranspiration rate was near its seasonal maximum (full cover, high irradiance, high temperature), near maximum competition for water should have been observed. However, the water stress found in this experiment was not sufficient to account for the drastic reductions in *H. leporinum* growth (Table 1). *H. leporinum* LAI on 21 August (74 DAP) was reduced to 80, 65, and 37 % of that of *H. leporinum* by 1, 4, and 12 *E. scordifolia* plants per m^2, while plant dry matter was reduced to 78, 34, and 17 %, respectively. This indicates that early season competition reduced leaf growth by *H. leporinum*, but subsequent shading by the taller *E. scordifolia* plants resulted in an even greater reduction in PAR interception by the *H. leporinum* plants. Head mass was reduced to 72, 34, and 17 % of that of *H. leporinum* for the respective *E. scordifolia* levels. Final grain yield was reduced to 74, 49, and 31 % of that of *H. leporinum* by populations of 1, 4, and 12 *E. scordifolia* plants per m^2.

In this study, the maximum effects of *E. scordifolia* competition on *H. leporinum* PAR absorption were found by monitoring PAR penetration into fully developed canopies. The effects of weed density were evident throughout the growing season. Once competition had caused reduced *H. leporinum* leaf area development, future

Table 2. Effect of *Euphorbia scordifolia* competition on *Hordeum leporinum* leaf temperature (T_l), stomatal conductance (g_s), net photosynthetic (P_N) and transpiration (E) rates, and their ratio in upper sunlit leaves. Means from five sets of reading taken between 15 and 21 August. Means followed by the same letter are not significantly different ($p<0.05$) as determined by the Student-Newman-Keuls Multiple Range Test.

E. scordifolia density [plants per m^2]	T_l [°C]	g_s [cm s^{-1}]	E [mg(H_2O) m^{-2} s^{-1}]	P_N [g(CO_2) m^{-2} s^{-1}]	P_N/E [mg(CO_2) g^{-1}(H_2O)]
0	32.27[a]	14.92[a]	247.0[ab]	1584.9[a]	6.614[a]
1	32.92[ab]	12.42[ab]	234.9[ab]	1366.2[b]	6.051
4	32.99[ab]	14.25[a]	251.6[a]	1411.0[b]	5.806[b]
12	33.34[b]	11.43[b]	215.1[b]	1238.6[b]	5.832[b]

potential PAR absorption was reduced also. On 45 DAP, prior to measurement of significant differences in *H. leporinum* LAI, midday leaf P_N was significantly reduced in all weed treatments, indicating possible competition for water at that time.

In work with *E. scordifolia*, foxtail (*Setaria spp.*), and (*Digitaria spp.*), Burnside and Wicks (1967) found that if *H. leporinum* was kept weed-free the first 4 weeks after planting, subsequent weed growth did not significantly reduce yield because the larger *H. leporinum* plants could out-compete the weeds. Using experimental results from numerous studies to determine critical periods of crop-weed competition, Van Heemst (1985) found *H. leporinum* to be very susceptible to weed competition, with a critical period of weed-crop competition extending to 21 % of the length of the total growth cycle. My study, however, indicated that *E. scordifolia* germinating early in the season competed with *H. leporinum* throughout the entire season. Conditions were uniform in all plots for the first 30 d of the growing season, but the plants were very sensitive to differential competition throughout the rest of the season.

My results show that competition for PAR is important in *H. leporinum-E. scordifolia* mixtures. Even in well-watered, fertilized plots, drastic dry matter and yield reductions were found, which corresponded to similar reductions in the amount of PAR intercepted by *H. leporinum*. Although there are many aspects of weed competition that are not well understood, the importance of PAR competition should not be underrated. Further studies are needed to describe the early effects and magnitude of competition for PAR and help to determine economically limiting threshold values or when the competition for PAR becomes limiting.

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