

ROOT DEVELOPMENT AND SOIL NITROGEN AVAILABILITY AS DRIVERS OF  
MAIZE-WEED COMPETITION

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by

Andrés Gustavo Berger Ricca

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## ABSTRACT

A mechanistic understanding of crop-weed interaction has been used in dynamic simulation models of the growth of crop-weed mixtures to estimate the outcomes of competition, including yield losses, and predict the effects of management practices. In the case of an annual crop such as maize, when plants in mixtures begin to compete for light during the early growing season, the relative position of the leaves of the crop and weeds determine the light captured by the plant and its subsequent growth and yield. Thus the total area and distribution of leaves, and factors that can change those characteristics will impact crop competitiveness. Below ground resources such as nitrogen or water availability, are thought to be among those factors that influence leaf area and distribution. However due to the complexity of studying competition for below ground resources, little information has been gathered to support this assumption.

The specific objectives of the present study are: i) to characterize early season root system growth for maize and four weed species and to determine the effects of above and belowground maize competition on maize and weed root system development; ii) characterize, in comparison with maize, the early and exponential growth phases of four weed species; iii) identify and quantify the changes induced by nitrogen stress in plant architecture and morphology that could be important in determining weeds and maize success in compete for resources in a mixed maize-weed stand. To achieve the first objective, this study utilized an herbicide injection technique to assess the comparative root geometries and temporal development patterns for redroot pigweed (*Amaranthus retroflexus* L.) and velvetleaf (*Abutilon theophrasti* Medic.) in association with maize (*Zea mays* L.); and redroot pigweed, velvetleaf, maize, common lambsquarters (*Chenopodium album* L.) and giant foxtail (*Setaria faberi* Herm.) in monoculture. The second and third objectives were addressed in a separate glasshouse experiment where

maize, *A. retroflexus*, *A. theophrasti*, *S. faberi* and *C. album* where grown in sand culture at varying soil solution nitrogen levels (0.2, 0.5, 2, 5 mM L<sup>-1</sup> NO<sub>3</sub>).

Root system vertical and lateral growth was more variable among species than between different soil types, suggesting that root development in the absence of important soil physical impediments is a plant intrinsic characteristic. For *A. theophrasti* and *A. retroflexus*, root system volume was proportional to plant above-ground biomass. Thus, plants growing under a competitive environment and having reduced above-ground biomass have a proportionally smaller root system, potentially compromising their ability to capture and compete for soil resources with their neighbors. This study also provides insights into the likelihood of belowground competition occurring between plants based on the likelihood of root system overlapping and exploring the same soil regions.

Increasing levels of soil nitrogen significantly increased relative above-ground plant biomass in a similar fashion for maize and the three broadleaf weeds, but *S. faberi* was comparatively unresponsive to higher levels of soil nitrogen. Diverse growth sensitivities to soil nitrogen may in part explain the variability of competitive relationships commonly observed under field conditions. Our results demonstrate that species do not respond uniformly to changes in soil nitrogen status and those differential responses must be addressed when considering the impact of soil fertility on competitive outcomes in agricultural systems. Furthermore, the root development study indicated that the chance of a crop-weed mixture exploiting a common region of soil or finding an enriched patch of soil are low at the early growth stages, suggesting that localized differences in nitrogen availability could drive the competitive relationship in favor of the crop or the weeds.

## BIOGRAPHICAL SKETCH

Andrés G. Berger was born April 24, 1976. He grew up in Colonia Valdense in the state of Colonia in the south west of Uruguay. He graduated from Liceo Daniel Armand Ugón in 1993 after which he moved to Montevideo to pursue undergraduate studies in Agronomy in Universidad de la República, Facultad de Agronomía. After his graduation he started to work in the same institution as a research associate working on soil fertility management of rice-pasture systems. He later appointed as entry-level professor, lecturing in courses at the undergraduate program. In 2003 he was awarded a Fulbright grant and an OAS grant and started a MS program in the Field of Soil and Crop Sciences at Cornell University.

To my wife Giovanna.

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## CHAPTER ONE

# ROOT SYSTEM DEVELOPMENT OF FOUR WEED SPECIES AND MAIZE IN MONOCULTURE OR MIXTURE

## INTRODUCTION

Plants root systems have evolved to serve the primary functions of anchoring and acquiring resources (i.e. water and mineral nutrients) from the soil. Both these functions are impacted by root system size (Harper et al., 1991). In the case of resource acquisition, the development of an extensive and structured root system represents the evolutionary response of plants to the spatio-temporal variability of resource availability and the associated constraints to growth (Harper et al., 1991; Robinson, 1991). While root system architecture is in part the result of ontogenetic development, the plastic response of root growth to environmental factors such as soil strength and resource availability (Gedroc et al., 1996) also influences root system structure.

In the case of annual crops, the root system initially develops in soil where, ideally, mutual competition between growing plants is absent or reduced. During early stages of growth, roots need to provide increasingly higher amounts of resources to satisfy the needs of a rapidly growing plant. In response to this need, extensive initial root development (Casper et al., 2003; Doussan et al., 2003; Fransen et al., 1999) and proliferation in enriched soil nutrient zones (ie. fertilizer band) (Chassot et al., 2001; Petersen, 2001; vanVuuren et al., 1996) have been observed. Thus, the ability of a plant to colonize the soil before its competitors and locate resource-rich regions in the soil will determine its success in competing for available soil resources relative to its neighbors (Baldwin, 1976).

Casper et al. (2003) introduced the concept of a belowground zone of influence, which is the potential area or volume of soil exploited by an individual plant at a given time, regardless of the root density. Implicit in this concept is the assumption that root length is of minor importance. This assumption is supported by the findings that, for some plant species, roots have the capacity to proliferate in nutrient-enriched soil regions once detected, although most of the available nutrients available in these enriched patches may be captured before extensive root proliferation occurs (vanVuuren et al., 1996). Unfortunately little information and data have been generated in this area probably due to the difficulties of studying root system development and morphology in the field. Furthermore, most of the studies on root system size and morphology were conducted on mature plants; there is limited information on the dynamics of root system development at early growth stages, especially in non-crop species.

It has been suggested that weeds growing with maize (*Zea mays* L.) modify its ability to compete for soil resources by stimulating reductions in its root/shoot ratio (Rajcan and Swanton, 2001; Rajcan et al., 2004). Evans et al. (2003) also speculated that weed infestation could alter maize and weeds root system size and morphology. However, there is no evidence that root development could be a significant driver of the competitive relationship between maize and weeds before above ground signs of competition are observed.

Spatial differences in nutrient availability due to fertilizer placement have been shown to be a significant modulator of crop-weed competition; small differences in the order of a few centimeters have been reported to preferentially influence the development of the crop versus weeds (Blackshaw et al., 2002; Petersen, 2001; Petersen, 2005). Thus, more in depth knowledge of root system development in different weed species is important to fully understand the expected crop response to both management practices and environmental growing conditions.

The objectives of this study are to (i) characterize early season root system development and expansion in the field for maize and four annual weed species, and (ii) determine the effects of above and below ground maize competition on root system development in two of the weed species.

## MATERIALS AND METHODS

Field experiments were conducted at two closely located experimental farms in Ithaca, NY (42° 27' N, 76° 27' W) during the 2004 growing season (May – August). The two farms had different soil types: an Arkport fine sandy loam soil (coarse-loamy, mixed, active, mesic Lamellic Hapludalfs ) (e.g. sandy loam) and a Williamson silt loam soil (coarse-silty, mixed, active, mesic Typic Fragiudepts ) (e.g. silt loam). An herbicide injection technique was used in these experiments to determine the root system dimensions of individual plants at the time they exhibited herbicidal damage (Khalifaoui and Havard, 1993; Trebuil et al., 1996). Average root system size and growth rate was estimated from measurements of several individual plants located at increasing distances from the herbicide injection point.

Experimental treatments were a factorial combination of species and test depths. Species grown in monoculture were maize cv. DK48-15, velvetleaf (*Abutilon theophrasti* Medic.), redroot pigweed (*Amaranthus retroflexus* L.), common lambsquarters (*Chenopodium album* L.) and giant foxtail (*Setaria faberi* Herm.). Intercrop (mixture) treatments were maize intercropped with *A. theophrasti* and maize intercropped with *A. retroflexus*. Treatments were arranged in a complete randomized block design with three replicates.

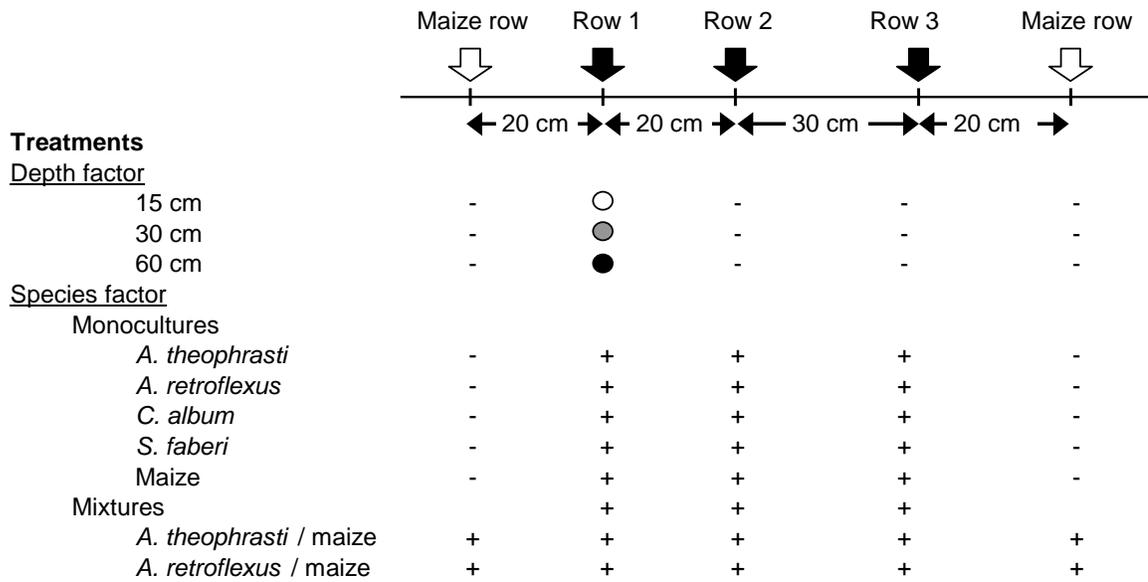


Figure 1.1 Row spacing and position of the herbicide injection points for the 21 injection depth by species treatment combinations. Symbols indicate presence (+) or absence (-) in the treatment. Circles indicate herbicide injections at 15 (○), 30 (●), and 60 (●) cm depth.

Weeds were sown with a small garden-type push planter in three rows, spaced 20 cm between the first and second row and 30 cm between the second and third row. For the mixture treatments, maize was planted 20 cm from the outer weed rows on both sides (Figure 1.1). In all treatments, the herbicide was placed underneath the first row (row 1 in Figure 1.1).

Treatments were planted on 9 June in the sandy loam site and 13 June in the silt loam site and emerged on 15 June and 18 June, respectively. Seeds were planted in excess and thinned to target densities on reaching the two-leaf stage (Table 1.1).

Table 1.1 Initial densities (mean  $\pm$  SE) of both maize and weeds in both monocultures and mixtures at the two sites.

	Sandy loam		Silt loam	
	— m <sup>2</sup> —		— m <sup>2</sup> —	
<i>A. theophrasti</i>	22	$\pm$ 1.2	24	$\pm$ 0.5
<i>A. theophrasti</i> (mixture plots)	22	$\pm$ 1.0	23	$\pm$ 0.8
<i>A. retroflexus</i>	18	$\pm$ 1.2	17	$\pm$ 2.1
<i>A. retroflexus</i> (mixture plots)	19	$\pm$ 0.7	13	$\pm$ 1.3
Maize	19	$\pm$ 0.5	23	$\pm$ 0.6
Maize (mixture plots)	9	$\pm$ 0.6	11	$\pm$ 0.5
<i>S. faberi</i>	23	$\pm$ 0.5	23	$\pm$ 1.2
<i>C. album</i>	16	$\pm$ 1.2	19	$\pm$ 1.1

Available mineral nitrogen at planting was  $15 \pm 3$  mg Kg<sup>-1</sup> for the sandy loam site and  $12 \pm 2$  mg Kg<sup>-1</sup> for the silt loam site; similarly, PSNT was  $19.7 \pm 7.8$  and  $34 \pm 6.9$  mg Kg<sup>-1</sup> respectively. Side dress nitrogen fertilizer at a rate of 22.5 Kg ha<sup>-1</sup> was broadcast applied when maize had approximately six ligulated leaves.

Herbicide injection points were 15 cm apart along a row with a total length of 90 cm. At each injection point, a 2 cm diameter core was drilled to the desired depth with a soil auger and 20 ml of herbicide metribuzin [4-Amino-6-(1,1-dimethylethyl)-3-(methylthio)-1,2,4-triazin-5(4H)-one] (20 g l<sup>-1</sup> a.i.) was injected. Injection depths were 15, 30 and 60

cm. Herbicide plume diameter was estimated  $15 \pm 5$  cm in parallel trials, in the same sites, with the injection of a dye instead of the herbicide.

The herbicide metribuzin was selected for use in this study because of its low mobility and high residuality (Henriksen et al., 2004; Junnila et al., 1993). To verify the presence of the herbicide and the possibility of herbicide leaching or lateral movement in the soil profile during the experiment, soil samples were taken at three locations with respect to the herbicide row (0, 20 and 40 cm from the herbicide row) in all replicates at the end of the experimental period. Two soil samples were taken for the 15 cm (from 15-22.5 cm and 22.5-30 cm) and 30 cm (from 30-37.5 cm and 37.5-45 cm) depth subplot. Soil samples were placed in a glasshouse and scarified *Abutilon theophrasti* seeds were sown and seedlings that emerged were observed for herbicide damage for a period of 15 days. Results were analyzed with multiple logistic regression.

Herbicide damage symptoms were assessed daily. When damage was detected, plant height, leaf count, and distance from the herbicide row was recorded. Plants were harvested, oven-dried at 70 °C, and weighed to determine biomass.

Plants growing in the same row as the herbicide injection row (row 1) were used to study vertical root growth (VRG), while of the plants growing in rows 2 and 3 were used to estimate lateral growth of the root system (LRG). Both groups of plants were used to estimate the volume of soil exploited by the root system (zone of influence) by calculating the volume of the frustum of a right cone for the intervals 0 to 15, 15 to 30 and 30 to 60 cm depth.

Thermistors were used to measure soil temperature at 10 cm depth. Weather data was obtained from a weather station located less than 1.5 Km from the two sites. The 2004 growing season was characterized by normal air temperatures and high rainfall throughout the season (Table 1.2). Based on daily soil average temperatures, cumulative growing degree days (GDD) were estimated using a common 8 °C base temperature for all species (Appendix 1.1).

Table 1.2 Mean air temperature and precipitation during the experimental period.

Month	Days	2004			30 yr. average		
		Mean air temperature	SD	Precipitation	Mean air temperature	SD	Precipitation
		°C		mm	°C		mm
MAY	1-15	15	6.1	49	12	4.9	43
	16-31	17	4.0	106	15	4.7	42
JUNE	1-15	16	4.1	40	17	4.2	42
	16-30	18	3.4	33	19	3.8	51
JULY	1-15	20	2.3	50	20	3.5	44
	16-31	20	2.5	129	21	3.2	52
AUGUST	1-15	19	3.2	63	20	3.3	47
	16-31	20	3.2	131	19	3.5	47
SEPTEMBER	1-15	19	1.9	49	17	4.0	43
	16-30	16	3.5	82	14	4.2	62

## RESULTS AND DISCUSSION

### **Herbicide placement and sensitivity**

Results from the bioassay indicated that the herbicide did not move in the soil profile to sample locations 20 or 40 cm laterally from the point of injection ( $\chi^2 = 10.9$ ,  $P=0.001$ ). However, the bioassay of samples taken at 7.5 to 15 cm below the injection point indicated the presence of herbicide ( $\chi^2 = 0.4035$ ,  $P=0.5253$ ). Though lateral or upward movement of the herbicide would have affected our results, downward movement would not.

Species sensitivity to the herbicide was high for all species except maize until the end of the experimental period. By approximately 35-45 days after application (six to seven ligulated leaves), maize was no longer sensitive to the herbicide.

### **Dynamics of root growth with depth**

Depth of rooting was determined for the different species grown in monoculture or mixtures with maize (Figure 1.2). In all cases, roots reached the 60 cm depth before the end of the experiment (78 and 93 days after emergence for the sandy loam and silt loam site, respectively), indicating that maximum rooting depth was greater than 60 cm for all species.

The variability associated with GDD required for the roots of different species to attain the test depths was larger than the variability associated with soil types, especially for the 15 and 30 cm test depths (Table 1.3). This suggests that a large component of root growth is an intrinsic characteristic of the species tested and soil texture likely plays a relatively smaller role in the dynamics of root growth.

Differences among species were already apparent when the roots reached the 15 cm depth (Figure 1.2, Appendix 1.2). In the sandy loam site, roots of all species except *C. album* and *S. faberi* reached a depth of 15 cm on average within 180 to 260 GDD. On average, roots of *C. album* and *S. faberi* did not reach the 15 cm test depth until 551 and 375 GDD respectively. With the exception of *C. album*, the roots of all species required on average, 170 GDD longer to reach the 15 cm test depth at the silt loam site compared with the sandy loam site.

Table 1.3 ANOVA summary of GDD when plant roots reached the test depths.

Source	Test depth (cm)					
	15		30		60	
	df	Type III sum of squares	df	Type III sum of squares	df	Type III sum of squares
Site	1	730037 ***	1	482646 ***	1	309525 ***
Species	6	1998704 ***	6	2173795 ***	6	494596 **
Site*Species	6	520929 ***	6	279638 *	6	422101 *
Residual	144	2535330	114	2580691	75	2690289

\*\*\* Significant at  $P < 0.001$ ; \*\* Significant at  $P < 0.05$ ; \* Significant at  $P < 0.10$

The greater GDD required for *A. retroflexus*, *C. album* and *S. faberi* to reach the 15 cm depth in comparison to *A. theophrasti* and maize may be due to their smaller seed size ( $A. retroflexus < C. album < S. faberi < A. theophrasti < maize$ ) (Harbur and Owen, 2004) and thus a slower initial root development (Wiese, 1968).

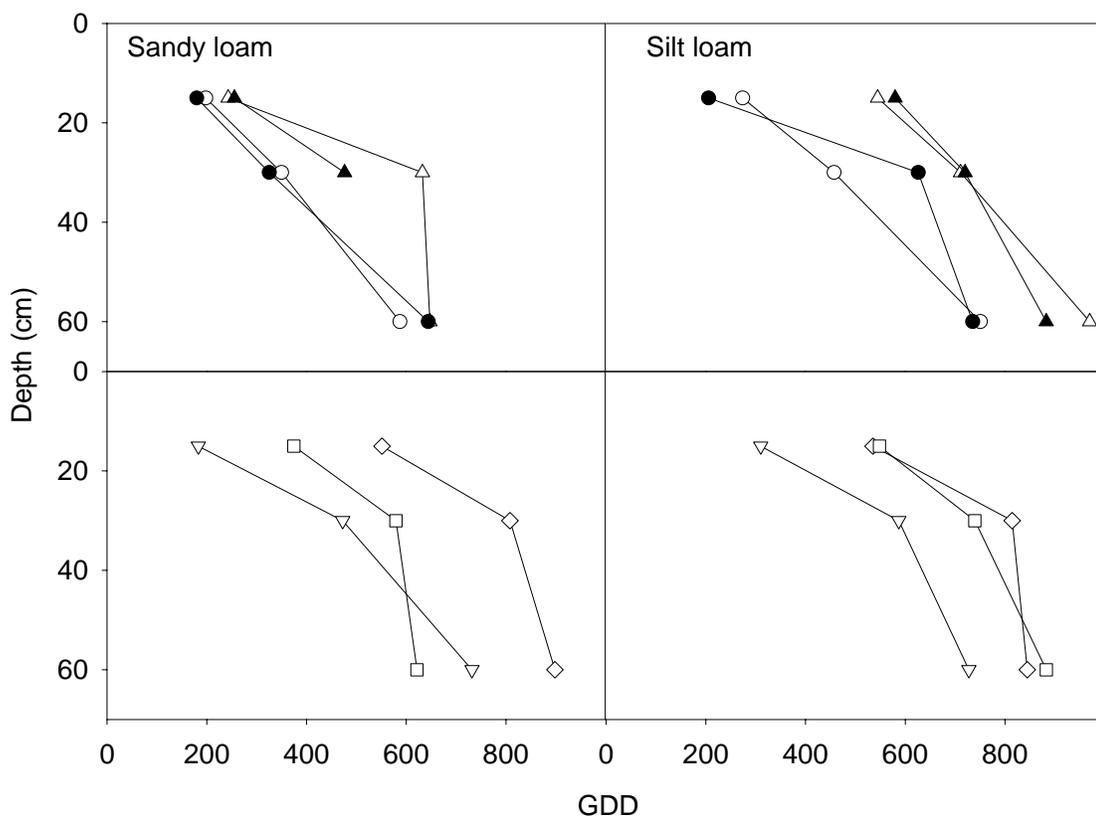


Figure 1.2 Mean cumulative growing degree days (GDD) for roots of the different species to reach the test depths in the two sites. *A. retroflexus* ( $\Delta$ ), *A. retroflexus* maize mixture ( $\blacktriangle$ ), *A. theophrasti* ( $\circ$ ), *A. theophrasti* maize mixture ( $\bullet$ ), maize ( $\nabla$ ), *C. album* ( $\diamond$ ), *S. faberi* ( $\square$ ).

To estimate differences in rates of vertical root growth (VRG) between the 15 cm depth and 60 cm depth, linear and exponential models were fitted for all species. Due to the large variability observed (Table 1.3); none of the parameters for either model were significantly different among species at  $\alpha=0.05$  (Table 1.4). In general, VRG assuming linear growth ranged from 0.7 to 1.5 mm GDD<sup>-1</sup> or approximately 8.5 to 17.8 mm day<sup>-1</sup> (Figure 1.3, Table 1.4). These figures are considerably smaller than those reported in previous studies (Evetts and Burnside, 1973; Wiese, 1968) for similar weed species (13 – 63 mm day<sup>-1</sup>), in which plants were grown in glass wall pots where space for the root system development was laterally restricted.

Table 1.4 Parameters for linear (Depth = a + b·GDD) and exponential (Depth = a·e<sup>b·GDD</sup>) models of vertical root growth between the 15 and 60 cm depths.

	Linear				Exponential			
	b	SE	a	SE	b	SE	a	SE
	— mm GDD <sup>-1</sup> —		— mm —		— GDD <sup>-1</sup> —		— mm —	
<u>Silt loam</u>								
<i>A. retroflexus</i>	1.1	0.1	-442	53	0.0032	0.0004	28	1.4
<i>A. retroflexus</i> (mixture plots)	1.5	0.2	-738	163	0.0046	0.0002	11	1.2
<i>A. theophrasti</i>	1.0	0.1	-120	29	0.0029	0.0004	73	1.2
<i>A. theophrasti</i> (mixture plots)	0.7	0.4	-22	231	0.0023	0.0008	88	1.6
Maize	1.0	0.4	-193	225	0.0032	0.0006	53	1.4
<i>C. album</i>	1.1	0.8	-447	583	0.0037	0.0017	20	3.6
<i>S. faberi</i>	1.3	0.4	-600	272	0.0041	0.0003	15	1.3
<u>Sandy loam</u>								
<i>A. retroflexus</i>	0.8	0.6	-44	340	0.0027	0.0014	78	2.2
<i>A. retroflexus</i> (mixture plots)	1.0	1.8	-30	686	0.0040	0.0047	66	6.1
<i>A. theophrasti</i>	1.2	0.1	-90	30	0.0035	0.0004	80	1.2
<i>A. theophrasti</i> (mixture plots)	1.0	0.0	-20	10	0.0029	0.0006	101	1.3
Maize	0.8	0.2	-26	95	0.0025	0.0001	93	1.0
<i>C. album</i>	1.1	0.6	-511	435	0.0037	0.0010	18	2.2
<i>S. faberi</i>	1.5	0.9	-428	487	0.0049	0.0019	23	2.7

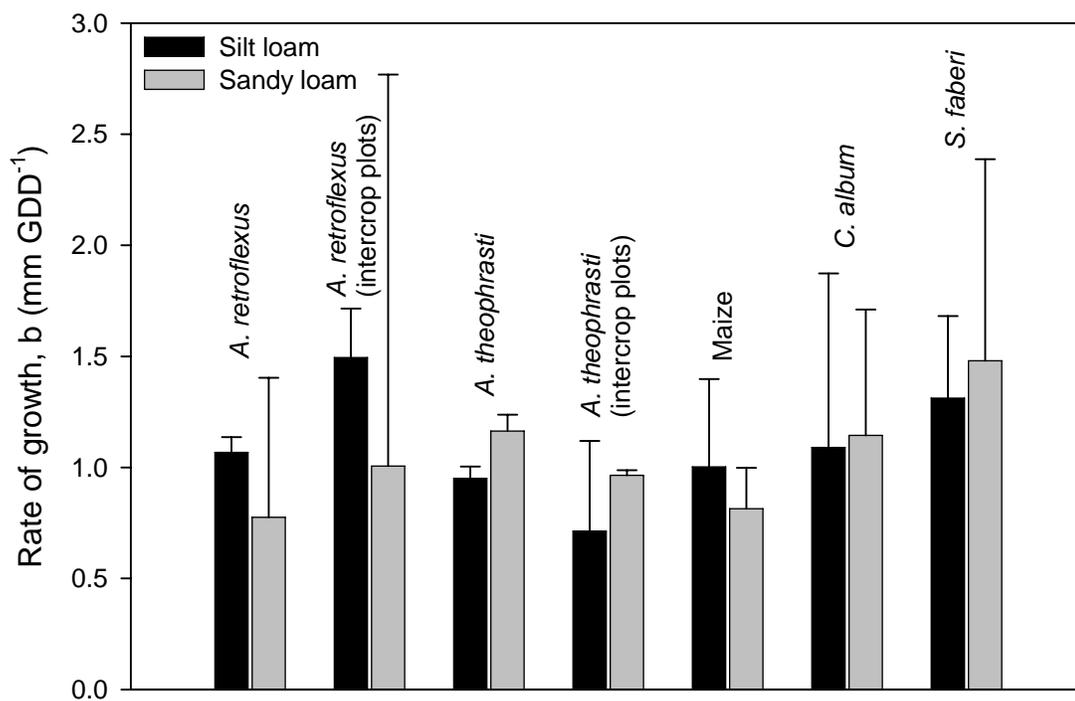


Figure 1.3 Rate of vertical root growth between the 15 and 60 cm depths (parameter  $b$  of the equation:  $\text{Depth} = a + b \cdot \text{GDD}$ ) for the tested species. (Parameters were not significantly different at  $\alpha = 0.05$ ). Bars are standard errors of the means ( $N=3$ ).

When comparing *A. theophrasti* in monoculture to the *A. theophrasti* maize mixture, no significant differences in the GDD for roots to reach the 60 cm depth were observed (at  $\alpha=0.1$ , Figure 1.2), although plants in the monoculture treatment were significantly larger (sandy loam, 20.4 g vs. 8.3 g,  $P<0.01$ ; silt loam, 18.2 g vs. 3.0 g,  $P<0.01$ ). These results indicate that VRG is independent of plant size, and suggest that VRG is primarily the result of ontogenetic development. In the case of *A. retroflexus* in monoculture and mixtures with maize the data suggests a similar behavior, although the number of observations was smaller with higher variability.

### **Dynamics of lateral root growth**

Lateral root growth (LRG) was assessed at 15, 30 and 60 cm depths. Since most of the lateral expansion of the root system occurred at the 15 cm depth, only the lateral root system growth at this depth will be discussed. By measuring the distance from the plant's stem base to the herbicide injection points, the root system size of a plant could be inferred when herbicide symptoms were observed. Plants were grouped by age (GDD) into equidistant groups of approximately equal number of observations to perform all the statistical analyses. Figure 1.4 and 1.5 present the values for all plants harvested during the experiment. Measurements were taken until the end of the growing season, when all plant species reached the reproductive phase; thus the maximum values represent the maximum observed LRG except for maize, which lost herbicide sensitivity by the time it had developed six to seven ligulated leaves.

Test species differed significantly in maximum LRG, and all species showed greater LRG in the sandy loam site than in the silt loam site. At both sites, the ranking of weed species according to maximum LRG was similar: *S. faberi*  $\approx$  *C. album*  $<$  *A. retroflexus*  $<$  *A. theophrasti*. Absolute values of LRG for a fully developed *A. theophrasti* plant found in this study (45-50 cm) are comparable to those found by Casper et al. (2003) using Sr as

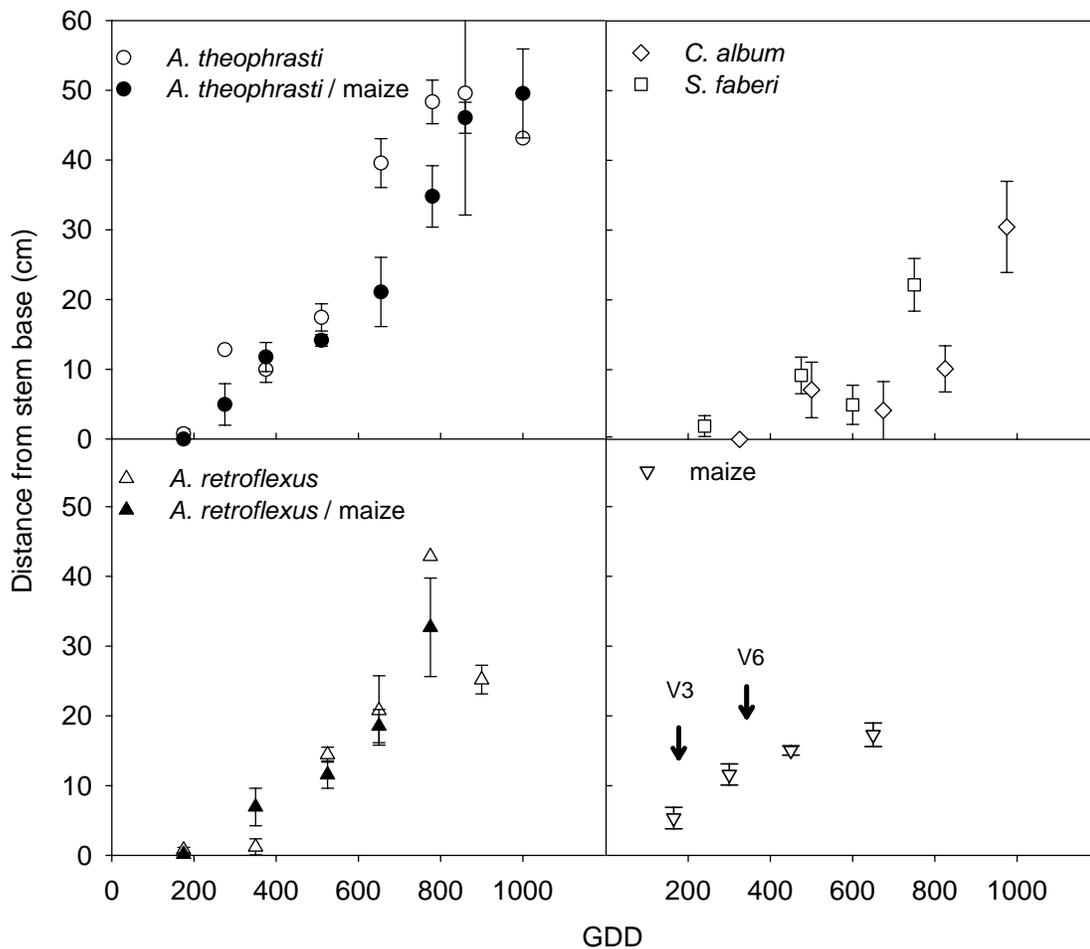


Figure 1.4 Mean cumulative growing degree days (GDD) for roots to reach the measured lateral growth at 15 cm depth in a sandy loam soil. *A. retroflexus* ( $\Delta$ , N=29), *A. retroflexus* intercropped with maize ( $\blacktriangle$ , N=27), *A. theophrasti* ( $\circ$ , N=56), *A. theophrasti* intercropped with maize ( $\bullet$ , N=44), maize ( $\nabla$ , N=63), *C. album* ( $\diamond$ , N=18), *S. faberi* ( $\square$ , N=32). Bars indicate standard errors of means.

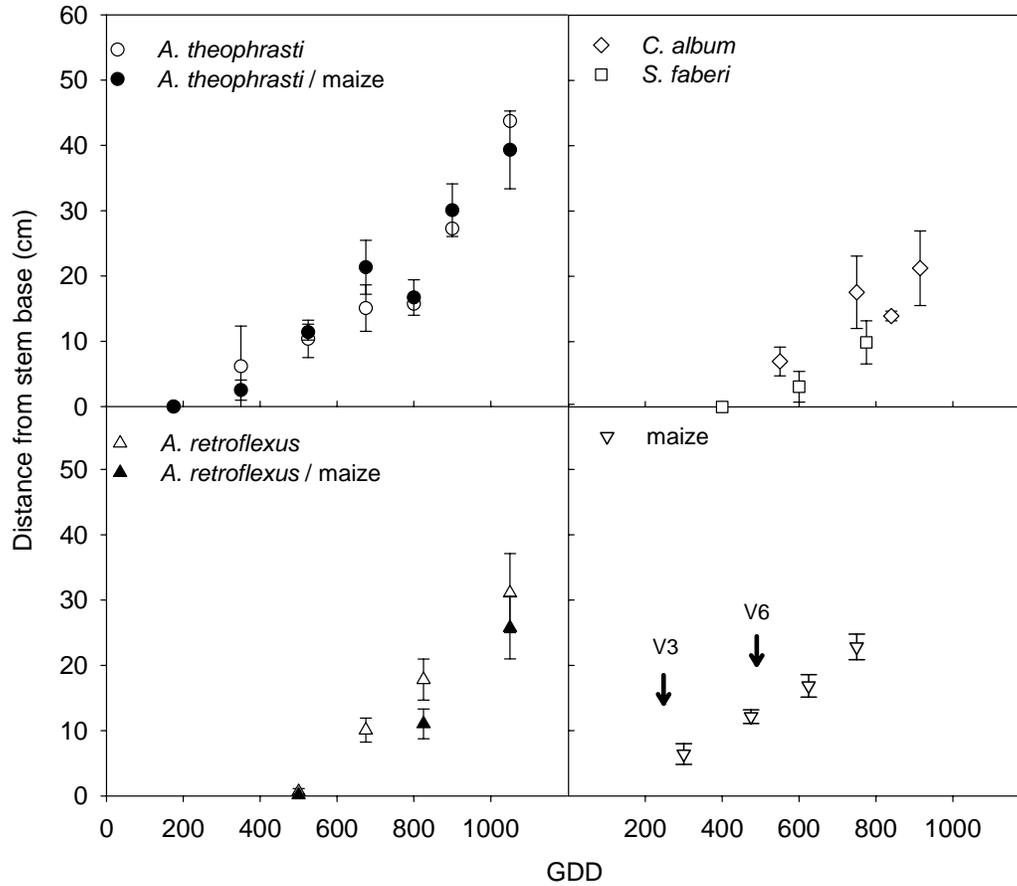


Figure 1.5 Mean cumulative growing degree days (GDD) for roots to reach the measured lateral growth at 15 cm depth in a silt loam soil. *A. retroflexus* ( $\Delta$ , N=39), *A. retroflexus* intercropped with maize ( $\blacktriangle$ , N=24), *A. theophrasti* ( $\circ$ , N=27), *A. theophrasti* intercropped with maize ( $\bullet$ , N=46), maize ( $\nabla$ , N=69), *C. album* ( $\diamond$ , N=24), *S. faberi* ( $\square$ , N=12). Bars indicate standard errors from mean.

a tracer. Differences in LRG could in part be explained by early differences in LRG, either due to species, site, or site-species effects (Appendix 1.3).

The rates of LRG at 15 cm depth ranged from 0.19 to 0.67 mm GDD<sup>-1</sup> and were not significantly different (at  $\alpha=0.01$ ) for the species when grown in monocrop or intercrop (Figure 1.4 and 1.5). Rates of LRG were similar across sites except for *A. theophrasti*, which had greater (at  $\alpha=0.01$ ) rates of LRG in the sandy loam site (Appendix 1.4).

### **Volume of soil exploited and plant size**

VRG and LRG (at 15, 30 and 60 cm) were both used to estimate the volume of soil roots occupied. Thus similar differences among species were found for volume of soil exploited as for LRG and VRG, with *A. theophrasti* occupying the largest volume of soil. The ability of *A. theophrasti* to develop an extensive root system could be a determinant of the observed high competitiveness, and relatively higher drought tolerance of this species compared to maize (McDonald et al., 2004).

For each treatment, plants were grouped by their age (GDD), and the average weight and the volume of soil exploited (estimated using VRG and LRG of multiple plants) was calculated for each age class (Figure 1.6 and 1.7). Weeds of similar age weighed less when growing in competition with maize than when growing in monocrop. For those weeds in competition with maize, the volume of soil exploited was smaller than their monocrop counterparts, due to lower but non significant ( $\alpha=0.05$ ) LRG at 15, 60 and especially 30 cm depth. There was a linear relationship between the volume of soil exploited (V) and above-ground biomass (AGB) for *A. theophrasti* ( $V = -1.44 + 5.62 \cdot \text{AGB}$ ,  $R^2=0.94$ ) (Figure 1.6) and *A. retroflexus* ( $V = -1.30 + 4.33 \cdot \text{AGB}$ ,  $R^2=0.84$ ) (Figure 1.7), indicating that volume of soil exploited (potential belowground resource acquisition) is symmetrically related to with plant size. This relationship was not altered by the different soil types (sandy loam vs. silt loam) or by contrasting competitive

environments (monocrop vs. intercrop). These findings suggest that for *A. theophrasti* and *A. retroflexus*, any reallocation of biomass between shoots and roots to optimize resource capture of the most limiting factor (i.e. light vs. soil resources) (Wilson, 1988) is of minor importance in comparison to the overall reduction in plant size due to lower light interception under the competitive environment of the intercrop plots.

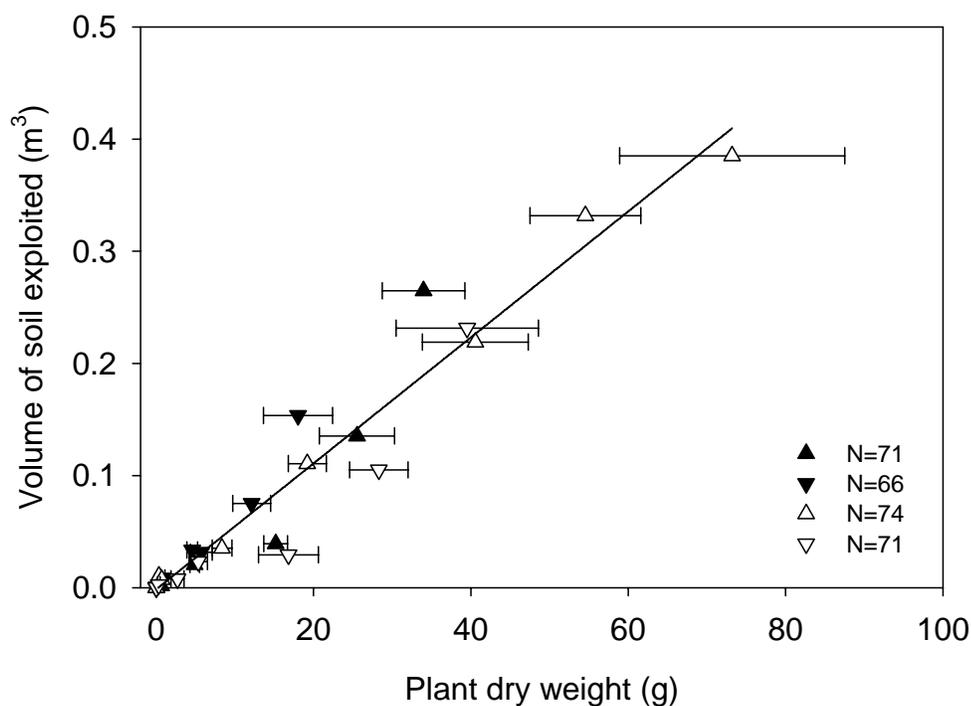


Figure 1.6 Mean volume of soil exploited by an individual *A. theophrasti* plant as a function of plant dry weight. *A. theophrasti* at the sandy loam site ( $\triangle, \blacktriangle$ ), *A. theophrasti* at the silt loam site ( $\nabla, \blacktriangledown$ ). Open and closed symbols indicate that plants were grown in monocrop or intercropped with maize respectively. Bars indicate standard errors of means.

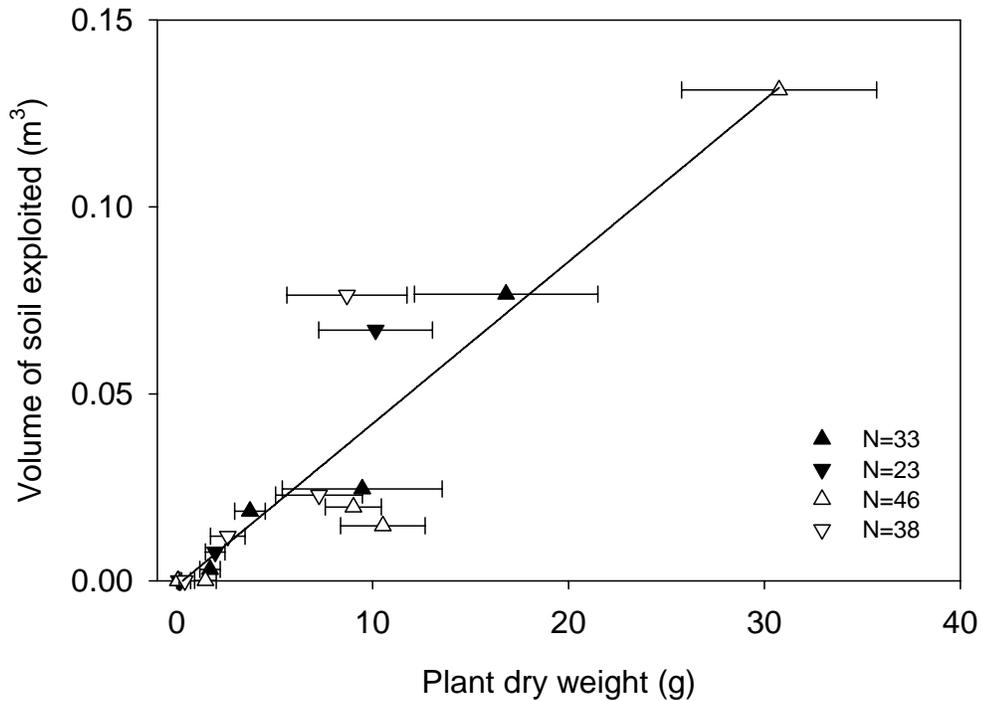


Figure 1.7 Mean volume of soil exploited by an individual *A. retroflexus* plant as a function of plant dry weight. *A. retroflexus* at the sandy loam site ( $\triangle$ ,  $\blacktriangle$ ), *A. retroflexus* at the silt loam site ( $\nabla$ ,  $\blacktriangledown$ ). Open and closed symbols indicate that plants were grown in monocrop or intercropped with maize respectively. Bars indicate standard errors from means.

## CONCLUSIONS

The herbicide approach used in this field study proved valuable in characterizing the expansion of root systems for a number of species. It was also capable of addressing the high variability associated with root system development by measuring a large number of plants per treatment.

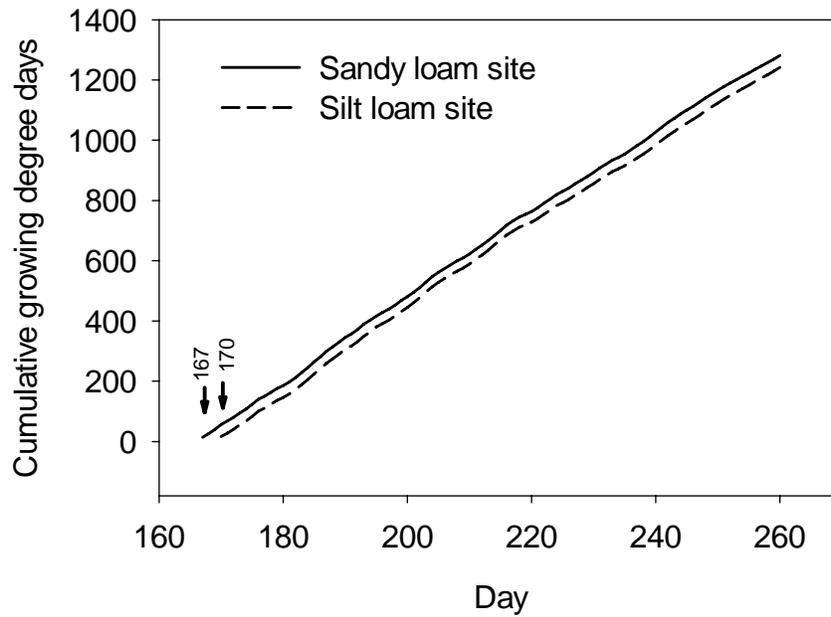
Root system growth was more variable among species than between different soil types, suggesting that root development in the absence of important soil physical impediments is a plant intrinsic characteristic. Early rates of root growth appear to play an important role on the later development of the plant and the root system at least for some of the investigated species (*A. retroflexus*, *C. album* and *S. faberi*). The differences in vertical root growth between sites should be attributed to other site-specific factors than soil or air temperature, and rainfall, which were similar among sites.

For *A. theophrasti* and *A. retroflexus*, root system volume was proportional to plant above ground biomass. Thus, plants growing under a competitive environment and having reduced above-ground biomass have a proportionally smaller root system, jeopardizing their ability to capture and compete for soil resources with their neighbors.

This study provides insights into the likelihood of belowground competition occurring between plants based on the likelihood of root system overlapping and exploring the same soil regions. During early stages of plant development, competition is likely to be low at low weed densities, and inherent LRG may limit the likelihood of weeds reaching enriched bands of fertilizer.

Differences among species in the volume of soil exploited might be an important factor determining the competitive ability of the different species; the ability to reach unexplored soil regions and thus to maintain high growth rates under soil resource shortages.

APPENDIX



Appendix 1.1 Cumulative growing degree days (based on soil temperature with  $t_b=8$  °C) during the 2004 growing season for the two field sites. Arrows indicate date of emergence of all species at that site.

Appendix 1.2 Least square means of cumulative growing degree-days (GDD) for roots to reach 15 cm depth.

Species	Sandy loam site	Silt loam site
	— GDD —	— GDD —
<i>A. theophrasti</i>	198	274
<i>A. theophrasti</i> (intercrop plots)	180	206
<i>A. retroflexus</i>	243	545
<i>A. retroflexus</i> (intercrop plots)	256	580
Maize	183	310
<i>C. album</i>	551	536
<i>S. faberi</i>	375	548

Appendix 1.3 ANOVA table for lateral root growth at 15 cm depth for the seven species combinations as a function of GDD.

Source	df.	Type III sum of squares	F	P
Site	1	293	4.5	0.0337
Species	6	2628	6.7	<0.0001
Species*Site	6	1046	2.7	0.0138
GDD	1	24450	378.1	<0.0001
GDD*Site	1	83	1.2	0.2576
GDD*Species	6	1518	3.9	0.0008
GDD*Species*Site	6	1305	3.3	0.0029
Residual	491	31748		

Appendix 1.4 Parameters for linear (Distance = a + b·GDD) model of lateral root growth at 15 cm depth for the seven species combinations under two soil types.

	b	SE	a	SE
	mm GDD <sup>-1</sup>		mm	
<u>Silt loam site</u>				
<i>A. theophrasti</i>	0.41	0.07	-92	78
<i>A. theophrasti</i> (intercrop plots)	0.42	0.05	-99	74
<i>A. retroflexus</i>	0.57	0.09	-279	98
<i>A. retroflexus</i> (intercrop plots)	0.48	0.10	-270	102
<i>C. album</i>	0.31	0.15	-101	129
Maize	0.29	0.08	-2	78
<i>S. faberi</i>	0.26	0.25	-115	163
<u>Sandy loam site</u>				
<i>A. theophrasti</i>	0.67	0.05	-100	72
<i>A. theophrasti</i> (intercrop plots)	0.61	0.06	-127	72
<i>A. retroflexus</i>	0.45	0.07	-98	76
<i>A. retroflexus</i> (intercrop plots)	0.52	0.08	-117	77
<i>C. album</i>	0.36	0.09	-133	88
Maize	0.19	0.08	62	72
<i>S. faberi</i>	0.36	0.11	-77	64

## REFERENCES CITED

- Baldwin, J.P. 1976. Competition for plant nutrients in soil - Theoretical approach. *Journal Of Agricultural Science* 87:341-356.
- Blackshaw, R.E., G. Semach, and H.H. Janzen. 2002. Fertilizer application method affects nitrogen uptake in weeds and wheat. *Weed Science* 50:634-641.
- Casper, B.B., H.J. Schenk, and R.B. Jackson. 2003. Defining a plant's belowground zone of influence. *Ecology* 84:2313-2321.
- Chassot, A., P. Stamp, and W. Richner. 2001. Root distribution and morphology of maize seedlings as affected by tillage and fertilizer placement. *Plant and Soil* 231:123-135.
- Doussan, C., L. Pages, and A. Pierret. 2003. Soil exploration and resource acquisition by plant roots: an architectural and modelling point of view. *Agronomie* 23:419-431.
- Evans, S.P., S.Z. Knezevic, J.L. Lindquist, and C.A. Shapiro. 2003. Influence of nitrogen and duration of weed interference on corn growth and development. *Weed Science* 51:546-556.
- Evetts, L.L., and O.C. Burnside. 1973. Early root and shoot development of 9 plant species. *Weed Science* 21:289-291.
- Fransen, B., H. De Kroon, C.G.F. De Kovel, and F. Van den Bosch. 1999. Disentangling the effects of root foraging and inherent growth rate on plant biomass accumulation in heterogeneous environments: A modelling study. *Annals of Botany* 84:305-311.
- Gedroc, J.J., K.D.M. McConnaughay, and J.S. Coleman. 1996. Plasticity in root shoot partitioning: Optimal, ontogenetic, or both? *Functional Ecology* 10:44-50.
- Harbur, M.M., and M.D.K. Owen. 2004. Light and growth rate effects on crop and weed responses to nitrogen. *Weed Science* 52:578-583.

- Harper, J.L., M. Jones, and N.R. Hamilton. 1991. The evolution of roots and the problem of analysing their behaviour, p. 3-24, In D. Atkinson, ed. *Plant Root Growth: An Ecological Perspective*, Vol. 10. Special publication of the British Ecological Society, Blackwell Scientific Pub., Cambridge, MA.
- Henriksen, T., B. Svensmark, and R.K. Juhler. 2004. Degradation and sorption of metribuzin and primary metabolites in a sandy soil. *Journal of Environmental Quality* 33:619-627.
- Junnila, S., H. Heinonen-Tanski, L.R. Ervio, and P. Laitinen. 1993. Phytotoxic persistence and microbiological effects of metribuzin in different soils. *Weed Research* 33:213-223.
- Khalfaoui, J.L.B., and M. Havard. 1993. Screening peanut cultivars in the field for root growth: a test by herbicide injection in the soil. *Field Crops Research* 32:173-179.
- McDonald, A.J., S.J. Riha, and C.L. Mohler. 2004. Mining the record: historical evidence for climatic influences on maize - *Abutilon theophrasti* competition. *Weed Research*. 44:439-445.
- Petersen, J. 2001. Recovery of N-15-ammonium-N-15-nitrate in spring wheat as affected by placement geometry of the fertilizer band. *Nutrient Cycling In Agroecosystems* 61:215-221.
- Rajcan, I., and C.J. Swanton. 2001. Understanding maize-weed competition: resource competition, light quality and the whole plant. *Field Crops Research* 71:139-150.
- Rajcan, I., K.J. Chandler, and C.J. Swanton. 2004. Red-far-red ratio of reflected light: a hypothesis of why early-season weed control is important in corn. *Weed Science* 52:774-778.
- Robinson, D. 1991. Roots and resource fluxes in plants and communities, p. 103-130, In D. Atkinson, ed. *Plant Root Growth: An Ecological Perspective*, Vol. 10. Special publication of the British Ecological Society, Blackwell Scientific Pub., Cambridge, MA.
- Trebuil, G.F., B. Courtois, and W. Herrera. 1996. Assessment of upland rice rooting depth: does the herbicide injection technique work? *Journal of Agronomy and Crop Science* 177:85-93.

vanVuuren, M.M.I., D. Robinson, and B.S. Griffiths. 1996. Nutrient inflow and root proliferation during the exploitation of a temporally and spatially discrete source of nitrogen in soil. *Plant and Soil* 178:185-192.

Wiese, A.F. 1968. Rate of weed root elongation. *Weed Science* 16:11-13.

Wilson, J.B. 1988. A review of evidence on the control of shoot-root ratio, in relation to models. *Annals Of Botany* 61:433-449.

## CHAPTER TWO

### COMPARATIVE GROWTH RESPONSE OF MAIZE AND FOUR ANNUAL WEEDS TO VARIATIONS IN SOIL NITROGEN CONCENTRATIONS.

#### INTRODUCTION

Though a large number of studies have addressed the impact of soil nutrient levels on crop-weed competition, the mechanisms of competition remain poorly understood. Most researchers agree that nitrogen fertilization management should be coupled with weed management to optimize nitrogen use efficiency and reduce weed interference (Evans et al., 2003; Hellwig et al., 2002; Liebman, 1989). Some studies (Sattin et al., 1992; Tollenaar et al., 1994) indicate that high soil nutrient levels will stimulate crop growth relative to weed growth and thus reduce weed induced yield loss. In contrast, other studies (Cathcart and Swanton, 2004; Cralle et al., 2003; Hellwig et al., 2002) suggest that high nutrient levels will favor weed growth, thus increasing the weed induced crop yield loss. It is evident that the impact of different nutrient levels on crop-weed competition is difficult to predict. This suggests that multiple factors are involved, such as other stress or growth factors (McDonald et al., 2004).

The most important factors determining maize tolerance to weeds have been thought to include timing of canopy closure, the leaf area index (LAI) of the closed canopy, and the height at which the leaf area (LA) is concentrated (Lindquist et al., 1998; Sattin et al., 1992). Although several recent studies have investigated the response of weeds to nutrient availability (Blackshaw et al., 2004; Blackshaw et al., 2003; Harbur and Owen, 2004), the effects of soil nutrient level on plant architecture or even yields still warrants further study. Liebman (1989) showed that increased soil nitrogen

availability promoted changes in barley plant architecture and leaf area distribution (through senescence), which in turn induced changes in light interception through the canopy profile, thus modifying weed growth and crop yield. There is evidence that weeds can take up nitrogen (N) more efficiently than crops, accelerating their rates of growth during the early stages of development (Blackshaw et al., 2003; Harbur and Owen, 2004). Since early N availability is extremely variable, even with heavy fertilization at planting, because of variable N losses (Sogbedji et al., 2001), it is possible that early N availability could modulate weed competitiveness. Furthermore, fertilizer banding applied at planting expose weeds to different nitrogen availabilities than the crop (Blackshaw et al., 2002; Petersen and Mortensen, 2002) usually enhancing the crop competitive ability. A more in depth mechanistic understanding of the effects of soil N on weeds and crops is required to better predict competitive interactions and outcomes.

The objectives of this work were to: i) characterize, in comparison with maize, the early and exponential growth phases of four common annual weed species of maize; ii) identify and quantify changes in weed and maize plant architecture and morphology induced by N stress that could be important in determining weeds and maize success in competing for resources in a mixed maize-weed stand.

## MATERIALS AND METHODS

Experiments were conducted in a glasshouse during autumn 2004 in Ithaca, NY. Plants were grown in 750 ml pots, which were automatically irrigated six to ten times a day with approximately 50 ml of a non-recyclable nutritive solution containing: 0.1, 0.25, 1 or 2.5 mM  $\text{Ca}(\text{NO}_3)_2$ , and 1mM  $\text{K}_2\text{SO}_4$ , 0.1 mM KCl, 0.1 mM  $\text{KH}_2\text{PO}_4$ , 0.6 mM  $\text{MgSO}_4$ , 36.09  $\mu\text{M}$   $\text{MnSO}_4$ , 27.49  $\mu\text{M}$   $\text{H}_3\text{BO}_4$ , 1.56  $\mu\text{M}$   $\text{CuSO}_4$ , 0.3  $\mu\text{M}$   $\text{MnNH}_4\text{Mo}$ , 1.53  $\mu\text{M}$   $\text{ZnSO}_4$  and 227  $\mu\text{M}$  EDTA-Fe (Engels and Kirkby, 2001). The growth media used was fine sand. Seedlings were thinned to one plant per pot at the one-to-two leaf stage. Pots

were arranged in a randomized complete block design with three replicates and were randomly rearranged twice during the experimental period. Treatments consisted of a factorial arrangement of five plant species, four soil solution nitrogen levels (0.2, 0.5, 2 and 5 mM L<sup>-1</sup> NO<sub>3</sub>, referred herein as N<sub>0.2</sub>, N<sub>0.5</sub>, N<sub>2</sub>, and N<sub>5</sub> respectively) and four harvest times (16, 31, 44 and 57 days after emergence, DAE). The N<sub>5</sub> nitrogen treatment was assumed non-limiting with respect to nutrients. The tested plant species were maize (*Zea mays* L.) cultivar DK48-15, velvetleaf (*Abutilon theophrasti* Medic.), redroot pigweed (*Amaranthus retroflexus* L.), common lambsquarters (*Chenopodium album* L.) and giant foxtail (*Setaria faberi* Herm.).

Plants were grown at air temperatures and photoperiod regime selected to match those typically found during the early summer in central New York State. Thus, the light/dark regime was 16/8 hours, light/dark air temperatures were 21/15 °C and supplemental lights provided a photon flux density of at least 300 μmol m<sup>-2</sup> s<sup>-1</sup> PAR.

Twice a week and at harvest (Table 2.1), plant height (the height to the tallest plant structure) and leaf number (LN, the number of macroscopically visible main stem leaves or ligulated leaves) were recorded for each plant. At each harvest, roots and shoots were collected. Shoots were divided into stem and leaf material, separating the leaf lamina from the stem or petiole. Stems, leaves and roots were oven-dried at 60 °C and weighed to determine biomass.

Specific leaf area (SLA) was estimated for each treatment combination by measuring the last fully developed leaf of harvested plants. Leaves were scanned with a desk scanner using Scion image analysis software (Scion Corporation, CT USA) and individually dried and weighed for dry weight estimations. Specific stem length (SSL) was estimated as the plant height per unit dry weight of shoot biomass, including leaves and stems. Chlorophyll content (Earl and Tollenaar, 1997) was estimated at the fourth harvest (i.e. 57 DAE) for all species by N treatments combinations using a SPAD 502 hand-held chlorophyll meter (Minolta Corporation, Ramsey, NJ USA).

Plant development was related to cumulative growing degree-days (GDD) as estimated by

$$GDD = \sum (t - t_b) \left( \frac{l}{24} \right) \quad (1)$$

where  $t$  is the measured air temperature in °C,  $t_b$  is the base temperature in °C, and  $l$  is the time interval between temperature measurements in hours. The base temperatures used were 10 °C for *A. theophrasti* (Lindquist et al., 1998; McDonald et al., 2004; Sattin et al., 1992), *S. faberi* (Conley et al., 2003; Forcella and Banken, 1996) and *A. retroflexus* (Oryokot et al., 1997; Steckel et al., 2004); 8 °C for maize (Birch et al., 2003); and 4 °C for *C. album* (Colquhoun et al., 2001; Kropff et al., 1992; Rohrig and Stutzel, 2001).

Table 2.1 Harvest timings in relation to days after emergence and GDD.

Harvest	Days after emergence	<i>A. theophrasti</i> , <i>S. faberi</i> , <i>C. album</i> , <i>A. retroflexus</i> , <i>Maize</i>		
		GDD		
1	16	159	255	191
2	31	305	491	367
3	44	433	697	521
4	57	542	882	655

To analyze the rates of growth across species and N treatments, expolinear (2) (Goudriaan and Monteith, 1990) and exponential (3) models were fitted to shoot biomass:

$$w = \frac{C_m}{r_m} \ln(1 + e^{r_m(t-t_0)}) \quad (2)$$

$$w = ae^{r_m t} \quad (3)$$

where  $w$  is shoot mass in grams,  $t$  is time in GDD or days,  $t_0$  is the moment at which the linear phase effectively begins, and  $c_m$  and  $r_m$  are the maximum growth rate in the ‘linear phase’ and maximum relative growth rate (RGR) in the ‘exponential phase’, respectively.

## RESULTS AND DISCUSSION

### Leaf appearance and number of tillers

Leaf appearance was linearly related to GDD throughout the experimental period at all N levels (Table 2.2). Thus, the phyllochron length, which is the time between consecutive leaves appearance, was estimated using the slope of that linear regression (1/b).

Table 2.2 Parameters for the linear model ( $LN = a + b \cdot GDD$ ) of leaf number for the  $N_5$  treatment for the five weed species and maize.

Species	a	SE	B	SE	R <sup>2</sup>
			—— GDD <sup>-1</sup> ——		
<i>A. theophrasti</i>	0.33	0.154	0.028	0.0005	0.99
<i>A. retroflexus</i>	-0.39	0.242	0.034	0.0007	0.98
<i>C. album</i>	-0.23	0.429	0.029	0.0008	0.97
<i>S. faberi</i>	0.06	0.357	0.022	0.0010	0.92
Maize	0.59	0.162	0.014	0.0004	0.97

Based on the length of their phyllochron period, the species could be ordered: *C. album* (2.4 days) < *A. retroflexus* (3.0 days) < *A. theophrasti* (3.7 days) < *S. faberi* (4.7 days) < maize (6.3 days) for the  $N_5$  treatment. Within each group, broadleaves species (*C. album*, *A. retroflexus* and *A. theophrasti*) and grasses (*S. faberi* and maize), the longest

phyllochron period corresponded to species having larger seed size and lower rates of growth (Harbur and Owen, 2004).

Limiting soil nitrogen availability lengthened the phyllochron period in all species, especially at the lowest N levels ( $N_{0.2}$ ) (Figure 2.1). The increase was larger for *A. theophrasti* and *A. retroflexus* compared with the other species, although at the  $N_{0.2}$  treatment, the phyllochron period of *S. faberi* did also increase. In addition, for *S. faberi* the number of tillers at the fourth harvest was reduced from  $19 \pm 1.7$  in the  $N_5$  treatment to  $4 \pm 0.3$  in the  $N_{0.2}$  treatment, indicating that limiting nitrogen nutrition affected more than one trait of growth development. These differences between species may imply different resource competition strategies. In the case of *S. faberi*, the growth of each individual tiller was little affected by N availability (except at  $N_{0.2}$ ); at low soil N levels, the number of tillers could potentially be compensated by increases in plant density (number of individuals per unit area), resulting in high competitive ability. While for the other weed species and maize, no matter the plant density of the stand, each individual plant will suffer a proportionally similar reduction in growth under low soil N.

### **Biomass production and allocation**

As expected, both the maize and weeds exhibited reduced growth as soil nitrogen availability was limited (Blackshaw et al., 2004; Blackshaw et al., 2003; Harbur and Owen, 2004; Teyker et al., 1991) (Figure 2.2). Plant growth was severely reduced at the  $N_{0.2}$  treatment, suggesting that N limitation at this concentration may have critically impaired a growth process, i.e. the photosynthesis, resulting in low plant radiation use efficiency as has been reported at low leaf nitrogen contents (Sinclair and Horie, 1989).

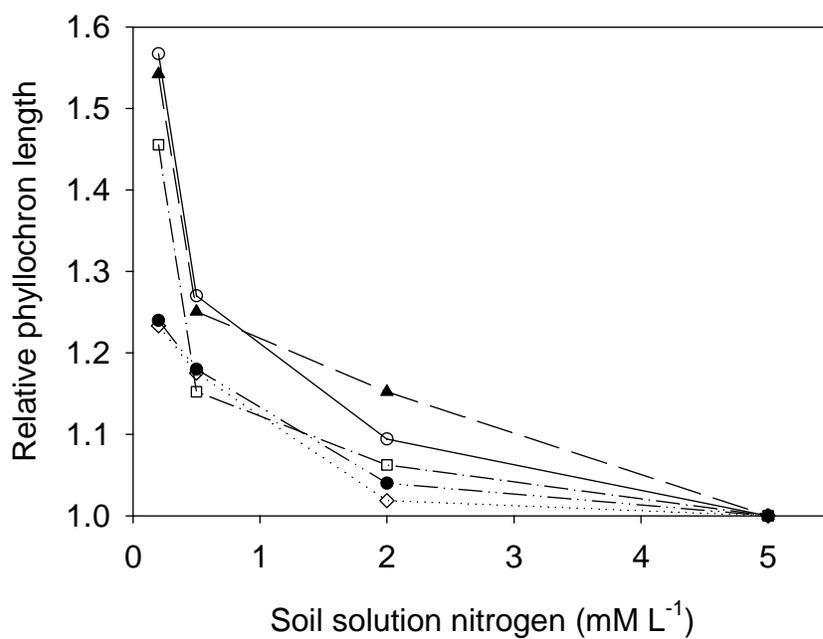


Figure 2.1 Length of the phyllochron period relative to the N<sub>5</sub> treatment for the five tested species. *A. retroflexus* (—▲—), *C. album* (··◇··), *A. theophrasti* (—○—), *S. faberi* (—□·—), and maize (—●·—).

Exponential fitting of shoot biomass with time (Appendix 2.1 and 2.2) indicated that biomass accumulation was exponential until the third harvest (44 DAE) for all species-nitrogen treatment combinations. By 44 DAE, mutual shading of leaves was occurring, suppressing exponential growth (Kropff et al., 1993). Therefore exponential growth equations were used to derive the relative growth rates only between the first (16 DAE) and third (44 DAE) harvests.

The responses to N levels relative to the N<sub>5</sub> treatment (Figure 2.2b) were similar for *A. theophrasti*, *A. retroflexus*, *C. album* and maize, however *S. faberi* produced almost the same biomass at N<sub>2</sub> as at N<sub>5</sub>. Relative growth rates indicate that this is not the result of low growth of *S. faberi* at high nutrient levels, but rather the maintenance of high growth rates at low nutrient levels (Table 2.3), suggesting that *S. faberi* can be an extremely competitive species for soil N. RGR in general followed the reported relationship with seed size (Harbur and Owen, 2004), where large seeded plants have lower RGR. However *S. faberi* had a larger RGR in relation to its seed weight, which could be the result of a larger initial lag phase of growth compared with *A. retroflexus* and *C. album* resulting in relatively smaller plants at the first harvest.

Relative yield responses to soil N and absolute plant dry weights of *A. retroflexus*, *C. album* and *S. faberi* were similar to those reported by Blackshaw et al. (2003) in a pot experiment where several plants were grown together with different N amendments. *A. retroflexus*, however grew relatively faster in their experiment than *C. album*, probably because of the higher air temperatures during the experiment (Percy et al., 1981).

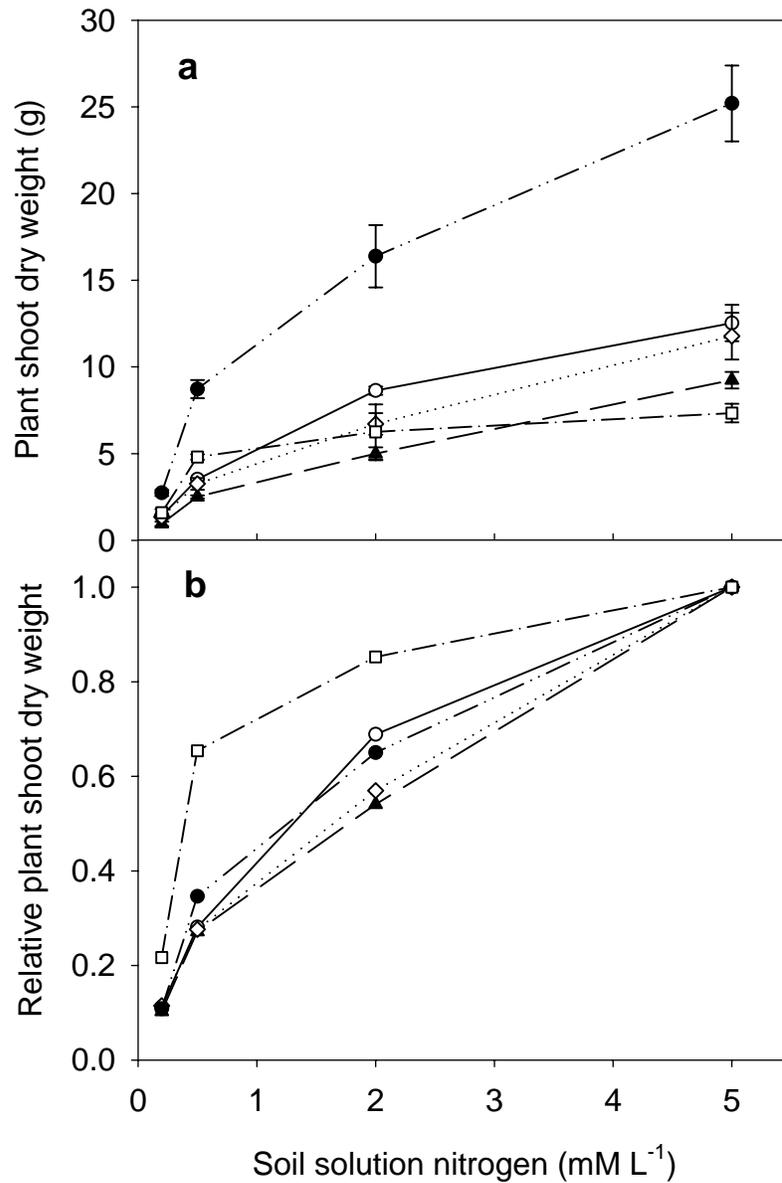


Figure 2.2 Shoot biomass (a) and shoot biomass relative to  $\text{N}_5$  shoot biomass (b) at the third harvest (44 DAE) for the five tested species. *A. retroflexus* (—▲—), *C. album* (··◇··), *A. theophrasti* (—○—), *S. faberi* (—□·—), and maize (—●·—). Error bars indicate standard error of the mean.

Table 2.3 Parameter estimates ( $\pm$  standard error) of the exponential growth equation fitted to shoot biomass as a function of days after emergence for the four weed species and maize.

	a — g —	$r_m$ — days <sup>-1</sup> —	$R^2$
<i>A. theophrasti</i>			
N <sub>5</sub>	0.0265 $\pm$ 0.6848	0.1441 $\pm$ 0.0211	0.98
N <sub>2</sub>	0.0304 $\pm$ 0.9408	0.1341 $\pm$ 0.0290	0.96
N <sub>0.5</sub>	0.0295 $\pm$ 0.3158	0.1106 $\pm$ 0.0097	0.99
N <sub>0.2</sub>	0.0250 $\pm$ 0.6648	0.0955 $\pm$ 0.0205	0.96
<i>A. retroflexus</i>			
N <sub>5</sub>	0.0031 $\pm$ 0.9447	0.1879 $\pm$ 0.0291	0.98
N <sub>2</sub>	0.0036 $\pm$ 0.6255	0.1684 $\pm$ 0.0193	0.99
N <sub>0.5</sub>	0.0035 $\pm$ 1.1155	0.1562 $\pm$ 0.0344	0.95
N <sub>0.2</sub>	0.0018 $\pm$ 0.8497	0.1471 $\pm$ 0.0262	0.97
<i>C. album</i>			
N <sub>5</sub>	0.0068 $\pm$ 1.0417	0.1757 $\pm$ 0.0321	0.97
N <sub>2</sub>	0.0059 $\pm$ 1.2160	0.1673 $\pm$ 0.0375	0.95
N <sub>0.5</sub>	0.0073 $\pm$ 0.9967	0.1446 $\pm$ 0.0307	0.96
N <sub>0.2</sub>	0.0034 $\pm$ 0.9684	0.1419 $\pm$ 0.0299	0.96
Maize			
N <sub>5</sub>	0.1332 $\pm$ 0.3037	0.1210 $\pm$ 0.0094	0.99
N <sub>2</sub>	0.1752 $\pm$ 0.5520	0.1065 $\pm$ 0.0170	0.98
N <sub>0.5</sub>	0.1153 $\pm$ 0.0503	0.0980 $\pm$ 0.0016	1.00
N <sub>0.2</sub>	0.0683 $\pm$ 0.1623	0.0849 $\pm$ 0.0050	1.00
<i>S. faberi</i>			
N <sub>5</sub>	0.0027 $\pm$ 1.0404	0.1862 $\pm$ 0.0321	0.97
N <sub>2</sub>	0.0026 $\pm$ 1.2496	0.1842 $\pm$ 0.0385	0.96
N <sub>0.5</sub>	0.0023 $\pm$ 1.5538	0.1827 $\pm$ 0.0479	0.94
N <sub>0.2</sub>	0.0043 $\pm$ 1.0385	0.1407 $\pm$ 0.0320	0.95

Allocation of assimilate to root biomass was severely reduced in all species at the  $N_{0.2}$  treatment (Figure 2.3). Root to shoot ratio was relatively constant for all the other N treatments except in *A. theophrasti*, whose root to shoot ratio increased as soil solution N increased. Compared with the test weed species, maize allocated less biomass to roots. This could be an important determinant of competitive outcomes between maize and weeds, especially *A. theophrasti* (Figure 2.3).

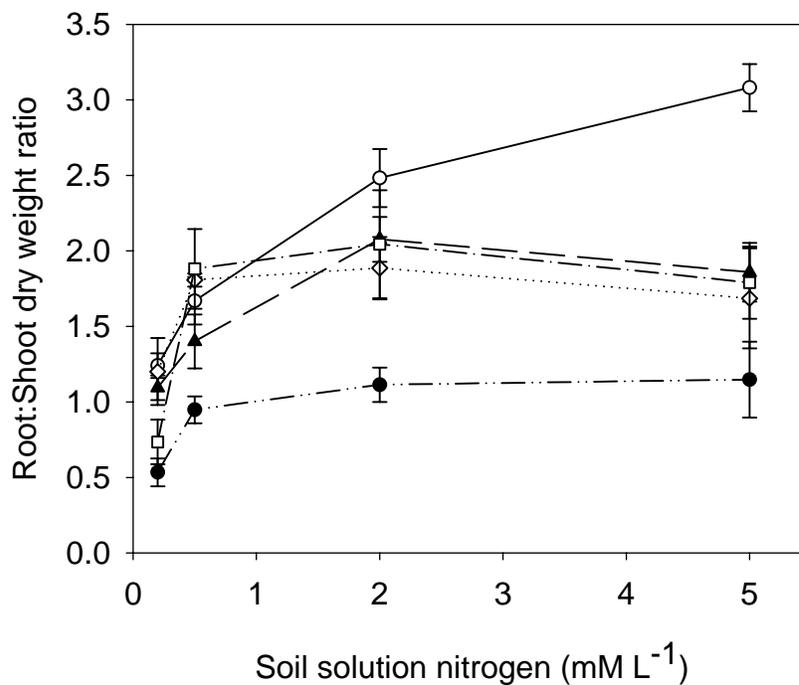


Figure 2.3 Root to shoot dry weight ratio at the second harvest (31 DAE) for the five tested species. *A. retroflexus* (—▲—), *C. album* (··◇··), *A. theophrasti* (—○—), *S. faberi* (—□·—), and maize (—●··—). Error bars indicate standard error of the mean.

As plants grew, allocation to leaf biomass was reduced in relation to the total shoot biomass (Figure 2.4). Of the four weed species, *A. theophrasti* had the largest decrease in leaf to total shoot weight, suggesting that the development of structural parts in this species represents a substantial cost in terms of photosynthate allocation. There were no significant differences ( $\alpha=0.01$ ) of N treatment on leaf to total shoot dry weight, although there was a tendency ( $P<0.05$ ) for *A. retroflexus* to have a smaller ratio at higher soil N levels.

### **Specific leaf area and chlorophyll contents**

There was a significant linear decrease ( $\alpha=0.01$ ) in specific leaf area (SLA) with time for all species (Figure 2.5). In the case of *A. retroflexus* and *A. theophrasti*, the decline was significantly ( $\alpha=0.05$ ) greater at the highest N levels.

Leaf chlorophyll content (SPAD readings) at the fourth harvest (57 DAE) showed the following order among species: *A. theophrasti* (36) < maize (42) < *S. faberi* (55) = *A. retroflexus* (60) < *C. album* (76) at  $\alpha = 0.01$ . Both the high SLA and SPAD readings for *A. retroflexus* and *C. album* suggest that these species may have a larger photosynthetic capacity per leaf area unit than the other species, thus allowing greater growth rates relative to the other species (Table 2.3).

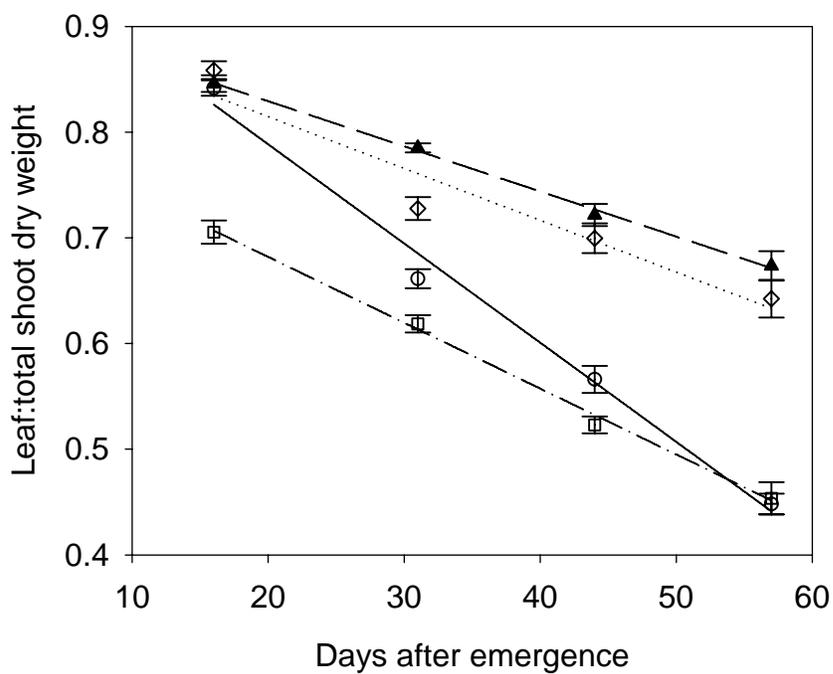


Figure 2.4 Average weed leaf to total shoot dry weight partition coefficients over time for the four weed species. *A. retroflexus* (—▲—)  $R^2=0.79$ , *C. album* (··◇··)  $R^2=0.68$ , *A. theophrasti* (—○—)  $R^2=0.94$ , and *S. faberi* (—□·—)  $R^2=0.87$ . Error bars indicate standard error of the mean.

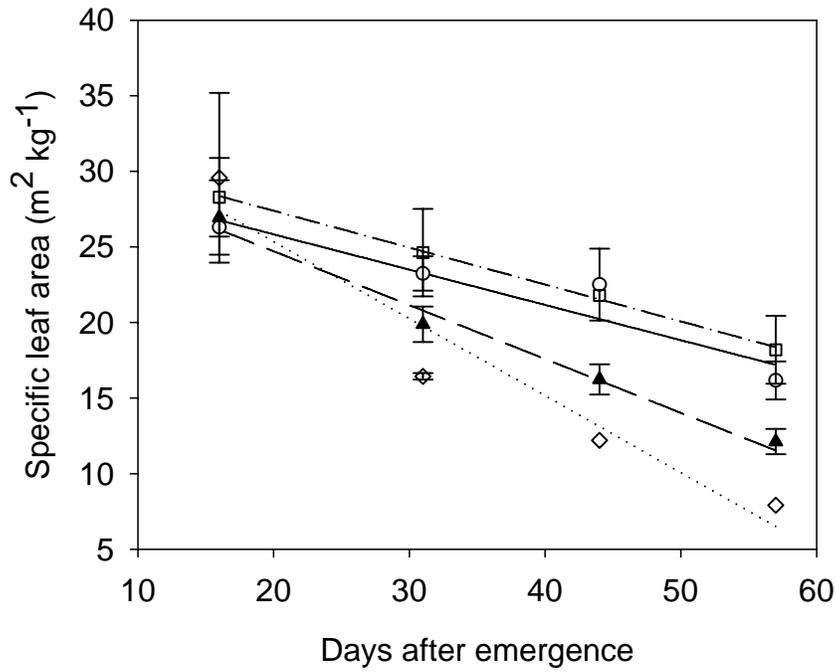


Figure 2.5 Specific leaf area over time for the newest developed leaves in treatment N<sub>5</sub> for the four weed species tested. *A. retroflexus* (—▲—), *C. album* (··◇··), *A. theophrasti* (—○—), and *S. faberi* (—□·—). SLA = 31.8364 - 0.3566 days, R<sup>2</sup> = 0.87; SLA = 35.5377 - 0.5095 days, R<sup>2</sup> = 0.71; SLA = 30.5033 - 0.2335 days, R<sup>2</sup> = 0.74; SLA = 32.2655 - 0.244 days, R<sup>2</sup> = 0.63, respectively.

### **Plant architecture, height and specific stem length**

Specific stem length (SSL) decreased with time as plants grew, developed laterally and increased biomass allocation to structural organs (Figure 2.6). The largest decrease was between 16 and 31 DAE, after which an apparently stable value was reached. Large differences were observed among species at the first sampling date (16 DAE) that were reduced as plants grew, and became less significant by the last harvest (57 DAE). Responses in SSL to N levels at the last harvest (57 DAE) differed between species (Figure 2.7a). *S. faberi* and *A. theophrasti* had the largest SSL values at all N levels and showed the greatest reduction in SSL with increased N availability. In contrast, *A. retroflexus* and *C. album* had the lowest SSL values at all N levels. This demonstrates the ability of *A. theophrasti* and *S. faberi* to maintain height growth at low N levels, thus maintaining its competitive ability for light at the canopy scale. It is well known that *A. theophrasti* is an excellent competitor for light (Hock, 2005; Lindquist and Mortensen, 1999; Sattin et al., 1992), but most of the research has been conducted under non-limiting soil N conditions. The previous results give insights on the behavior of this species under non-optimal soil nitrogen conditions.

Interestingly, maize had the largest SSL at N<sub>5</sub> and one of the lowest at N<sub>0.2</sub>, indicating a high sensitivity to soil N (Figure 2.7a). When comparing the absolute height of maize with the absolute height of the weed species (Figure 2.7b) it is evident that maize responses to soil N in height are larger, suggesting high competitive ability for light of maize. Height includes the effects of soil nitrogen availability on plant biomass accumulation and plant morphology (SSL), in the case of maize both effects are enhanced at high soil N levels.

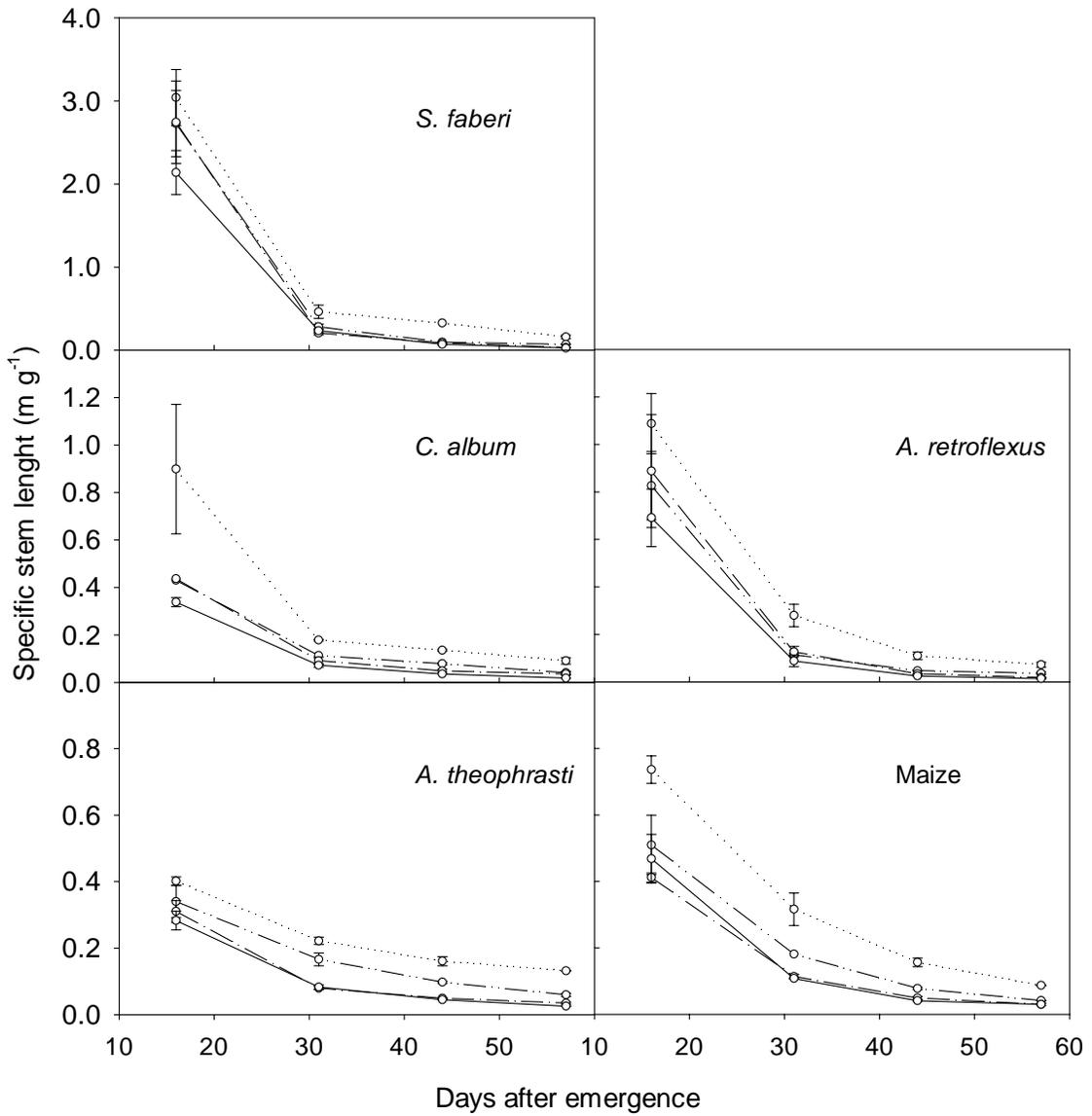


Figure 2.6 Specific stem length of plants grown at 0.2 (·····), 0.5 (— · — · — · —), 2 (— — —), and 5 (—) mM L<sup>-1</sup> N in soil solution at different harvest intervals. Bars indicate standard errors of mean.

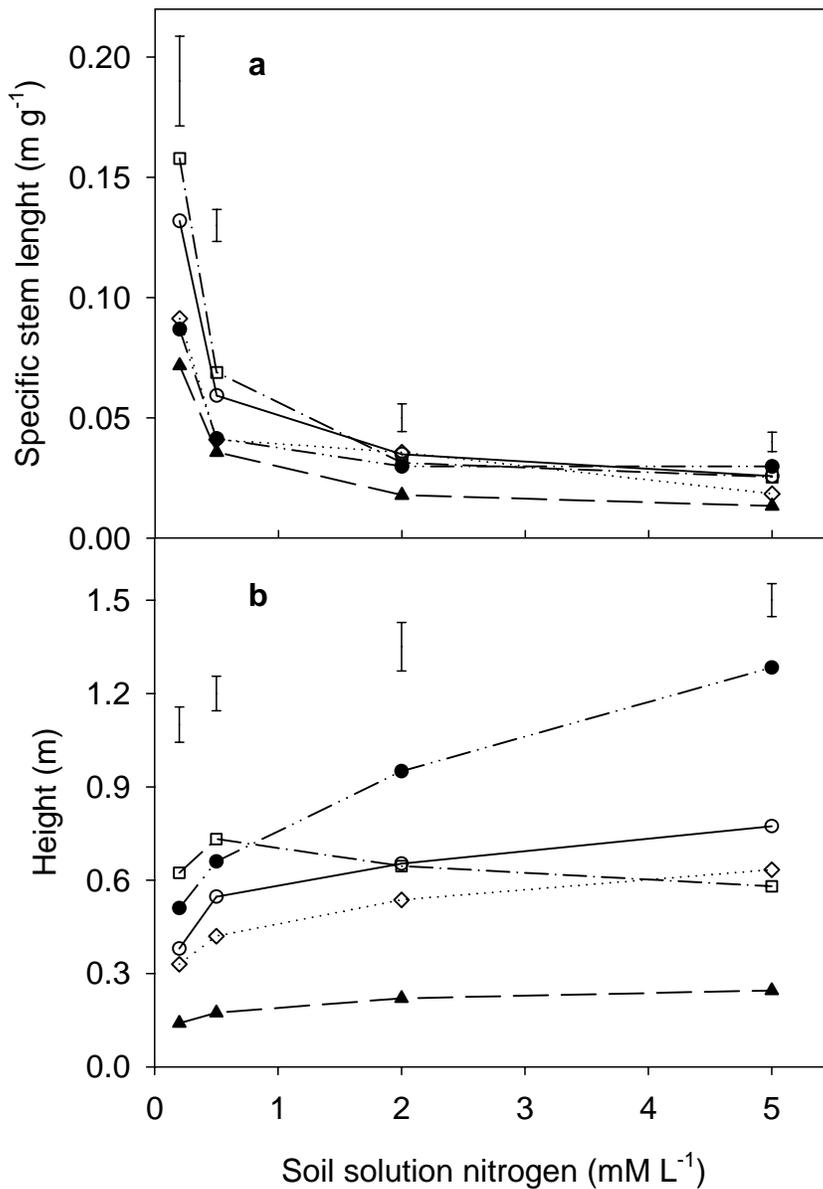


Figure 2.7 Specific stem length (a) and plant height (b) at the fourth harvest (57 DAE) as a function of nitrogen in soil solution for the five tested species. *A. retroflexus* (—▲—), *C. album* (··◇··), *A. theophrasti* (—○—), *S. faberi* (—□·—), and maize (—●····—). Bars indicate LSD (P=0.05) at each N level.

## CONCLUSIONS

Relative responses to soil N availability were similar for all species except for *S. faberi*. This species maintained high growth at low N levels, suggesting that it will be highly competitive for soil N. Shoot dry weight at 57 DAE was more dependent on the initial plant size (seed size) than on the relative growth rate or soil N status, indicating that large seeded crops maintained an early advantage in terms of dry weight accumulation and ability to capture light and soil resources compared with small seeded species.

Soil N status induced changes in several plant traits such as leaf appearance rate, tillering, SLA, chlorophyll content and SSL. These findings suggest that effects of soil N status on plant growth are multiple and more plant parameters than merely shoot or root dry weight should be considered if the objective is to determine the competitive ability of the weed species in mixed crop-weed stands.

Results indicate the important effect of nitrogen on plant architecture. Most importantly, different responses to nitrogen additions in plant architecture were observed (i.e. height). We propose that height response to nitrogen availability could be a major determinant of a species relative position when interspecific height hierarchies are formed, thus affecting light interception when plants begin to compete for light. This response could be important in field situations, considering that N availability could differ substantially both spatially and temporally early in the growing season due to weather conditions, and that starter banded fertilizer potentially establishes differences in N availability for crops and weeds.

APPENDIX

Appendix 2.1 Parameter estimates ( $\pm$  standard error) of the expolinear growth equation fitted to shoot biomass as a function of GDD for the four N treatments.

	t — GDD —	$r_m$ — GDD <sup>-1</sup> —	$c_m$ — g GDD <sup>-1</sup> —	R <sup>2</sup>
<i>A. retroflexus</i>				
N <sub>5</sub>	329 ± 19	0.0235 ± 0.0069	0.0856 ± 0.0083	0.99
N <sub>2</sub>	404 ± 93	0.0169 ± 0.0103	0.0867 ± 0.0462	0.95
N <sub>0.5</sub>	343 ± 49	0.0149 ± 0.0050	0.0239 ± 0.0053	0.98
N <sub>0.2</sub>	375 ± 71	0.0140 ± 0.0054	0.0113 ± 0.0039	0.97
<i>A. theophrasti</i>				
N <sub>5</sub>	439 ± 55	0.0129 ± 0.0024	0.2479 ± 0.0751	0.99
N <sub>2</sub>	478 ± 303	0.0103 ± 0.0063	0.1838 ± 0.2870	0.92
N <sub>0.5</sub>	605 ± 355	0.0102 ± 0.0032	0.2241 ± 0.5664	0.98
N <sub>0.2</sub>	572 ± 388	0.0078 ± 0.0028	0.0384 ± 0.0720	0.96
<i>C. album</i>				
N <sub>5</sub>	773 ± 152	0.0083 ± 0.0021	0.2288 ± 0.1383	0.99
N <sub>2</sub>	658 ± 200	0.0079 ± 0.0040	0.0623 ± 0.0381	0.96
N <sub>0.5</sub>	1112 ± 1307	0.0065 ± 0.0026	0.3306 ± 2.2213	0.99
N <sub>0.2</sub>	958 ± 640	0.0062 ± 0.0025	0.0468 ± 0.1217	0.97
Maize				
N <sub>5</sub>	349 ± 62	0.0186 ± 0.0155	0.1438 ± 0.0327	0.95
N <sub>2</sub>	462 ± 128	0.0091 ± 0.0033	0.1511 ± 0.0693	0.97
N <sub>0.5</sub>	384 ± 42	0.0135 ± 0.0043	0.0584 ± 0.0090	0.99
N <sub>0.2</sub>	637 ± 185	0.0073 ± 0.0015	0.0564 ± 0.0436	0.99
<i>S. faberi</i>				
N <sub>5</sub>	590 ± 1375	0.0126 ± 0.0178	0.7020 ± 8.8859	0.83
N <sub>2</sub>	604 ± 572	0.0121 ± 0.0063	0.6406 ± 3.2355	0.97
N <sub>0.5</sub>	416 ± 75	0.0124 ± 0.0033	0.0752 ± 0.0288	0.99
N <sub>0.2</sub>	602 ± 557	0.0096 ± 0.0048	0.0869 ± 0.3082	0.96

Appendix 2.2 Parameter estimates ( $\pm$  standard error) of the expolinear growth equation fitted to shoot biomass as a function of days after emergence for the four N treatments.

	t — days —	$r_m$ — days <sup>-1</sup> —	$c_m$ — g days <sup>-1</sup> —	$R^2$
<i>A. retroflexus</i>				
N <sub>5</sub>	39 ± 3.5	0.1401 ± 0.0273	1.6549 ± 0.2720	0.99
N <sub>2</sub>	41 ± 17.8	0.1120 ± 0.0718	1.0849 ± 0.8276	0.92
N <sub>0.5</sub>	49 ± 14.1	0.1078 ± 0.0342	0.8229 ± 0.5990	0.98
N <sub>0.2</sub>	43 ± 17.3	0.0861 ± 0.0320	0.1699 ± 0.1130	0.97
<i>A. theophrasti</i>				
N <sub>5</sub>	31 ± 1.6	0.3010 ± 0.1239	0.7001 ± 0.0528	0.99
N <sub>2</sub>	38 ± 6.6	0.1831 ± 0.1155	0.6418 ± 0.2108	0.95
N <sub>0.5</sub>	31 ± 3.6	0.1755 ± 0.0712	0.1852 ± 0.0271	0.98
N <sub>0.2</sub>	34 ± 5.1	0.1586 ± 0.0690	0.0841 ± 0.0181	0.97
<i>C. album</i>				
N <sub>5</sub>	45 ± 6.8	0.1373 ± 0.0355	2.6009 ± 0.9614	0.99
N <sub>2</sub>	38 ± 9.4	0.1353 ± 0.0711	0.7820 ± 0.3260	0.96
N <sub>0.5</sub>	73 ± 90.0	0.0939 ± 0.0365	4.7651 ± 32.3549	0.99
N <sub>0.2</sub>	88 ± 252.5	0.0813 ± 0.0327	3.7618 ± 69.8241	0.97
Maize				
N <sub>5</sub>	27 ± 4.5	0.3370 ± 0.5882	1.4773 ± 0.2680	0.95
N <sub>2</sub>	34 ± 7.5	0.1208 ± 0.0474	1.3488 ± 0.3963	0.97
N <sub>0.5</sub>	30 ± 2.9	0.1884 ± 0.0759	0.5821 ± 0.0671	0.99
N <sub>0.2</sub>	80 ± 83	0.0677 ± 0.0157	2.0386 ± 10.4422	0.99
<i>S. faberi</i>				
N <sub>5</sub>	68 ± 239.7	0.1039 ± 0.1405	8.8362 ± 183.7672	0.83
N <sub>2</sub>	51 ± 21.7	0.1260 ± 0.0656	2.1806 ± 2.9367	0.97
N <sub>0.5</sub>	37 ± 5.1	0.1369 ± 0.0386	0.5198 ± 0.1141	0.99
N <sub>0.2</sub>	48 ± 24.0	0.1026 ± 0.0516	0.3309 ± 0.3919	0.96

## REFERENCES CITED

- Birch, C.J., J. Vos, and P.E.L.v.-d. Putten. 2003. Plant development and leaf area production in contrasting cultivars of maize grown in a cool temperate environment in the field. *European Journal of Agronomy* 2:173-188.
- Blackshaw, R.E., G. Semach, and H.H. Janzen. 2002. Fertilizer application method affects nitrogen uptake in weeds and wheat. *Weed Science* 50:634-641.
- Blackshaw, R.E., R.N. Brandt, H.H. Janzen, and T. Entz. 2004. Weed species response to phosphorus fertilization. *Weed Science* 52:406-412.
- Blackshaw, R.E., R.N. Brandt, H.H. Janzen, T. Entz, C.A. Grant, and D.A. Derksen. 2003. Differential response of weed species to added nitrogen. *Weed Science* 51:532-539.
- Cathcart, R.J., and C.J. Swanton. 2004. Nitrogen and green foxtail (*Setaria viridis*) competition effects on corn growth and development. *Weed Science* 52:1039-1049.
- Colquhoun, J., D.E. Stoltenberg, L.K. Binning, and C.M. Boerboom. 2001. Phenology of common lambsquarters growth parameters. *Weed Science* 49:177-183.
- Conley, S.P., L.K. Binning, C.M. Boerboom, and D.E. Stoltenberg. 2003. Parameters for predicting giant foxtail cohort effect on soybean yield loss. *Agronomy Journal* 95:1226-1232.
- Cralle, H.T., T.B. Fojtasek, K.H. Carson, J.M. Chandler, T.D. Miller, S.A. Senseman, R.W. Bovey, and M.J. Stone. 2003. Wheat and Italian ryegrass (*Lolium multiflorum*) competition as affected by phosphorus nutrition. *Weed Science* 51:425-429.
- Earl, H.J., and M. Tollenaar. 1997. Maize leaf absorptance of photosynthetically active radiation and its estimation using a chlorophyll meter. *Crop Science* 37:436-440.
- Engels, C., and E.A. Kirkby. 2001. Cycling of nitrogen and potassium between shoot and roots in maize as affected by shoot and root growth. *Journal of Plant Nutrition and Soil Science* 164:183-191.

- Evans, S.P., S.Z. Knezevic, J.L. Lindquist, and C.A. Shapiro. 2003. Influence of nitrogen and duration of weed interference on corn growth and development. *Weed Science* 51:546-556.
- Forcella, F., and K.R. Banken. 1996. Relationships among green foxtail (*Setaria viridis*) seedling development, growing degree days, and time of nicosulfuron application. *Weed Technology* 10:60-67.
- Goudriaan, J., and J.L. Monteith. 1990. A mathematical function for crop growth based on light interception and leaf-area expansion. *Annals of Botany* 66:695-701.
- Harbur, M.M., and M.D.K. Owen. 2004. Light and growth rate effects on crop and weed responses to nitrogen. *Weed Science* 52:578-583.
- Hellwig, K.B., W.G. Johnson, and P.C. Scharf. 2002. Grass weed interference and nitrogen accumulation in no-tillage corn. *Weed Science* 50:757-762.
- Hock, S.M., Knezevic, Stevan Z., Martin, Alex R., Lindquist, John L. 2005. Influence of soybean row width and velvetleaf emergence time on velvetleaf (*Abutilon theophrasti*). *Weed Science* 53:160-165.
- Kropff, M.J., H.H.v. Laar, and H.H. Van Laar. 1993. *Modelling Crop-Weed Interactions* CAB International, Wallingford; UK.
- Kropff, M.J., C.J.T. Spitters, B.J. Schneiders, W. Joenje, W.d. Groot, and W. De Groot. 1992. An eco-physiological model for interspecific competition, applied to the influence of *Chenopodium album* L. on sugarbeet. *Weed Research* 32:451-463.
- Liebman, M. 1989. Effects of nitrogen fertilizer, irrigation, and crop genotype on canopy relations and yields of an intercrop/weed mixture. *Field Crops Research* 22:83-100.
- Lindquist, J.L., D.A. Mortensen, and B.E. Johnson. 1998. Mechanisms of corn tolerance and velvetleaf suppressive ability. *Agronomy Journal* 90:787-792.
- McDonald, A.J., S.J. Riha, and C.L. Mohler. 2004. Mining the record: historical evidence for climatic influences on maize - *Abutilon theophrasti* competition. *Weed Research* 44:439-445.

- Mohler, C.L. 2001. Enhancing the competitive ability of crops, p. 269-321, In M. Liebman, et al., eds. Ecological Management of Agricultural Weeds. Cambridge University Press, Cambridge, UK.
- Oryokot, J.O.E., S.D. Murphy, A.G. Thomas, and C.J. Swanton. 1997. Temperature- and moisture-dependent models of seed germination and shoot elongation in green and redroot pigweed (*Amaranthus powellii*, *A. retroflexus*). Weed Science 45:488-496.
- Pearcy, R.W., N. Tumosa, and K. Williams. 1981. Relationships between growth, photosynthesis and competitive interactions for a C3-plant and a C4-plant. Oecologia 48:371-376.
- Petersen, J., and J.V. Mortensen. 2002. Dry matter production and N-15 recovery in spring wheat as affected by placement geometry of the fertilizer band. Communications in Soil Science and Plant Analysis 33:163-178.
- Rohrig, M., and H. Stutzel. 2001. Canopy development of *Chenopodium album* in pure and mixed stands. Weed Research 41:111-128.
- Sattin, M., G. Zanin, and A. Berti. 1992. Case-history for weed competition population ecology - velvetleaf (*Abutilon theophrasti*) in corn (*Zea mays*). Weed Technology 6:213-219.
- Sinclair, T.R., and T. Horie. 1989. Leaf nitrogen, photosynthesis, and crop radiation use efficiency - A review. Crop Science 29:90-98.
- Sogbedji, J.M., H.M.v. Es, S.D. Klausner, D.R. Bouldin, W.J. Cox, and H.M. van Es. 2001. Spatial and temporal processes affecting nitrogen availability at the landscape scale. Soil and Tillage Research 58:233-244.
- Steckel, L.E., C.L. Sprague, E.W. Stoller, and L.M. Wax. 2004. Temperature effects on germination of nine *Amaranthus* species. Weed Science 52:217-221.
- Teyker, R.H., H.D. Hoelzer, and R.A. Liebl. 1991. Maize and pigweed response to nitrogen supply and form. Plant and Soil 135:287-292.

Tollenaar, M., S.P. Nissanka, A. Aguilera, S.F. Weise, and C.J. Swanton. 1994. Effect of weed interference and soil nitrogen on four maize hybrids. *Agronomy Journal* 86:596-601.