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## Corn and Velvetleaf (*Abutilon theophrasti*) Transpiration in Response to Drying Soil

Jared J. Schmidt, Erin E. Blankenship, and John L. Lindquist\*

Soil water availability is the most important factor limiting crop yield worldwide. Understanding crop and weed transpiration in response to water supply may provide valuable insight into the mechanisms of crop yield loss in water-limited environments. A greenhouse experiment was conducted to quantify corn and velvetleaf transpiration in response to drying soil. Five plants of each species were well watered by adding back the equivalent water loss each day to reach field capacity, and five plants were subjected to drought stress (dry-down) by not replacing lost water. Normalized daily transpiration of dry-down plants was regressed on soil water content expressed as the fraction of transpirable soil water (FTSW). The critical soil water content below which plants begin to close their stomates occurred at  $FTSW_{cr} = 0.36 \pm 0.015$  for corn and  $0.41 \pm 0.018$  for velvetleaf. Total water transpired did not differ among species. Velvetleaf also responded to drought by senescing its oldest leaves, whereas corn mainly maintained its leaf area but with rolled leaves during peak drought stress. During a short-term drought, corn is expected to perform better than velvetleaf because it maintains full transpiration to a lower FTSW and does not senesce its leaves. Under severe long-term drought, the species that closes its stomates at greater  $FTSW_{cr}$  will conserve water and increase its chances of survival. Moreover, senescing all but the youngest leaves may ensure at least some seed production. Research is needed to evaluate the effects of soil water supply on corn–velvetleaf interference in the field.

**Nomenclature:** Corn, *Zea mays* L.; velvetleaf, *Abutilon theophrasti* Medic., ABUTH; soybean, *Glycine max* (L.) Merr.

**Key words:** Soil water supply, transpiration efficiency, competition.

Weeds cause crop loss by reducing the quantity of available resources to which the crop responds. Therefore, predicting the impact of weeds on crops can only be achieved through a quantitative understanding of resource depletion by both crop and weed species and their unique response to resource supply. Soil water availability is the most important factor limiting crop yield worldwide (Begg and Turner 1976; Boyer 1982). Crop production in the Great Plains region of the United States is characterized by highly variable rainfall and, consequently, variable soil water availability (Ruiz-Barradas and Nigam 2005). A comparative understanding of crop and weed transpiration in response to water availability may provide valuable insight into the mechanisms of crop yield loss in water-limited environments and provide the background for predicting crop–weed competition for soil water.

When soil water supply is not sufficient to meet plant demand, transpiration is reduced (Kropff 1993; Sadras and Milroy 1996). Kropff (1993) suggested that under water-limiting conditions, plant growth is reduced in proportion to the reduction in whole-plant transpiration rate. Therefore, actual plant growth can be predicted as the product of potential growth under non-water-limiting conditions and the ratio of actual to potential transpiration ( $T_a/T_p$ ). The response of the  $T_a/T_p$  of a species to the progressive drying of soil varies little across a wide range of conditions when expressed as a function of transpirable soil water content (FTSW; Sinclair 2005; Sinclair et al. 1998).

Velvetleaf is a detrimental weed in corn, soybeans, cotton, and sorghum in the United States (Bridges 1992, Spencer 1984). Patterson and Flint (1983) found little variation in transpiration efficiency (dry-matter production/transpiration) among five  $C_3$  weeds (including velvetleaf) and soybean. However, smooth pigweed (*Amaranthus hybridus* L.), a  $C_4$  species, had approximately twice the transpiration efficiency

of the  $C_3$  species. Plants that exhibit  $C_3$  and  $C_4$  photosynthetic pathways differ in how they fix  $CO_2$  during photosynthesis, which subsequently affects stomatal conductance and transpiration (Monson et al. 1984). In general, the transpiration efficiency of  $C_4$  plants is twice that of  $C_3$  plants (Begg and Turner 1976). We know of no reports of the comparative water use of velvetleaf ( $C_3$ ) and corn, a  $C_4$  species. Thus, the objective of this research was to determine the relative transpiration of corn and velvetleaf as the plants were subjected to drought stress by limiting soil water availability.

### Materials and Methods

A greenhouse experiment was conducted at the University of Nebraska–Lincoln to evaluate the relative transpiration of velvetleaf and corn as plants were subjected to drying soil. The experiment was conducted as a randomized complete block with two species (corn and velvetleaf), two treatments (well-watered and dry-down) and five replicate blocks. An experimental unit was a pot with a single plant. To test whether the relationship between  $T_a/T_p$  and FTSW varied with greenhouse conditions and plant development stage at which dry-down was initiated, the experiment was conducted by initiating treatments at two development stages within each of two planting dates. Corn (DKC 60-18<sup>1</sup>) and a locally collected population of velvetleaf were sown into 10-L (28-cm diameter) pots filled with 13.5 kg of an 8:1:1 mixture of dry silty clay loam soil : sand : perlite on 10 October, 2006 (fall) and 31 January, 2007 (winter). The pots were then watered to saturation and allowed to drain overnight, then weighed to determine pot mass at field capacity. Corn and velvetleaf plants were thinned to one plant per pot within 10 d of emergence. Plants were fertilized with a 20–20–20 (N–P–K) commercial plant fertilizer<sup>2</sup> and watered daily until treatments were imposed. Plants were fertilized with 2 g nitrogen (N) at emergence and, if treatments were initiated after V9 stage of corn development, treated with a second

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application of fertilizer to apply 2 g N 3 d prior to initiation of treatments. Pots were placed in blocks in greenhouse benches and the location of plants within a replicate block was randomized daily and the location of blocks was randomized weekly. The greenhouse was maintained at 25/20 C day/night temperature regime with a 14-h day supplemented with sodium halide lamps.

Within each sowing date, water stress treatments were imposed at two stages of development. Stress treatments were imposed at 49 d after planting (DAP) (V7 leaf stage of corn; fall early) and 61 DAP (V13 leaf stage of corn; fall late) in the fall sowing date, and at 36 DAP (V6 leaf stage of corn; winter early) and 55 DAP (V10 leaf stage of corn; winter late) for the winter sowing date. The evening before initiating stress treatments, uniformly sized plants of each species were selected based on visual observation, and pots were watered to saturation and allowed to drain overnight. Then the pots were enclosed in black plastic bags and the bag opening sealed around the plant stem with twist ties to minimize water loss due to evaporation. The bags on the control plants were fitted with resealable plastic access tubes (bulk density soil sampling tubes, sealed on the open end using the accompanying rubber caps) to facilitate watering. The access tubes were inserted through the bag and the junction was taped to maintain the seal.

Soil water content was quantified as volumetric water content ( $\theta$ ) with the use of

$$\theta = \frac{M_l}{M_s} \rho_s,$$

where  $M_l$  is the mass of water,  $M_s$  is the mass of dry soil, and  $\rho_s$  is the bulk density of the greenhouse soil (1.53 g cm<sup>3</sup>). Newly bagged pots were weighed to obtain an estimate of the volumetric water content at field capacity ( $\theta_{fc}$ ). Pots were weighed daily at the same time and in the same order for the duration of the experiment, and daily transpiration was calculated as the difference in mass on successive days. For the well-watered control plants, the equivalent water that had transpired during the previous 24 h was added via the access tube. Water was completely withheld from the dry-down treatments and actual daily volumetric soil water content ( $\theta$ ) was calculated based on the pot mass obtained for that day.

Treatments were maintained within an experiment until velvetleaf plants in the dry-down treatment approached final wilting point, at which time the final pot mass was determined and volumetric water content at permanent wilting point ( $\theta_{pwp}$ ) calculated. Final wilting point was the point at which all fully developed velvetleaf leaves had senesced. Although corn leaves had not completely senesced,  $T_a/T_p$  was below 0.1 indicating that very little transpiration occurred, so the experiment was terminated. This took 11 and 6 d for the fall sowing date (early and late) and 18 and 11 d for the winter sowing date (early and late). Area of senescent leaves was measured daily during the experiment with the use of an area meter,<sup>3</sup> and the final remaining leaf area determined at the termination of the experiment. At final harvest, plants were clipped at the soil surface, separated into leaves and stems, and dried at 60 C to constant mass.

Leaf area on a particular day was estimated in the dry-down treatments by summing the total leaf area remaining on the final day of the experiment and the area of leaves that had senesced after that particular day. Leaf area of the well-watered plants was estimated assuming these plants had a leaf area at

the initiation of treatments equal to the average total leaf area of the dry-down plants. This assumption is based on the observed lack of growth during the dry-down period in those treatments. Leaf area on a given day was then estimated for each control plant with the use of a linear interpolation between starting leaf area and the measured final leaf area. Transpiration per unit leaf area was then calculated by dividing the daily transpiration rate by the estimated leaf area on a given day. The ratio of daily transpiration per unit leaf area in the dry-down treatments ( $T_a$ ) to that in the well-watered treatments ( $T_p$ ) provides an estimate of the daily transpiration ratio (i.e., DTR =  $T_a/T_p$ ; Ray and Sinclair 1997). A normalized transpiration ratio (NTR) was then obtained by dividing the DTR of each individual stressed plant by the average transpiration per unit leaf area of that particular plant when treatments were initiated, when plants were not yet drought stressed (Ray and Sinclair 1997, 1998).

Obtaining a consistent plant physiological response to water availability among species is best achieved when compared on the basis of the fraction of total extractable water in the root zone (Ray et al. 2002; Ray and Sinclair 1997; Sinclair et al. 1998). The quantity of soil water available to the plant on any given day was therefore normalized with the use of the fraction of transpirable soil water (FTSW):

$$FTSW = \frac{\theta - \theta_{pwp}}{\theta_{fc} - \theta_{pwp}}, \quad [1]$$

where  $\theta$ ,  $\theta_{pwp}$ , and  $\theta_{fc}$  are defined as above (Van den Berg and Driessen 2002). The relationship between NTR and FTSW for each species was quantified with the use of the logistic equation (Ray and Sinclair 1997):

$$NTR = \frac{1}{1 + \exp(b - cFTSW)}, \quad [2]$$

where  $b$  and  $c$  are shape coefficients (Hunt 1982). Equation 2 was fit to NTR in relation to FTSW for each sowing date and growth stage with the use of the NLMIXED procedure in SAS,<sup>4</sup> and coefficient estimates were compared among sowing dates and growth stages with the extra sum-of-squares procedure (Lindquist et al. 1996). Assumptions of normality and homogeneity of variances were met, and coefficient estimates did not differ among sowing dates and stage of development at which dry-down was initiated, so Equation 2 was fit to the pooled data from all experiments. Goodness of fit for each species was determined with the use of the pseudo- $R^2$  (Schabenberger and Pierce 2002). The parameters of Equation 2 provide an estimate,  $(b + 2)/c$ , of the point at which the curve diverges from the upper asymptote, providing an estimate of the critical FTSW below which transpiration begins to decline (FTSW<sub>cr</sub>).

Total shoot dry mass (DW), daily transpiration ratio (DTR), volumetric water content on the final day of treatment ( $\theta_{pwp}$ ), volumetric water content at saturation ( $\theta_{fc}$ ), and total transpirable soil water (TSW) were compared among sowing dates, growth stages, and species by ANOVA with the use of the MIXED procedure in SAS assuming a randomized complete block design, where block nested in sowing date was treated as a random effect. Differences among growth stages, sowing dates, and species were compared with the use of the Tukey test at a  $P < 0.05$  level of significance. The fraction of leaf area that senesced during dry-down also

Table 1. Least-squares means of corn and velvetleaf shoot biomass (DW, g), daily transpiration ratio (DTR), and volumetric soil water content ( $\theta_{pwp}$ ) in dry-down treatments on the final day of each experiment, volumetric water content at saturation ( $\theta_{fc}$ ), and total amount of transpirable soil water (TSW, kg).

Time of sowing	Development stage at treatment initiation	DW <sup>a</sup>		DTR		$\theta_{pwp}$		$\theta_{fc}$		TSW	
		Corn	Velvetleaf	Corn	Velvetleaf	Corn	Velvetleaf	Corn	Velvetleaf	Corn	Velvetleaf
		g				v/v				kg	
Fall	Early	38.6	22.3*	0.03	0.02*	0.12	0.07*	0.45	0.40*	2.65	2.58
	Late	56.3	42.5*	0.15	0.09*	0.15	0.07*	0.41	0.40	2.00	2.58*
Winter	Early	12.6	10.0*	0.02	0.01	0.06	0.04	0.38	0.38	2.58	2.78
	Late	32.8	34.7	0.05	0.03*	0.05	0.04	0.38	0.38	2.64	2.65
	SE (diff) <sup>b</sup>	4.44	3.15	0.012	0.006	0.011	0.014	0.015	0.010	0.150	0.129

<sup>a</sup> An asterisk (\*) indicates a difference among species within an experiment at  $P < 0.05$  level of significance.

<sup>b</sup> The SE (diff) is the standard error of the difference among experiments within species.

was compared among sowing dates, growth stages, and species with the use of similar procedures.

## Results and Discussion

Corn and velvetleaf in dry-down treatments reached aboveground biomass up to  $56 \pm 3.7$  and  $43 \pm 3.7$  g plant<sup>-1</sup>, respectively (Table 1). These greenhouse-grown plants are comparable to plants at a similar stage of development growing in the field (Bonifas et al. 2005), suggesting that the growing conditions in the greenhouse did not substantially inhibit either corn or velvetleaf growth. Shoot biomass of plants in the dry-down treatment differed among sowing dates, development stage at which treatments were initiated, and species, owing to the different growth stages at which each experiment was initiated. Within an experiment, variation in biomass among experimental units was relatively small (coefficient of variation ranged from 3.8 to 11.7%).

Sinclair (2005) defined the lower limit of available soil water for transpiration as the volumetric water content at which DTR declines below 0.1. Transpiration of stressed corn and velvetleaf plants on the final day of each experiment was generally less than 5% of the well-watered plants (DTR < 0.05), indicating that stomatal conductance was severely reduced (Table 1). Corn DTR on the final day of the experiment was greater than 0.1 in the fall-sown, late-development-stage experiment, indicating that this experiment may have been terminated prematurely for corn. Therefore, the lower limit of volumetric soil water content ( $\theta_{pwp}$ ) may not accurately reflect the permanent wilting point of corn in that experiment. Excluding the fall late experiment, permanent wilting point in this greenhouse soil occurred at about  $\theta_{pwp} = 0.074 \pm 0.010$  (SE) and  $0.056 \pm 0.005$  cm<sup>3</sup>/cm<sup>3</sup> for corn and velvetleaf, respectively, which are within the range predicted for sandy soils by Sinclair (2005). We are not aware of similar published values for silty clay loam soils.

Volumetric water content at field capacity ranged from 0.38 to 0.45 cm<sup>3</sup>/cm<sup>3</sup>, which is within the range of values reported for well-drained soils by Sinclair et al. (1998). Corn and velvetleaf did not differ in the quantity of total soil water extracted from pots (TSW) in all but the fall-sown late-development-stage experiment, where corn TSW was 24% lower, owing to the greater water content at the termination of this experiment (Table 1). The fact that TSW generally did not differ among species or experiments indicates that, over time, these species will extract an equivalent quantity of water

from severely water-limited soil regardless of plant size or development stage at the start of the drying period.

Equation 2 provided a good fit to the NTR versus FTSW relationship for both corn ( $R^2 = 0.89$ ) and velvetleaf ( $R^2 = 0.79$ ) (Figure 1). Even though plant size varied greatly among sowing dates and development stage at treatment initiation, the shape coefficients  $b$  and  $c$  did not differ among experiments, so results were pooled for comparison among species. Both coefficients differed among species. The better fit obtained for corn may be expected, because a corn hybrid is

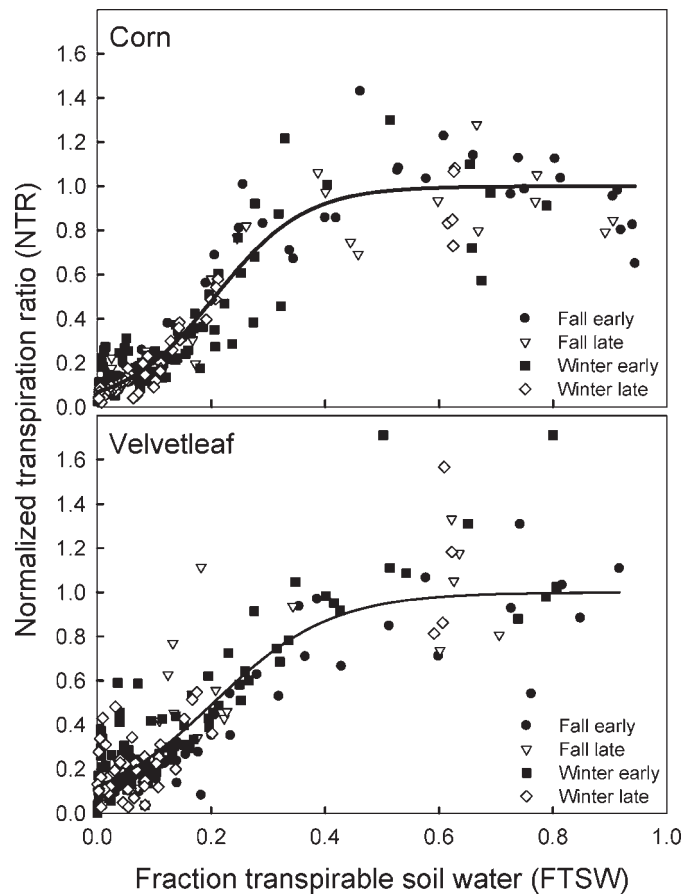


Figure 1. Corn and velvetleaf normalized transpiration ratio (NTR) in relation to the fraction of transpirable soil water (FTSW) in a greenhouse experiment. The line represents the nonlinear regression of NTR on FTSW across sowing dates and development stages at which treatments were initiated with the use of Equation 2.  $NTR = 1/(1 + \exp(2.61(0.12) - 12.67(0.69) FTSW))$ ;  $R^2 = 0.89$ ,  $RMSE = 0.0132$  for corn and  $NTR = 1/(1 + \exp(1.98(0.12) - 9.71(0.74) FTSW))$ ;  $R^2 = 0.79$ ,  $RMSE = 0.0257$  for velvetleaf.



Table 2. Least-squares mean percent of total leaf area senesced during the dry-down period of each experiment.

	Leaf area senesced			
	Fall		Winter	
	Early	Late	Early	Late
	%			
Corn				
Well watered	0	0	0	1
Dry-down	3	0	1	3
Velvetleaf				
Well watered	3	1	2	4
Dry-down	42	25	28	71
SE (diff) <sup>a</sup>	4.3	3.9	3.2	5.4

<sup>a</sup> The SE (diff) is the standard error of the difference among species and treatment within an experiment at the  $P < 0.05$  level of significance.

genetically uniform, whereas velvetleaf is not; therefore, velvetleaf is subject to greater variability among individual plants.

The critical soil water content below which the plants begin to close their stomates occurred at  $FTSW_{cr} = 0.36 \pm 0.015$  for corn and  $0.41 \pm 0.018$  for velvetleaf. The  $FTSW_{cr}$  obtained for corn were within the range of values reported by Ray and Sinclair (1997) and Ray et al. (2002). The greater  $FTSW_{cr}$  obtained for velvetleaf indicates that velvetleaf stomates begin to close at a greater fraction of transpirable soil water than corn. The stomatal closure of corn at lower  $FTSW_{cr}$  may be due in part to the higher expected efficiency of the C4 photosynthetic pathway when stomatal conductance is low (Hetherington and Woodward 2003).

Ray and Sinclair (1997) suggested that even small differences in  $FTSW_{cr}$  among species can have important impacts under field conditions because premature closing of stomata during a temporary soil drying cycle will be translated into lost productivity. Under monoculture conditions, the species (like velvetleaf) that closes its stomates at greater  $FTSW_{cr}$  will conserve water and increase its chances of survival during a long-term drought. However, this would not provide a benefit for a velvetleaf plant growing within the corn canopy because the corn will continue to transpire at its potential until the  $FTSW_{cr}$  for corn is reached.

Leaf senescence occurred in both species, but velvetleaf plants subjected to drying soil senesced a much greater proportion of their leaves than corn (Table 2). Differences in percent of leaf area senesced prior to harvest of each species existed between experiments, probably as the result of differences in plant development stage and greenhouse conditions during the dry-down period. The high senescence observed in velvetleaf is consistent with previous research on velvetleaf grown under soil water deficit (Salisbury and Chandler 1993). Velvetleaf generally began to senesce its oldest leaves as soon as NTR diverged from 1.0, but senescence was most rapid when FTSW neared 0.1 (data not shown). Corn subjected to drought stress also responded by senescing some of its oldest leaves, but far less so than velvetleaf (Table 2). The most significant visual response of corn to drought stress was the rolling of its leaves. The shedding of only the older leaves by velvetleaf may contribute to its survival under water stress conditions.

Several implications can be drawn from the results of this experiment. Corn is expected to have a superior response to

drought stress of short duration compared to velvetleaf because (1) it continues to transpire normally at lower soil water content than velvetleaf and (2) the minimal leaf senescence indicates that once soil water is replenished, productive growth would fully recover over the entire leaf surface of the plant. Velvetleaf, on the other hand, would begin to close its stomates at higher soil water content and immediately begin senescing its lower leaves. The decrease in transpiration may result in lower than optimal photosynthetic rates in productive leaves and the senesced leaves cannot be regained except by producing new leaves, which may reduce its capacity for seed production.

The velvetleaf response to soil drying may be advantageous in the case of a severe drought of long duration, where early conservation of available soil water would result in maintaining at least some soil water for transpiration later. Reducing leaf area by senescing leaves in order to reduce whole plant transpiration while maintaining some leaf area to support even a small amount of seed production is an effective weedy characteristic (Baker 1974). Under severe drought of long duration, the lack of leaf senescence and rapid decline in corn transpiration may simply result in the plants aborting all reproductive activity or result in death before reproduction can occur (Sinclair et al. 1990).

Predicting the effects of differential corn and velvetleaf transpiration in a competitive situation is more difficult. Senescence of the oldest velvetleaf leaves in response to drying soil may not impact its ability to compete with corn for light because the uppermost (youngest) leaves are expected to intercept the greatest fraction of light (Lindquist and Mortensen 1999). Moreover, it is likely the continuing transpiration of a high density velvetleaf stand would compound the depletion of soil water and further reduce corn transpiration even under relatively minor drought conditions. A situation where the soil water was below the critical FTSW for velvetleaf, yet still above the critical FTSW for corn, might result in a competitive advantage for corn, as it would be photosynthesizing at a more optimum level than velvetleaf.

This study on the relative transpiration of corn and velvetleaf in response to drying soil provides useful insights into the relative responses of these species when subjected to a drought. Although this study does not examine competition for water between the two species, the experiment furthers our understanding of how these species individually respond to drying soil. Further experiments are needed to examine the nature of competition for water between these species.

## Sources of Materials

<sup>1</sup> DKC 60-18, DeKalb Brand, 800 N. Lindbergh Blvd., St. Louis, MO 63167.

<sup>2</sup> Peters Professional Allrounder, Scotts International B.V., P.O. Box 40, 4190 CA Geldermalsen, The Netherlands.

<sup>3</sup> LI-3000, Li-Cor Biosciences, 4647 Superior St., Lincoln, NE 68504.

<sup>4</sup> SAS Institute Inc., 100 SAS Campus Dr., Cary, NC 27513-2414.

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