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Water Deficit Stress Effects on Corn (*Zea mays*, L.) Root:Shoot Ratio

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Abstract

A study was conducted at Akron, CO, USA, on a Weld silt loam in 2004 to quantify the effects of water deficit stress on corn (*Zea mays*, L.) root and shoot biomass. Corn plants were grown under a range of soil bulk density and water conditions caused by previous tillage, crop rotation, and irrigation management. Water deficit stress (D_{stress}) was quantified by the number of days when the water content in the surface 0.3 m deviated from the water content range determined by the Least Limiting Water Range (LLWR). Root and shoot samples were collected at the V6, V12, and R1 growth stages. There was no significant correlation between D_{stress} and shoot or root biomass at the V6 growth stage. At the V12 and R1 growth stages, there were negative, linear correlations among D_{stress} and both root biomass and shoot biomass. The proportional decrease of shoot biomass was greater than the proportional decrease in root biomass, leading to an increase in the root:shoot ratio as water deficit stress increased at all growth stages. Determining restrictive soil conditions using the LLWR may be useful for evaluating improvement or degradation of the soil physical environment caused by soil management.

1. Introduction

There are mixed reports in the literature on the effects of water deficit stress on crop production, and how different plants respond to water deficits by changing root:shoot ratios. Amos and Walters [1] summarized the effects of several soil environmental variables on corn root:shoot ratios. They found that the average root:shoot ratio varied from 0.68 at plant emergence to 0.16 at physiological maturity for unstressed plants.

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Environmental stresses on the plant generally decreases both root growth and shoot growth. In field studies, Allmaras and Nelson [2] and Allmaras and Nelson [3] showed little difference in corn root distribution caused by differences in soil matric suction in a Nicollet soil in southwestern Minnesota, but the differences in matric suction were minimal among treatments. In their studies, the hydraulic head was greater than −40 kPa for all observations and only varied between −40 and −10 kPa during the two years of the study. Kondo *et al.* [4] measured a decrease in root:shoot ratio as corn experienced greater water stress. Gregory [5] concluded that dry soils induce plants to develop a more extensive root system and include deeper rooting, greater total weight, and greater total root length when compared with well-watered plants.

Water deficit and excessive soil strength are two factors that affect plant growth. In a growth chamber study using a silty clay loam soil, King and Greer [6] found that, at physiological maturity, a low water regime had no significant effects on root biomass but the plants had lower shoot growth compared with a fully watered regime. Calculations of soil environmental conditions from information given in the paper indicated that the plants were grown in a soil with a bulk density (ρ_b) of 0.61 g·cm^{-3} and the initial volumetric water content (θ_v) was 0.35 cm^3·cm^{-3}. Water stress was imposed by not replacing all the water transpired by the plant, but no specific θ_v measurements during the study were given in the report.

High soil ρ_b, an indicator of high soil strength, may also limit root growth. In a growth chamber study using a sandy loam soil, Tubeileh *et al.* [7] showed the effects of high soil ρ_b on root and shoot growth, even under adequate soil water conditions. In their study, both root growth and shoot growth were reduced due to higher soil ρ_b. Root growth decreased more, proportionately, to shoot growth so that they observed a 13% decrease in root:shoot ratio as ρ_b increased from 1.3 to 1.45 Mg·m^{-3}. Measurements of total CO_2 assimilation were similar under both bulk densities. More of the assimilated CO_2 was found in microbial biomass, indicating that the roots growing under high ρ_b exuded more of the C allocated to root by the plant.

It is difficult to quantify the response of root systems of many species to water deficit stress in the field because soil θ_v and soil strength are inexorably linked. One method to link plant growth with soil physical conditions is to define soil physical quality of a particular management scheme in terms of the Least Limiting Water Range (LLWR). The LLWR combines the soil physical conditions of soil water holding capacity, soil aeration, and soil strength into a numerical range that estimates the soil water contents that minimize physical limitations on plant growth [8].

The objective of this study was to determine the effects of deficit water stress on corn root distribution, corn root surface area density, and root:shoot ratio using the LLWR as the criteria to evaluate water deficit stress.

2. Materials and Methods

The study was conducted at the USDA-ARS Central Great Plains Research Station near Akron, Colorado. The station lies at 40.15°N lat and 103.15°W long. The elevation of the station is 1384 m above mean sea level. The research station location is within a semi-arid climate with approximately 400 mm annual precipitation. The soil is a Weld silt loam (fine, smectitic, mesic Aridic Paleustolls). This soil has a silt loam Ap horizon from about 0 to 120 mm with fine granular structure. A silty clay loam Bt1 horizon with fine to medium subangular blocky structure extends from about 120 to 240 mm with a smooth boundary to a silty clay loam Bt2 horizon, also with fine to medium subangular blocky structure to about 410 mm. A silty clay loam Btk horizon with fine to medium subangular blocky structure extends to about 640 mm.

The irrigation-tillage-crop rotation experiment started in 2001. The experiment was organized as a split-plot design with three replications. The main plot was an irrigation treatment of either full irrigation or delayed irrigation. Irrigation treatments in 2001 to 2003 included a fully irrigated treatment that supplied water based on the evapotranspiration (ET) demand for the crop grown and a delayed irrigation treatment that used no irrigation during the vegetative portion of the growth cycle and then added irrigation water equivalent to the fully irrigated plots during the reproductive stage of the crop grown. All plots were fully irrigated in 2004.

Crop rotation and tillage subplots were randomized within the main irrigation plots. Two levels of tillage were used. A no-till (NT) system consisted of directly planting into the previous crop residues. A chisel tillage system (CT) consisted of a fall chisel plow operation 0.35 m deep with a parabolic shank deep ripper. The shanks on the ripper had 0.6-m centers. Chisel tillage was followed in the spring by one or two passes with a mulch treader to break up clods and smooth the soil surface in preparation for planting. Depth of operation of the mulch treader was approximately 50 mm. Two crop rotations were used in a factorial arrangement with tillage. One consisted

of continuous corn production (CC). The other was a crop rotation (Rot) of red kidney bean (*Phaseolus vulgaris* L.) in 2001, spring barley (*Hordeum vulgare* L.) in 2002, sunflower (*Helianthus annuus* L.) in 2003 and corn in 2004. Details of the cropping history and management leading to the 2004 crop year are shown in **Table 1**. Plot size and machinery working widths are such that the wheel tracks for field operations follow a controlled wheel traffic pattern.

The least limiting water range was determined for this soil using the methods described in Benjamin, *et al.* [8]. The θ_v at field capacity was determined by removing undisturbed cores and placing the cores in individual water desorption chambers to equilibrate at 33 kPa pressure potential. Water content at wilting point was determined by placing disturbed samples in a pressure chamber equilibrated to 1500 kPa pressure potential. Measurements of cone penetration resistance, θ_v and ρ_b were made in each plot to determine the strength characteristics of the soil. Water contents defining the upper limit of the LLWR (θ_{UL}) and the lower limit of the LLWR (θ_{LL}) were determined for the range of ρ_b found in the field based on limitations of aeration, soil strength and water holding capacity.

Irrigation was applied to supplement natural rainfall. Irrigation was applied weekly based on evapotranspiration demand (**Figure 1**). Soil θ_v measurements were taken during the 2004 growing season with a neutron probe. Water measurements were taken from the center of a row at 0.3 m, 0.6 m, 0.9 m, 1.2 m, 1.5 m, and 1.8 m depths. Water content measurements were taken immediately before irrigation and as soon after irrigation as field entry was possible.

A simple method to quantify soil environmental stress experienced by the plant was used. The θ_{UL} and θ_{LL} for each sampling position were averaged across the row and also averaged for the 0 to 22.5 cm and 22.5 to 45 cm
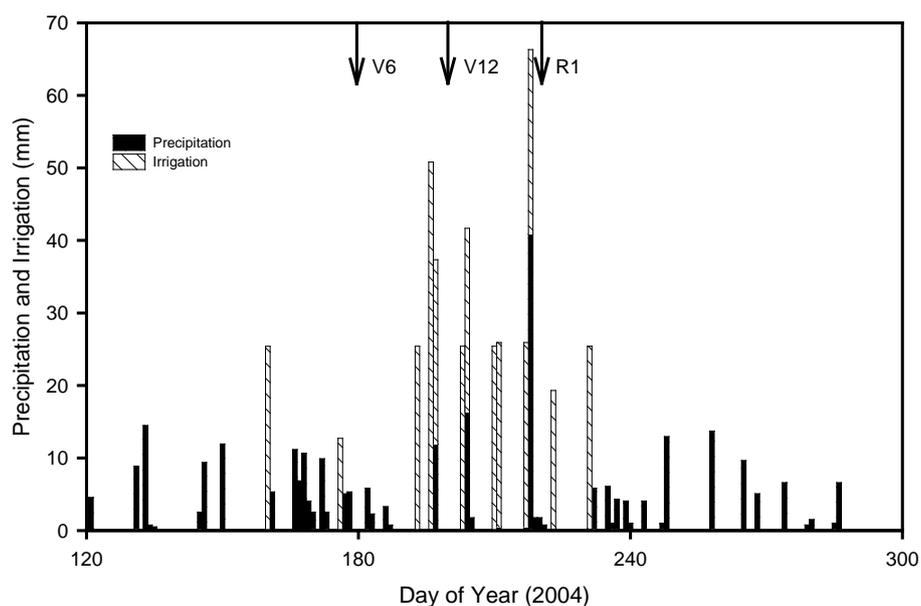
Figure 1. Precipitation and irrigation amounts applied to all plots in 2004. Sampling dates for the V6, V12, and R1 growth stages are indicated by the arrows.

Table 1. Details of cropping history for rotations, 2003 to 2004.

Year	Rotation	Crop	Variety	Row Spacing	Population	N-P-K-Zn
				m	plants·ha^{-1}	kg·ha^{-1}
2003	CC	Corn	NK N42-B7	0.75	86,000	215-22-0-0
	Rot	Sunflower	Triumph 567	0.75	70,000	34-22-0-0
2004	CC	Corn	Laser L62-C2	0.75	86,000	215-22-0-0.6
	Rot	Corn	Laser L62-C2	0.75	86,000	215-22-0-0.6

depth increments. The θ_v at each measurement time during the growing season was determined to either lie within the LLWR or lie outside the LLWR. Each day that the soil θ_v in the 0 to 30 cm depth was outside the LLWR was considered one day of water stress. When θ_v for one water content measurement lay within the LLWR and the next θ_v lay outside the LLWR, a linear change in θ_v was assumed and the stress days were calculated accordingly. The days of stress were summed from planting until the date of sampling to determine the total number of days of soil physical stress (D_{stress}) experienced by the plant.

Soil samples to determine root distribution were collected at the V6 (June 30), V12 (July 26) and R1 (August 8) growth stages. Corn growth stages were determined from the description in Ritchie and Hanway [9]. A hydraulic probe with a sampling tube 75 mm in diameter and 1.125 m long was used for sampling. A corn plant was selected in the plot that had no wheel traffic on either side of the plant. The plant material was clipped level with the soil surface and removed before sampling. Any loose plant residue on the soil surface was also brushed away from the sampling site. The probe was positioned directly over the corn plant for sampling. A second probe taken in the same hole produced samples to a 1.8-m depth. Additional samples were taken 150 mm on each side of the same plant. Each core was sectioned into 0- to 0.225-, 0.225- to 0.45-, 0.45- to 0.675-, 0.675- to 0.9-, 0.9- to 1.125-, 1.125- to 1.35-, 1.35- to 1.575-, and 1.575- to 1.8-m lengths. The sample was weighed for ρ_b determination and a small subsample was removed to determine soil θ_v. The sample was then placed in a plastic, sealable bag and the bags placed in a polystyrene cooler for transport from the field. After each half day's sample collecting, the samples were placed in refrigerated storage until washing the next day. Roots were washed from the soil cores and root surface area measurements were made using digital image analysis techniques as described in Benjamin and Nielsen [10].

A subset of the root samples were used to determine root weight-root surface area relationships. Roots and debris were separated manually by placing the sample in a tray and examining the sample with the aid of a 3X lighted magnifier. All roots, including large primary roots, were included in the sample. Scans were made with an Agfa Snapscan[TM] E40 flatbed scanner at 118 pixels per cm (300 dpi). A grid overlay technique was used to determine root surface area [10]. After scanning, the roots were removed from the sample tray, dried and weighed.

Root surface area density (R_{den}, m$^2 \cdot$m^{-3}) for each sampling position was calculated by:

$$R_{den} = R_{sam}/V_{sam} \qquad (1)$$

where R_{sam} is the total root surface area in the sample (m^2) and V_{sam} is the sample volume (m^3). The representative soil volume (V_{rep}) for each sample was considered to be 0.25 m wide, 0.225 m deep, and 1 m in length along the row. Total root surface area (R_{pos}) at each sample location was calculated by:

$$R_{pos} = R_{den} * V_{rep} . \qquad (2)$$

Total roots per unit area (R_{tot}, m$^2 \cdot$m^{-1}) was calculated by adding the root contents from the 24 sampling positions by

$$R_{tot} = 1.33 \sum_1^{24} R_{pos} \qquad (3)$$

where 1.33 converts the representative surface area of sampling to m^2.

Four representative whole plants were collected at each root sampling time. The shoots were dried at 60°C and weighed to give above-ground biomass production. Total average shoot density (TS_{avg}) was calculated by

$$TS_{avg} = S_{avg} P A^{-1} \qquad (4)$$

where S_{avg} is the average shoot weight per plant (kg), P is the plant population in each plot (plant$\cdot$m^{-2}) and A is the area of land surface (m^2).

An analysis of variance was conducted using a mixed statistical analysis in SAS. The F-test of main effect of irrigation was tested using the rep by irrigation error term. The F-test for interactions with irrigation was tested using the rep by interaction error term. Soil depth was treated as a repeated measure so the F-test for depth was determined using the rep by depth error term. The F-test for interactions with depth was tested using the rep by interaction error term. Least squares means were used to determine specific treatment differences when there was a significant F-test. Analyses of variance were conducted to determine irrigation, crop rotation, and tillage effects on total root density under a plant and root density in each layer. A protected LSD test was used to de-

termine treatment differences. The LSD was used to distinguish treatment effects only if the F-test was significant at the 0.05 probability level. Regression analysis was used to correlate D_{stress} with root and shoot production.

3. Results

The plots receiving CT had lower ρ_b than the NT plots in the 0- to 0.225-m depth (**Table 2**), but not in the 0.225- to 0.45-m depth. Lower ρ_b in the CT plots was evident at all sampling times. The CT tillage had less root surface area in the 1.8 m soil profile than the NT plots at the V6 growth stage (**Table 3**), while previous irrigation or

Table 2. Tillage effects on bulk density (ρ_b) distribution. NT denotes the no till system and CT denotes the chisel tillage system. Means followed by the same letter within growth stage and depth increment are not significantly different at P = 0.05.

Growth Stage	V6			V12			R1		
Tillage	NT	CT	lsd$_{0.05}$	NT	CT	lsd$_{0.05}$	NT	CT	lsd$_{0.05}$
Depth									
m					Mg·m^{-3}				
0 - 0.225	1.41a	1.36b	0.04	1.46a	1.39b	0.05	1.47a	1.34b	0.05
0.225 - 0.45	1.44a	1.42a	0.04	1.40a	1.39a	0.03	1.41a	1.40a	0.04
0.45 - 0.675	1.40a	1.40a	0.03	1.41a	1.38a	0.04	1.39a	1.38a	0.04
0.675 - 0.90	1.40a	1.40a	0.03	1.34a	1.39a	0.05	1.40a	1.37a	0.11
0.90 - 1.125	1.37b	1.43a	0.05	1.39a	1.40a	0.06	1.41a	1.39a	0.06
1.125 - 1.35	1.41a	1.40a	0.06	1.45a	1.44a	0.07	1.44a	1.37a	0.11
1.35 - 1.575	1.36a	1.40a	0.08	1.44a	1.46a	0.06	1.43a	1.46a	0.09
1.575 - 1.80	1.48b	1.54a	0.05	1.44b	1.57a	0.06	1.54a	1.51a	0.12

Table 3. Total root surface area in a 1.8 m soil profile for corn at V6, V12, and R1 growth stages as affected by previous irrigation history, previous cropping rotation and tillage system. Within each growth stage, treatment means followed by the same letter are not significantly different at the 0.05 probability level.

Treatment		Root Surface Area		
		V6	V12	R1
			m^2·m^{-2}	
Previous Irrigation (PI)	Full	218a	738a	1148a
	Delayed	196a	461b	1214a
Previous Crop (PC)	Corn	199a	659a	1323a
	Sunflower	215a	541a	1139b
Tillage (T)	No Till	253a	609a	1172a
	Chisel Plow	161b	591a	1190a
	LSD	25	235	144
Source	df		P > f	
PI	1	0.4457[†]	0.0379	0.7986
PC	1	0.1733	0.2378	0.0055
T	1	0.0006	0.8388	0.7427
PC × PI	1	0.6400	0.2243	0.0866
T × PI	1	0.5713	0.4715	0.3640
PC × T	1	0.0723	0.2475	0.5193
PI × PC × T	1	0.1524	0.6982	0.1101

[†]The test for significance of previous irrigation effects on total roots used the irrigation × rep interaction for the error term, crop × irrigation effects were tested using the irrigation × crop × rep interaction for the error term and tillage × irrigation effects were tested using the irrigation × tillage × rep interaction for the error term.

previous crop had no significant effect on total root surface area. There was less root surface area with delayed irrigation at the V12 growth stage in the surface 1.8 m soil profile than the full irrigation, while tillage or previous crop had no significant effect on total root surface area. At the R1 growth stage, plots with the previous crop as sunflower had less root surface area than the CC plots, while previous irrigation or tillage had no significant effect.

Previous irrigation history and crop rotation resulted in different water environments in the 0- to 0.3-m depth for root growth during the 2004 growing season (**Figure 2**). The average initial water contents of Rot were approximately 0.04 $m^3 \cdot m^{-3}$ less than the average water contents in the CC plots at the 0.3 m depth. As the growing season progressed, the treatment differences in θ_v decreased, but significant differences between Rot and CC continued throughout the growing season.

The combination of different ρ_b and water contents in the 0- to 0.3-m layer resulted in differences of D_{stress} during the growing season (**Figure 3**). Plants grown under conditions of Rot and delayed irrigation in 2003 had greater D_{stress} in 2004 at each sampling time than plants grown under conditions of CC and full irrigation in 2003, even though all plots were irrigated the same in 2004. Plants grown in plots with Rot with full irrigation in 2003 and CC with delayed irrigation in 2003 showed intermediate D_{stress} in 2004 compared with the other treatments.

The correlation between root weight and root surface area did not change due to growth stage of the crop (**Figure 4**). There was no difference in slope or intercept at the p = 0.05 level so all data were combined to estimate the relationship between root weight and surface area for subsequent analysis of root:shoot ratios.
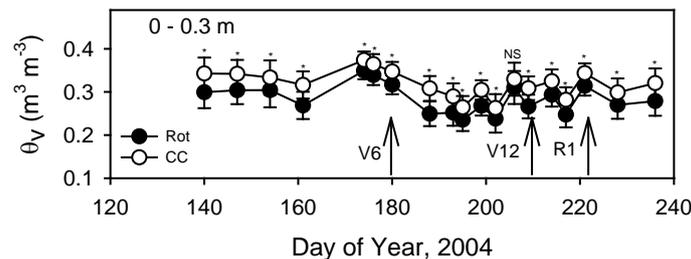
Figure 2. Mean soil volumetric water content (θ_v) in the 0- to 0.3-m depth interval during the growing season for the rotation (Rot) and continuous corn (CC) treatments. * indicates a significant difference between treatment means at p = 0.05. NS indicates no significant difference between treatment means at p = 0.05. Dates of sampling at the V6, V12, and R1 growth stages are indicated by the arrows.
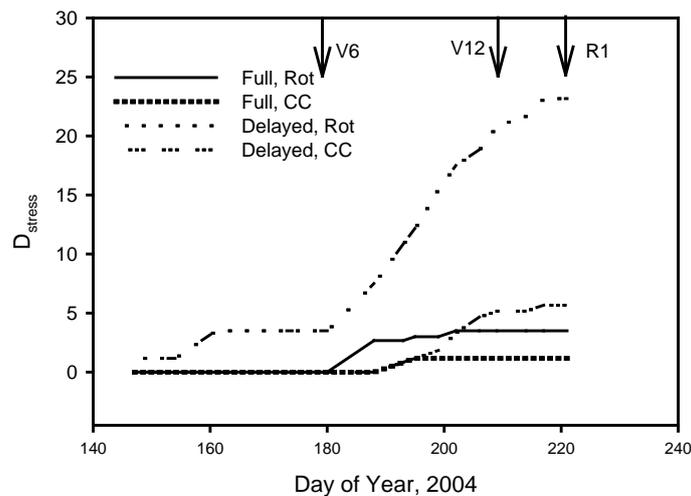
Figure 3. Effects of multi-crop (Rot) and continuous corn (CC) rotations and delayed and full irrigation in 2003 on cumulative days of water stress (D_{stress}) in 2004. Dates of sampling at the V6, V12, and R1 growth stages are indicated by the arrows.
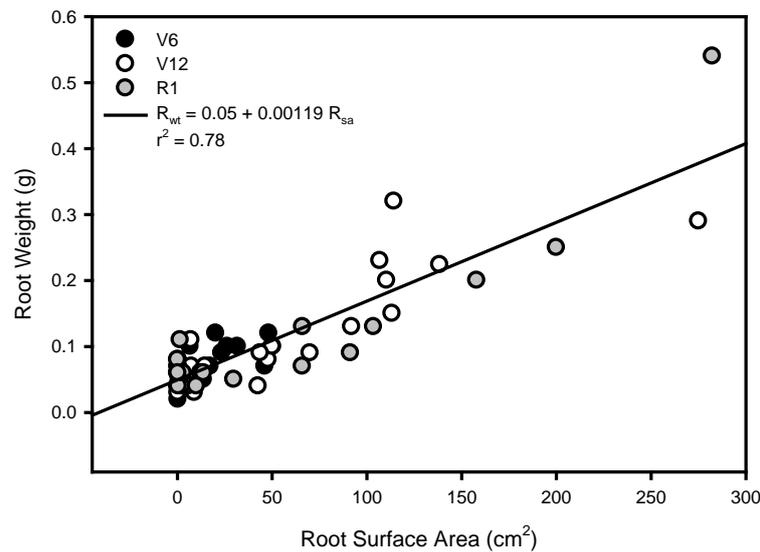
Figure 4. Correlation between measured root surface area and root weight for selected samples at the V6, V12, and R1 growth stages.

Root biomass was linearly correlated with D_{stress} at the V12 and R1 growth stages, but not at the V6 growth stage (**Figure 5**). The slope of the regression of root biomass to D_{stress} at the V6 growth stage was not significantly different (p = 0.22) from zero. The slope of the regression of root biomass to D_{stress} at the V12 growth stage was significantly different (p = 0.02) from the slope at the V6 growth stage and indicated a linear decline of root biomass as stress increased. The slope of the regression of root biomass to D_{stress} at the R1 growth stage was not significantly different (p = 0.75) from the slope at the V12 growth stage, however, the intercepts were different (p < 0.0001) as total root biomass increased with time.

Shoot biomass was linearly correlated with D_{stress} at the V12 and R1 growth stages, but not at the V6 growth stage (**Figure 6**). The slope of the regression of shoot biomass to D_{stress} at the V6 growth stage was not significantly different (p = 0.09) from zero. The slope of the regression of shoot biomass to D_{stress} at the V12 growth stage was significantly different (p = 0.003) from the slope at the V6 growth stage and indicated a linear decline of shoot biomass as stress increased. The slope of the regression of shoot biomass to D_{stress} at the R1 growth stage was not significantly different (p = 0.95) from the slope at the V12 growth stage, however, the intercepts were different (p = 0.004) as total shoot biomass increased with time.

The calculated root:shoot ratio declined as the plant developed (**Figure 7**). The root:shoot ratio for unstressed plants decreased from 0.5 at the V6 growth stage to 0.21 at the V12 growth stage, indicating more shoot growth relative to root growth at later growth stages. The lowest root:shoot ratio occurred at the V12 growth stage relative to the other measurement times. At the V12 growth state the root, shoot ratio was about 0.21 for unstressed plants and the root:shoot ratio increased slightly to 0.27 at the R1 growth stage.

The calculated root:shoot ratio increased as D_{stress} increased at all growth stages. The root:shoot ratio at the V6 growth stage increased from about 0.5 at no stress to 0.63 with 35 days of stress. The root:shoot ratio at the V12 growth stage increased from 0.21 for unstressed plants to 0.47 for plants with 55 days of stress. The root:shoot ratio at the R1 growth stage increased from 0.27 for unstressed plants to 0.47 for plants with 65 days of water stress.

4. Discussion

Many studies have shown that the root:shoot ratio of unstressed plants decreases as the plant develops. The root:shoot ratio of unstressed plants from this study was similar to those found by Allmaras *et al.* [11], and Mengel and Barber [12] for field root studies on corn. In the Allmaras *et al.* [11] study, soil monoliths were excavated and whole root systems were extracted. No growth stage information was given in the paper, but the root:shoot ratio of 0.40 at 59 days after planting was similar to the 0.50 found in this study at the V6 growth stage. The root:shoot ratio of 0.25 at 73 days after planting was similar to the root:shoot ratio of 0.21 found at the V12 growth
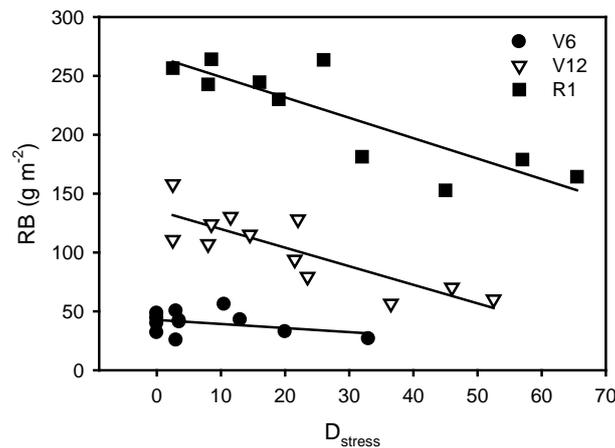
Figure 5. Correlation between root biomass (RB) and days of water stress (D_{stress}) at the V6, V12, and R1 growth stages. Root biomass at the V6 growth stage was RB = 42.7 - 0.34 D_{stress}, $r^2 = 0.14$. Root biomass at the V12 growth stage was RB = 135.6 - 1.58 D_{stress}, $r^2 = 0.69$. Root biomass at the R1 growth stage was RB = 266.4 - 1.73 D_{stress}, $r^2 = 0.74$.
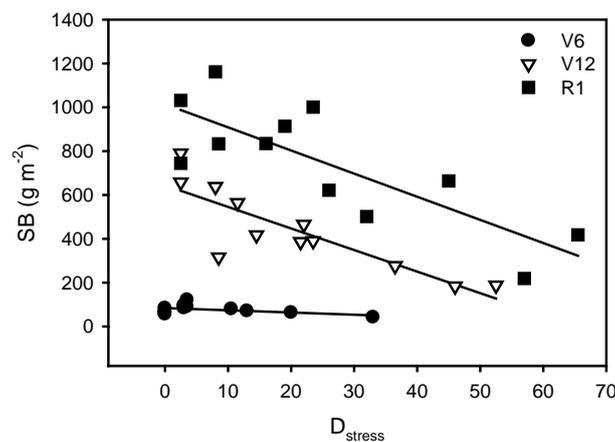
Figure 6. Correlation between shoot biomass (SB) and days of water stress (D_{stress}) at the V6, V12, and R1 growth stages. Shoot biomass at the V6 growth stage was SB = 84.0 - 1.0 D_{stress}, $r^2 = 0.25$. Shoot biomass at the V12 growth stage was SB = 135.6 - 9.8 D_{stress}, $r^2 = 0.72$. Shoot biomass at the R1 growth stage was SB = 1014.0 - 10.6 D_{stress}, $r^2 = 0.64$.

stage in this study. In the Mengel and Barber [12] study, no growth stage information was given except the date of the R1 growth stage. In the first year, the root:shoot ratio was 0.13 at 23 days after planting and 0.15 at 49 days after planting. The root:shoot ratio the second year was 0.64 at 34 days after planting and 0.40 at 42 days after planting. In this study, the root:shoot ratio at the V6 growth stage (40 days after planting) was 0.51. In the Mengel and Barber [12] study, the root:shoot ratio at the R1 growth stage was 0.10 the first year and 0.19 the second year. In this study, the root:shoot ratio was 0.26 at R1 for unstressed plants. Differences in soil temperature, corn hybrid, insect activity, or possible other reasons may account for differences in root:shoot ratios found among the studies.

There are few studies that measured the change of root biomass or shoot biomass under gradients of water deficit stress. Durieux *et al.* [13] measured about two thirds to one half the root weight in the surface 0.6 m from corn plants experiencing visual water stress symptoms than plants that indicated no water stress at the R1 growth stage. In this study, plants with long-term stress conditions, as indicated by days of water contents outside the
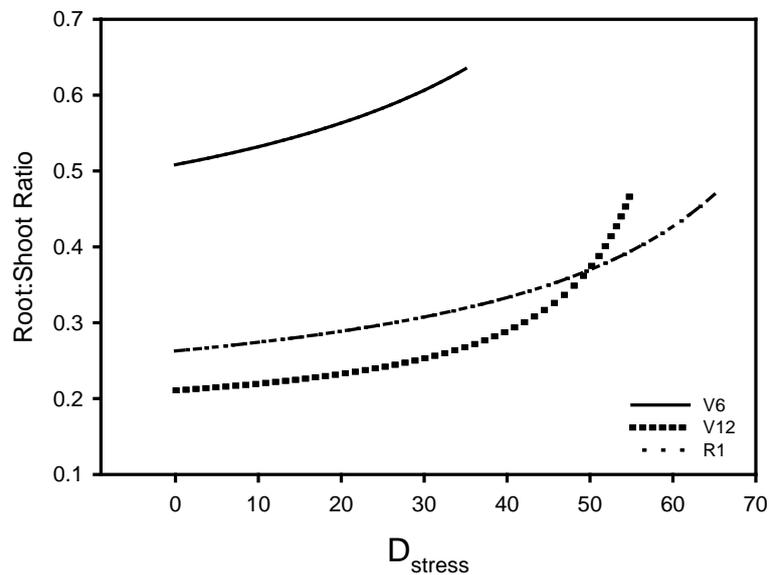
Figure 7. Calculated root:shoot ratios at the V6, V12, and R1 growth stages.

LLWR, had about 60% of the root biomass as unstressed plants, with a linear decline as water stress increased. Using D_{stress} as criteria for adverse soil environmental conditions appears useful for estimating the decline in both root and shoot growth.

Stress, as measured by D_{stress}, affected shoot growth and root growth to different degrees. Shoot growth was more affected by water deficit stress than root growth, leading to an increase in the root:shoot ratio. The percentage change of root:shoot ratio caused by D_{stress} was very similar among the growth stages, except for plants with high D_{stress}. At the V6 growth stage, the root:shoot ratio increased by 5% with 10 D_{stress}, by 11% with 20 D_{stress} and by 20% with 30 D_{stress}. At the V12 growth stage, the root:shoot ratio increased by 4% with 10 D_{stress}, by 10% with 20 D_{stress}, by 18% with 30 D_{stress}, but increased by 70% with 50 D_{stress}. At the R1 growth stage, the root:shoot ratio increased by 4% with 10 D_{stress}, by 9% with 20 D_{stress}, by 16% with 30 D_{stress}, and increased by 39% with 50 D_{stress}. Estimates of root biomass based on shoot biomass measurements may be more accurate if the changing root:shoot ratio caused by water deficit stress were considered.

These results are at odds with those of Kondo *et al*. [4] who showed a decrease of root:shoot ratio as water stress increased. The differences in the studies may lie in the way water stress was estimated. In the Kondo [4] study, water stress was imposed by limiting the amount of irrigation water to replenish water use by the crop. Water content measurements showed that there were differences in soil water matric potential between the two treatments, but the time the plant was under a specific stress was not noted. Using an estimate of the cumulative stress encountered by the plant by a means such as D_{stress} may improve our understanding of the effects of poor environmental conditions on plants.

5. Conclusion

This study showed a linear response of decreasing root growth and shoot growth to water deficit stress as indicated by days of water contents outside the LLWR. Shoot growth was proportionately more affected than root growth, leading to an increased root:shoot ratio as stress increased. The criteria for determining restrictive soil conditions defined by the LLWR may be useful for evaluating improvement or degradation of the soil physical environment caused by soil management. With rain fed agricultural management, soil management schemes that result in a larger LLWR have the potential for growing plants under soil water conditions that are less restrictive than soils with a smaller LLWR. Under irrigated management schemes, care should be taken to maintain soil water contents within the LLWR for the greatest root and shoot growth.

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