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Optimum versus non-limiting water contents for root growth, biomass accumulation, gas exchange and the rate of development of maize (*Zea mays* L.)

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Abstract

Many biological processes vary in a curvilinear manner, reaching a maximum rate at an optimum water content. Optimum conditions commonly extend across a range in water contents, and providing there are no soil-related limitations to biological processes, this range can be referred to as the non-limiting water range (NLWR) of a soil. The rate of a biological process would be expected to be similar in soils with different structure when the water content is in the NLWR and soils are under similar environmental conditions. This range potentially is a useful characteristic to describe the quality of soil structures with respect to a biological process—the larger the range the higher the quality. The distinction between optimum and NLWR has received little attention. The objective of this study was to determine if gas exchange rates, biomass accumulation in shoots and roots, root morphology and rate of development of maize (*Zea mays* L.) vary among soils under optimum soil water contents. Plants were grown to the 12-leaf stage under controlled environment conditions in four soils of different texture, packed to two levels of compaction with two rates of N addition and maintained at three different water contents. The optimum water content, for processes involving both shoots and roots, bracketed an air content of 0.15 for the different soils. The magnitude of the plant responses at optimum water content varied among soils and with relative compaction. Plant responses were largest in the Conestogo (loam soil) and smallest in soils with the highest clay contents. The magnitude of several responses decreased with increasing compaction. In the process of determining the NLWR, it is not appropriate to assume that either shoot or root characteristics are similar in soils of different structure when the water content of each soil is within a range that is optimum for that soil. The largest root and shoot growth that can be achieved at optimum water content across a range of soil conditions must be determined and NLWR determined on soils exhibiting these growth rates. Soils at their optimum water content with root and shoot growth

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that are less than the largest values imply the existence of soil-related limitations and therefore, by definition, have a value of zero for NLWR.

Keywords: Non-limiting water range; Soil structure; Leaf area; Root length; Transpiration; Photosynthesis

1. Introduction

Physiological processes in plants are affected by limited aeration at high soil water contents and by limitations in the supply of water and/or soil resistance to root penetration at low water contents (Letey, 1985; Boone et al., 1987). Within the intervening water contents, there is a range in any soil that is optimum for physiological processes. The processes in this range are independent, or have minimal dependence, on water content. If the processes are not limited by any soil physical conditions, the range can be referred to as the non-limiting water range (NLWR).

The magnitude of the NLWR is defined on the basis of threshold water contents at which limitations to physiological processes begin to be manifested. After rapid drainage has ceased, the water content at the upper end of the range is defined by the threshold water content for the onset of changes in the rates of physiological processes due to inadequate aeration. If this water content is greater than that when rapid drainage has ceased, the latter is taken as the upper limit. The lower limit of the NLWR is the threshold water content at which water supply and/or soil resistance to root penetration begins to limit physiological processes. The limits of the NLWR may vary with species, physiological process and environment (particularly temperature and evaporative demand). The NLWR is distinguished from the least limiting water range (da Silva et al., 1994; da Silva and Kay, 1997), which is focused on extreme response of physiological processes to limiting factors (e.g., cessation of root elongation due to large soil resistance) rather than the onset of response of the processes to these factors.

The magnitude of the NLWR potentially is a very useful way to characterize the quality of soil structure for different biological processes. Although soil structure is strongly influenced by texture, organic carbon (OC) content, tillage and traffic, the impact of structure on physiological processes in a soil is determined by soil water content. Use of the NLWR as a characteristic of soil structure has two particularly appealing aspects. First, it can be directly linked to physiological processes that have a strong influence on yield. This is in contrast to characteristics of soil structure such as bulk density or the distribution in sizes of pores or aggregates. Secondly, it integrates the effects of soil water content and different soil physical characteristics on these physiological processes into a single characteristic. Potential applications of the concept of NLWR include assessing the impact of compaction and tillage of different soils on the early growth of plants and interpreting crop response to spatial variability in texture and OC contents. The concept of a NLWR, with particular emphasis on the lower limit of the range, has also been used by plant physiologists to assess the response of cultivars to drought (Ray and Sinclair, 1997).

The NLWR would be of greatest practical utility as a measure of soil structure if it could be predicted from other readily measurable soil characteristics using pedotransfer functions. However, this first requires an understanding of the response of different physiological processes to changes in water content in various soils of different structure. The direct measurement of the NLWR of a given soil involves determining the relation between the rates of the physiological processes and soil water content and identifying the range in water contents in which the processes are proceeding at their maximum rates. Physiological processes would be expected to proceed at the same rate in soils of different structure assuming that the water content was within the NLWR, other environmental conditions were the same and there were no additional limitations such as availability of nutrients. However, processes will proceed at different rates in soils of different structure if the water contents in the different soils were in their optimum range but one or more limitations persisted across the range in optimum water contents. For instance, Donald et al. (1987) and Alexander and Miller (1991) found that the early growth of maize (*Zea mays* L.) in beds of different sized aggregates varied with aggregate size. Shoot weight, proportion of fine roots, total root length and shoot: root ratio of maize decreased as aggregate diameter increased under two different watering regimes (−5 to −15 kPa and −15 to −25 kPa). These results suggested that water contents in both studies were in the optimum range. Alexander and Miller (1991) found no evidence that nutrition could account for differences in root and shoot growth. Donald et al. (1987) noted that a combination of increased endogenous ethylene in roots in the finest aggregates (due to entrapment by water) and increased mechanical resistance of the coarsest aggregates would be compatible with the observed effects on root morphology. This would imply that limitations persisted in the optimum range in water content and therefore that the NLWR was zero.

The extent to which limitations in physiological processes persist across the range in optimum water contents in different soils is unknown. However, the usefulness of the NLWR as a characteristic of soil structure would need to be reappraised if the observations of Donald et al. (1987) and Alexander and Miller (1991) extended to a broader range of conditions in which soil structure varied due to differences in texture, organic carbon content, tillage or compaction. The NLWR would be of little value as a characteristic of soil structure if it had a value of zero for many soils.

The objective of this study was to determine if gas exchange rates, biomass accumulation in shoots and roots, root morphology, nutrient uptake and rate of development of maize varied among soils at optimum water contents.

2. Materials and methods

Plants were grown under controlled environmental conditions, in soils of different structure that were maintained at different water contents and to which different levels of N were added. Variation in soil structure (particularly related to the textural and structural porosity) was achieved using four different soils that were sieved and packed to two different levels of relative compaction. Air content (volume air-filled pores/total volume of soil) was used as the water variable rather than water potential because of the role of air-filled pores on aeration (Grable and Siemer, 1968; Linn and Doran, 1984). Values of air content (θ_a) were selected to bracket the optimum values for these soils, i.e., to be sufficiently small that soil resistance to penetration or water potential would not be limiting and yet large enough that aeration would not be limiting. Two N treatments were imposed since preliminary studies indicated that differences in physiological processes in these soils might have been linked to N dynamics and N availability.

Samples of soils were collected from the A horizon (0–20 cm) of fields that had been conventionally tilled (ploughed in the fall or spring followed by secondary tillage in the spring) and under either a corn/soybean (*Glycine max* L.)/wheat (*Triticum aestivum* L.) or corn/soybean rotation, for several years. The soils (Table 1) represented a range in texture (70–377 g kg^{-1} clay) and OC contents (13–28 g kg^{-1}) but were similar in pH and mineralogy (dominantly poorly weathered micas). The Brookston was from the Eugene Whalen Experimental Farm, Agriculture and Agri-Food Canada, and was an Orthic Humic Gleysol. The Perth came from a privately owned field on which detailed studies relating plant growth to soil structure have been conducted (da Silva and Kay, 1996). The Conestogo was from the Elora Research Station, University of Guelph, and was a Gleyed Orthic Melanic Brunisol. The Fox was from the Cambridge Research Station, University of Guelph, and was a Brunisolic Grey Brown Luvisol.

Table 1
Selected characteristics of soils

Soil name	Clay (g kg^{-1})	Silt (g kg^{-1})	Sand (g kg^{-1})	Textural class	OC[a] (g kg^{-1})	Total N (g kg^{-1})	BD (Mg m^{-3}) at		P (mg kg^{-1})	K (mg kg^{-1})	pH (mg kg^{-1})
							RC = 0.83[a]	RC = 0.91[a]			
Brookston	377	358	265	Clay loam	18.0	1.54	1.26	1.38	24	206	7.5
Perth	272	485	243	Loam	15.0	0.99	1.28	1.40	13	126	7.7
Conestogo	153	441	407	Loam	28.1	1.61	1.21	1.33	35	146	6.5
Fox	70	162	768	Sandy loam	13.0	0.64	1.41	1.55	55	120	6.9

[a] OC, BD, and RC are organic carbon, bulk density and relative compaction, respectively.

The soils were air-dried, sieved (<6 mm) and selected physical and chemical properties determined (Table 1). Sub-samples were used to characterize soil texture (Gee and Bauder, 1986), OC content (Nelson and Sommers, 1986), plant available P (sodium bicarbonate extractable, Schoenau and Karamanos, 1993), plant available K (ammonium acetate extractable, Simard, 1993), pH (water saturated paste, Hendershot et al., 1993), and total N (Dumas method, McGill and Figueiredo, 1993) using a Leco FP428 auto analyzer. Available micronutrient levels were also determined but not reported. Reference bulk density was determined using a modification of Håkansson (1990) in which about 100 g oven dry equivalent weight of soil was puddled, vacuum saturated, poured into a Rowe cell (7 cm inside diameter), a load of 200 kPa applied until drainage had ceased, the pressure released and bulk density determined after 15 min. Soils were packed to a relative compaction (bulk density/reference bulk density) of 0.83 or 0.91. These values of relative compaction represent values commonly found under conventional till (0.83) and no-till (0.91) across a range of soil textures, OC contents and climates (Kay et al., 1997). A water release curve was determined for each soil (Klute, 1986). Soil resistance to penetration (using a cone penetrometer with a 30° angle, 4 mm basal diameter cone on a recessed shaft) was measured as a function of water content (da Silva and Kay, 1997) on each of the soils at their respective bulk densities.

Nutrients were added to the soil and then the soil packed in 6-L plastic pots. The amount of soil required to fill a volume of 4.18 L in a pot at the required bulk density was determined and nutrients, in the form of dry reagent grade chemicals (NH_4NO_3, $Ca(H_2PO_4)_2 \cdot 2H_2O$, and K_2SO_4) were mixed with the soil for each pot. Nutrients were added to the soil at rates of 2.5 and 1.25 g N per pot, 150 mg P per kg soil and 50 mg K per kg soil (P and K were added on a unit soil weight basis recognizing that these nutrients would be more reactive with the soil than N and the pots contained different weights of soil). Soils were then packed to the required bulk density in 3 cm depth increments in pots. Supplementary tests showed little radial or vertical variation in bulk density when this technique was used. Pots were wetted from the base to saturation with distilled water and submerged for 1–3 days (depending on texture). Pots were then removed from the containers in which they were saturated, covered with plastic to prevent evaporation, and allowed to drain until there was no further water loss. Equilibrium water content (normally achieved with 2 days) was about equal to the water content at a θ_a of 0.10 in the coarse-textured soils. Pots were then transferred to growth cabinets and evaporation allowed to continue until the desired air contents were established.

A short-season maize hybrid Pioneer 3902 was used in this experiment. Seeds were sterilized in a 1:1 bleach to water solution, stirred for 15 min to sterilize, rinsed thoroughly with de-ionized water, and then soaked in an aerated beaker for 48 h for pre-germination. Prior to sowing, seeds were immersed in a 2% solution of Benelate (Dupont Canada Inc.) for 20 min to prevent Fusarium infection. Three pre-geminated seeds were planted in each pot and seedlings were thinned to one plant at the three-leaf stage. Three hundred gram of sand was used to cover the pot surface to minimize evaporation and soil crusting once the desired water contents had been achieved.

The experiment was conducted in controlled-environment growth cabinets with 26 °C/16 °C day/night temperature, a 16-h photoperiod, and a relative humidity of approximately 75%. The photosynthetic photon flux density was maintained at approximately 650 μmol m^{-2} s^{-1} at the top of the canopy, with a mixture of 'cool white' fluorescent tubes and 'inside frost' tungsten bulbs. Air temperature in each growth cabinet was continuously monitored with thermocouples placed close to the whorls of four plants. The experiment was laid out as a randomized complete block design with four soils (S), two levels of relative compaction (RC), two levels of nitrogen addition (N), three air contents (θ_a) and three replications (R). Each replication of the θ_a treatment was contained in one growth cabinet in which the 16 treatments (4S*2N*2RC) were randomly assigned.

Pots were watered twice a week at the beginning of the growing period and increased in frequency to daily measurements by the 12-leaf stage. Weights were determined before the end of the light period and water added to return the water content to that equivalent to an air content of 0.10, 0.15 and 0.20. This timing maximized the opportunity for water redistribution in the pots prior to the start of the next light period. The amount of water to be added was calculated from pot weight, weight of oven dry soil in each pot, volume of soil, density of water and estimated fresh weight of plants. Plant fresh weight at different leaf stages and days after sowing was estimated according to previous maize physiological studies (Tollenaar and Migus, 1984; Tollenaar, 1989, 1999).

Days elapsed from emergence to the 12-leaf stage (i.e., tip of the 12th leaf was visible in the whorl) was taken as a measure of the rate of plant development. Once the plants reached the 12-leaf stage, pots were completely enclosed in white plastic bags and the bags tightened around the base of the stem to prevent evaporation. Rates of transpiration and carbon exchange were measured daily thereafter for 7 days. Transpiration was measured on a whole plant basis and on a unit leaf area basis (in conjunction with carbon exchange measurements). Whole plant transpiration measurements were based on weight difference on successive days minus the plant weight increase. Leaf carbon exchange rate (CER) at 650 μmol m^{-2} s^{-1} was measured using a portable, open-flow gas exchange system LI-6400 (LI-COR Inc., Lincoln, NE). Measurements were taken on the youngest, fully expanded leaf at the middle of the light period daily for all treatments. Exchange of CO_2 between the leaf sample and the measuring chamber air was measured for a 6 cm^2 area of the leaf, excluding the midrib. The flow rate of air through the chamber and sample side of the infrared gas analyzer were set to the 500 μmol s^{-1} in order to minimize the system response time to a change in CER. The CO_2 concentration of the intake air was maintained at 350 ppm using the 6400–01 CO_2 injector (LI-COR Inc. Lincoln, NE). Leaf temperature was maintained at 26 ± 1 °C by Peltier thermoelectric coolers. All CER and leaf transpiration rates were calculated by the LI-6400 operating software following the method of von Caemmerer and Farquhar (1981).

After completion of gas exchange measurements, above-ground plant material was harvested, leaves and stems separated and fresh weights determined, leaf area measured, shoot tissue dried (80 °C), ground (to pass 1-mm sieve) and the concentration of major and minor nutrients in the leaves determined. Tissue concentrations of N, P, K Ca and Mg were determined after digestion with sulfuric acid and hydrogen peroxide (Thomas et al., 1967). Concentrations of N and P were determined colorimetrically using a Technicon auto analyzer. Tissue concentrations of Zn, Cu, B and Mn were determined by atomic adsorption spectrophotometry after ashing the plant material for 16 h at 425 °C and dissolving the residue in 2N HCl.

Roots were separated from soil by soaking for 24 h and then carefully separating roots from soil and other residues using gentle washing under a flow of swirling water. Fresh root mass was determined and then the roots distributed on shallow trays in water, placed on a scanner and morphology of the roots determined using WinRHIZO For Root Morphology and Architecture Measurement (Regent Instruments Inc.). After morphological determinations, roots were dried (80 °C) and weighed.

Fresh weight of the harvested shoots and roots were used to update plant weights that had been calculated through the growing period as previously described. Any errors in these calculations would be expected to increase as the plants increased in size. These analyses showed that minimum air content treatments of 0.10, 0.15 and 0.20 were actually 0.11, 0.16 and 0.20 through the 7 days measurement period.

To test the significance of treatments and their interactions an analysis of variance was conducted using the Proc Mixed/GLM procedures of SAS/STAT software (SAS Institute, 1999). The statistical model was a factorial design. The procedure was initially run with the treatment terms and all possible interaction terms. Non-significant interaction terms were then progressively removed and the model rerun. Multiple comparisons on interactions as well as main effects were performed using the least squares mean statement. Statistically significant relations were identified at $P \leq 0.05$.

3. Results and discussion

3.1. Descriptive statistics

Descriptive statistics for the means of each measured variable are given in Table 2. The magnitude of the overall variability in measured plant characteristics that was introduced by the treatments was assessed using the coefficient of variability (CV) of the means of the reps.

Table 2
Descriptive statistics for means of reps of selected shoot and root variables and leaf tissue nutrient concentrations ($N = 48$)

Variable	Mean	Minimum	Maximum	CV (%)
Shoot weight (g plant^{-1})	24.1	14.5	34.7	20
Leaf area (cm^2 plant^{-1})	2533	1764	3326	15
C exchange rate (μmol m^{-2} s^{-1})	17.9	15.4	21.4	8
Leaf transpiration rate (mmol m^{-2} s^{-1})	2.2	1.7	2.7	10
Whole plant transpiration rate (g plant^{-1} day^{-1})	227	81	453	32
Plant development (days to 12-leaf stage)	30.7	26.7	35.3	8
Root weight (g plant^{-1})	6.1	2.8	9.7	27
Shoot:root ratio	4.4	2.4	8.4	31
Total root length (cm plant^{-1})	18557	6775	33366	36
Average root diameter (mm)	0.073	0.061	0.091	8
Length 1 (cm plant^{-1})	9895	3580	18793	41
Length 2 (cm plant^{-1})	5750	2186	9877	33
Length 3 (cm plant^{-1})	2914	1010	4697	30
Prop. 1	0.52	0.40	0.62	8
Prop. 2	0.31	0.26	0.39	10
Prop. 3	0.16	0.11	0.22	12
N (%)	3.2	1.6	3.9	14
P (%)	0.23	0.15	0.3	13
K (%)	2.1	1.4	2.6	15
Ca (%)	1.0	0.5	1.4	20
Mg (%)	0.4	0.1	0.5	22
Cu (mg kg^{-1})	10.2	6.0	13.5	19
Zn (mg kg^{-1})	52.1	16	174	63
Mn (mg kg^{-1})	56	20	92	31
B (mg kg^{-1})	17	14	23	11

Note: CV is coefficient of variability. Length 1, 2 and 3 are the lengths of roots with diameters <0.5, 0.5–1.0 and >1.0 mm, respectively. Prop. 1, 2 and 3 are the lengths of roots with diameters <0.5, 0.5–1.0 and >1.0 mm as a proportion of total root length, respectively.

Root parameters generally exhibited more variation due to treatments than shoot parameters, including leaf nutrient concentrations (Table 2). The total length of roots, the length of roots in different diameter size classes and root dry weight were the most responsive root parameters (average CV = 33%). These parameters were also strongly correlated with one another. However, average root diameter was much less responsive (CV = 8%) and was less strongly correlated with the preceding root parameters.

Shoot parameters with the most variability across treatments were whole plant transpiration, shoot weight and leaf area (average CV = 22%). Not surprisingly, these variables were also strongly correlated. Rates of carbon exchange, leaf transpiration and plant development were less strongly influenced by treatment variables (average CV = 9%).

With the exception of Zn, variations in leaf tissue nutrients across treatments were similar and had an average CV of 18%. The high CV for Zn (63%) reflected the unusually high concentrations found in all treatments with the Conestogo soil. The high tissue concentrations reflected concentration of extractable Zn in the soil, which was nearly an order of magnitude larger than the concentrations in the other soils (data not shown).

Minimum concentrations of nutrients in leaf tissue were above deficiency levels for all nutrients with the possible exception of N and P (Jones et al., 1990). However, the possibility of nutrient deficiency at minimum concentrations for both of these nutrients is small. Supplemental studies indicated that plant characteristics were only adversely affected when N concentration was <1.2% under the conditions of this study (Novosad and Kay, in preparation). There was a weak but significant positive relation between root length and total amount of P in leaves, reflecting reduced accessibility of P in soils with restricted root systems (Lipiec and Stępniewski, 1995). However, there was no correlation between shoot dry weight and

Table 3a
ANOVA indicating significance level of the main and interaction effects on root variables

Source	Root dry weight	Total root length	Average diameter	Length[a]			Prop.[b]		
				1	2	3	1	2	3
θ_a	0.004	0.0002	ns	0.004	<0.0001	<0.0001	0.02	ns	0.05
Soil	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
RC	0.01	0.04	0.03	0.005	ns	ns	0.0002	0.0002	0.02
N	0.04	ns	ns	ns	ns	ns	0.02	<0.0001	ns
θ_a*Soil	ns	ns	ns	ns	ns	ns	ns	0.0005	ns
θ_a*RC	ns	ns	ns	ns	ns	ns	ns	ns	ns
θ_a*N	ns	ns	ns	ns	ns	ns	ns	ns	ns
Soil*RC	ns	ns	ns	ns	ns	ns	ns	<0.0001	ns
Soil*N	ns	ns	ns	ns	ns	ns	ns	ns	ns
RC*N	ns	ns	ns	ns	ns	ns	ns	ns	ns
θ_a*Soil*RC	ns	ns	ns	ns	ns	ns	ns	ns	ns
θ_a*Soil*N	ns	ns	ns	ns	ns	ns	ns	ns	ns
θ_a*RC*N	ns	ns	ns	ns	ns	ns	ns	ns	ns
Soil*RC*N	ns	ns	ns	ns	ns	ns	ns	ns	ns
θ_a*Soil*RC*N	ns	ns	ns	ns	ns	ns	ns	ns	ns

ns indicates the effect is not significant at $P < 0.05$.
[a] Length 1, 2 and 3 are the lengths of roots with diameters <0.5, 0.5–1.0 and >1.0 mm, respectively.
[b] Prop. 1, 2 and 3 are the lengths of roots with diameters <0.5, 0.5–1.0 and >1.0 mm as a proportion of total root length, respectively.

P concentration, suggesting that P concentrations did not curtail shoot biomass accumulation.

3.2. Analysis of variance (ANOVA)

The ANOVA of root- and shoot-related characteristics is given in Table 3. All of the root-related characteristics were influenced by soil (Table 3a). Air content and compaction affected most root characteristics. The N treatment affected only a small number of root characteristics. Root characteristics were generally not affected by treatment interaction terms. Most shoot variables were significantly affected by θ_a, soil and RC (Table 3b). Nitrogen affected only shoot dry weight, whole plant transpiration and plant development. Shoot characteristics were not consis-

Table 3b
ANOVA indicating significance level of the main and interaction effects on shoot variables

Source	Leaf area	Shoot dry weight	Whole plant transpiration	Leaf transpiration	Carbon exchange	Plant development	Shoot:root ratio
θ_a	<0.0001	<0.0001	0.0001	0.001	<0.0001	<0.0001	<0.0001
Soil	<0.0001	<0.0001	<0.0001	0.03	<0.0001	<0.0001	<0.0001
RC	0.004	<0.0001	<0.0001	ns	0.001	0.002	0.04
N	ns	0.001	0.001	ns	ns	0.006	ns
θ_a*Soil	ns	ns	ns	ns	ns	ns	0.002
θ_a*RC	0.0009	ns	<0.003	ns	ns	0.02	ns
θ_a*N	ns	ns	ns	ns	ns	ns	ns
Soil*RC	ns	0.04	ns	ns	ns	ns	ns
Soil*N	ns	ns	ns	ns	ns	ns	ns
RC*N	ns	ns	ns	ns	ns	ns	ns
θ_a*Soil *RC	ns	ns	ns	ns	ns	ns	ns
θ_a*Soil*N	ns	ns	ns	ns	ns	ns	ns
θ_a*RC*N	ns	ns	ns	ns	ns	ns	ns
Soil*RC*N	ns	ns	ns	ns	ns	ns	ns
θ_a*Soil*RC*N	ns	ns	ns	ns	ns	ns	ns

ns indicates the effect is not significant at $P < 0.05$.

Table 4
Means of selected shoot and root parameters as affected by treatment variables (no treatment interaction effects)

Treatment	Carbon exchange rate (μmol m^{-2} s^{-1})	Leaf transpiration (mmol m^{-2} s^{-1})	Total root length (cm)	Root dry weight (g $plant^{-1}$)	Length[a] (cm)			Average diameter (cm)	Prop.[b]	
					1	2	3		1	3
θ_a										
0.10	18.1^{a}	2.3^{a}	15547^{b}	5.4^{a}	8589^{b}	4701^{b}	2273^{b}	0.0718^{b}	0.54^{a}	0.15^{b}
0.15	18.3^{a}	2.3^{a}	20443^{a}	6.5^{b}	10857^{a}	6324^{a}	3263^{a}	0.073^{ab}	0.52^{ab}	0.16^{ab}
0.20	17.1^{b}	2.1^{b}	19660^{a}	6.2^{b}	10248^{a}	6223^{a}	3189^{a}	0.075^{a}	0.51^{b}	0.17^{a}
Clay content										
70	18.1^{b}	2.2^{ab}	16313^{b}	5.5^{b}	8320^{b}	5175^{a}	2826^{b}	0.076^{a}	0.50^{b}	0.18^{a}
153	19.1^{a}	2.3^{a}	27692^{a}	8.1^{a}	15730^{a}	8240^{b}	3738^{a}	0.066^{b}	0.57^{a}	0.13^{b}
272	17.1^{c}	2.2^{b}	16421^{b}	5.6^{b}	8462^{b}	5223^{a}	2735^{b}	0.075^{a}	0.51^{b}	0.17^{a}
377	17.1^{c}	2.1^{b}	13774^{b}	5.00^{b}	7080^{b}	4361^{c}	2333^{b}	0.076^{a}	0.51^{b}	0.17^{a}
RC										
0.83	18.3^{a}	ns	19601^{a}	6.4^{a}	10706^{a}	ns	ns	0.071^{b}	0.54^{a}	0.16^{b}
0.91	17.4^{b}		17483^{b}	5.7^{b}	9089^{b}			0.074^{a}	0.51^{b}	0.17^{a}
N										
Low				6.3^{a}					0.53^{a}	
High	ns	ns	ns	5.8^{b}	ns	ns	ns	ns	0.51^{b}	ns

ns indicates the effect is not significant at $P < 0.05$; means followed by different superscript letters indicate significant difference at $P \leq 0.05$ within a treatment for a characteristic.
[a] Length 1, 2 and 3 are the lengths of roots with diameters <0.5, 0.5–1.0 and >1.0 mm, respectively.
[b] Prop. 1 and 3 are the lengths of roots with diameters <0.5, 0.5–1.0 and >1.0 mm as a proportion of total root length, respectively.

tently influenced by any single treatment interaction term although the θ_a*RC term was significant most often. Treatment means of shoot and root variables that were not significantly affected by treatment interactions are given in Table 4.

3.3. Optimum air content

A significant increase in root weight and root length characteristics occurred as θ_a increased from 0.10 to 0.15 (Table 4). None of the root characteristics showed a significant change as θ_a increased from 0.15 to 0.20.

Shoot characteristics exhibited less sensitivity to θ_a than the root characteristics at low θ_a, and were generally similar in magnitude at θ_a of 0.10 and 0.15. However, in contrast to the root characteristics, the magnitude of most shoot characteristics declined as θ_a increased from 0.15 to 0.20. These trends were most obvious for CER and leaf transpiration (Table 4).

The shoot:root (S:R) ratio tended to decline with increasing θ_a as a consequence of root weight increasing as θ_a increased from 0.10 to 0.15 (Table 4) and shoot dry weight decreasing as θ_a increased from 0.15 to 0.20. The S:R ratio was influenced by the θ_a*soil interaction term (Table 3b), because of the large S:R ratio in the Fox and Brookston soils at θ_a of 0.10. The largest decrease in S:R ratio occurred between θ_a of 0.10 and 0.15 and was primarily due to the increase in root weight.

The increase in root weight and the decline in S:R ratio as θ_a increased from 0.10 to 0.15 is consistent with aeration limitations at $\theta_a = 0.10$. Roots have been reported to be more sensitive to anaerobic conditions than shoots (Meek and Stolzy, 1978; Bennicelli et al., 1998) with anaerobic conditions resulting in decreased root growth (Bennicelli et al., 1998), reduced root numbers (Lizaso and Ritchie, 1997), increased root branching (de Wit, 1978) and increased S:R ratio (Huang et al., 1994).

Differences in the response of shoots and roots to increasing θ_a suggest that the range in optimum water content may be different for different plant organs. However, since the optimum range in water content for both root and shoot characteristics encompassed $\theta_a = 0.15$ (Table 4), this value was used as the optimum water content when root characteristics were related to shoot characteristics.

3.4. Effects of soil, relative compaction and N at $\theta_a = 0.15$

The effect of soil, RC and N treatment at $\theta_a = 0.15$ on plant parameters was assessed from the statistical analysis of the entire data set when no interaction term involved θ_a. In the case of variables significantly influenced by interaction terms involving θ_a, an ANOVA was run for the data at $\theta_a = 0.15$ only (Table 5).

Soils were primarily distinguished on the basis of clay content and to a lesser degree on the basis of OC content. Shoot and root variables were greatest in the Conestogo soil which had a clay content of 153 g kg^{-1} and the largest OC content (28.1 g kg^{-1}). Root characteristics varied little in the other soils (Table 4). Shoot characteristics tended to be greater in the Fox soil than the Perth and Brookston soils. Shoot weight was influenced by the soil*compaction interaction term (Table 3b) due to a greater difference between RC in the Fox than in the other soils. The decline in shoot weight with increasing clay content at $\theta_a = 0.15$ was greatest at the smaller relative compaction.

Increasing RC decreased the magnitude of many plant variables although the impacts were most consistent on root characteristics. Increased compaction reduced total root length, root dry weight, the length of roots <0.5 mm diameter, and the proportion of the total root length made up of roots <0.5 mm diameter by 11, 10, 15, 6%, respectively (Table 4). The response of average root diameter and the proportion of the total length of roots with a diameter >1.0 mm increased by 4 and 9%, respectively. The CER decreased by 4% as RC increased (Table 4). Leaf area, whole plant transpiration and plant development decreased by 7, 23, and 5%, respectively, as RC increased (Table 5). All of the trends in root and shoot characteristics were consistent with previously described compaction-induced increases in soil resistance to root penetration and concomitant effects on shoot characteristics (Lipiec et al., 1996; Young et al., 1997; Passioura, 2002).

The nitrogen treatment had a small but significant effect on most shoot characteristics but on fewer root characteristics (Table 3). The cause for adverse effects of the larger rate of N addition (Tables 4 and 5) was not identified.

Table 5
Means of selected shoot parameters as affected by treatment variables at $\theta_a = 0.15$ (no treatment interaction effects)

Treatment[a]	Leaf area (cm^2)	Whole plant transpiration[a] (g $plant^{-1}$ day^{-1})	Plant development[a] (days)
Clay content			
70	2753[a]	230[b]	28.8[b]
153	2948[a]	282[a]	28.5[b]
272	2485[b]	202[bc]	31.0[a]
377	2532[b]	192[c]	31.3[a]
RC			
0.83	2776[a]	256[a]	29.2[b]
0.91	2582[b]	198[b]	30.6[a]
N			
Low	2756[a]	247[a]	29.3[b]
High	2602[b]	206[b]	30.5[a]

[a] Means followed by different superscript letters indicate significant difference at $P \leq 0.05$ within a treatment for a characteristic.

3.5. Root–shoot relations in the $\theta_a = 0.15$ treatment

Experimental treatments were all soil-related and therefore any limitations on physiological processes would have been expected to be manifested in root characteristics. Shoot characteristics could have also responded to soil conditions through a variety of mechanisms that include hormone-based signals generated in the roots (Passioura, 2002). Whole plant transpiration and root length were the characteristics showing most variation due to treatment (Table 2). A strong relation existed between these characteristics at $\theta_a = 0.15$ and this relation was similar to that between leaf area and root length (Fig. 1). Although the levels of RC are not identified in Fig. 1, the largest value of a shoot characteristic for a given soil was in the least compacted soil (RC = 0.83). Leaf transpiration (on a unit area basis) was not correlated to root length implying that the relation between whole plant transpiration and root length was largely due to the relation between leaf area and root length. Similar relations were obtained if root weight or the length of roots with diameters <0.5 mm were used as the independent variable instead of root length. Neither the length of roots with diameters <0.5 mm as a proportion of the total root length or average root diameter were correlated with whole plant transpiration or with leaf area. Relations between CER and root length were similar to those between shoot weight and root length

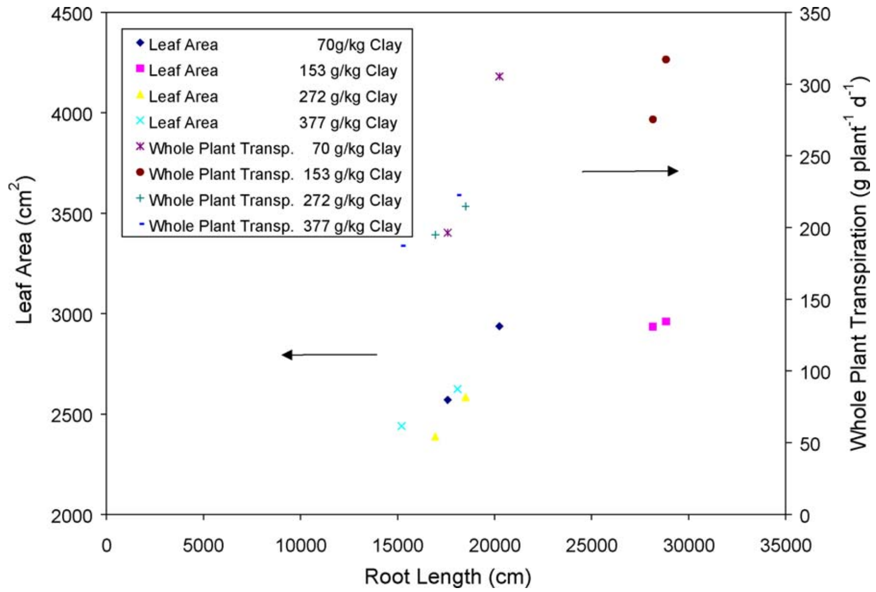

Fig. 1. Variation in whole plant transpiration and leaf area with root length in soils with different clay contents and relative compaction in the air content treatment of 0.15 (averaged across N treatments).

(Fig. 2) and followed exactly the same pattern as in Fig. 1. Rate of plant development (days to 12-leaf stage) followed a similar pattern and showed a significant decline with increasing root length.

The range in magnitude of root and shoot characteristics (Figs. 1 and 2) suggested that physiological processes were limited in some of the soils. The largest root length occurred in the

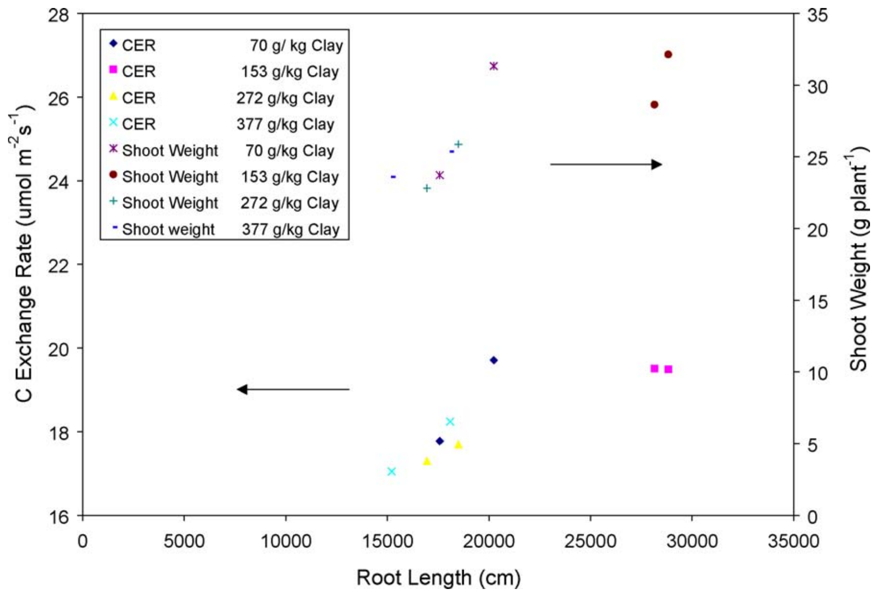

Fig. 2. Variation in leaf carbon exchange rates and shoot dry weight with root length in soils with different clay contents and relative compaction in the air content treatment of 0.15 (averaged across N treatments).

Conestogo soil whereas the largest shoot characteristics were associated with Conestogo (both values of RC) and Fox soils (RC = 0.83) (Figs. 1 and 2). The shoot characteristics declined as root length decreased from about 20,250 cm. A ratio of root length to leaf area (Lipiec et al., 1996; Lizaso and Ritchie, 1997) was not significantly different among Fox (6.9, 6.8), Perth (7.1, 7.1) and Brookston (6.9, 6.3) soils at an RC of 0.83 and 0.91, respectively, but significantly smaller than that of Conestogo soil (9.8, 9.6).

3.6. Optimum versus non-limiting water contents

In comparison with the Conestogo soil, processes associated with the shoot were apparently limited by one or more factors at $\theta_a = 0.15$ in the Perth and Brookston soils at both levels of RC and in the Fox at RC = 0.91. The existence of a limitation means either that the NLWR fell outside of $\theta_a = 0.15$ or that the NLWR was zero on these soils. There was no evidence that values of θ_a different from 0.15 would have resulted shoot or root characteristics of these soils increasing to those of the Conestogo soil. Consequently, we assume that the NLWR of these soils was zero.

Limitations to physiological processes at $\theta_a = 0.15$ may have been due to inadequate supplies of nutrients, oxygen, water or high soil resistance to root penetration. There were no significant effects of either soil or RC on concentrations of N and P at $\theta_a = 0.15$ and there was no additional evidence that small values root and shoot characteristics were caused by nutrient limitations. Although studies on net N mineralization in these soils (Drury et al., 2003) would suggest less likelihood of O_2 limitations in the Brookston than in the Conestogo soil, an inadequate supply of O_2 in the finer textured soils cannot be completely discounted. Soil water potential in all treatments was always >-160 kPa although the water supply may have been limited by low unsaturated hydraulic conductivity in the Fox soil. Maximum soil resistance (determined from minimum daily water content after reaching the 12-leaf stage) reached 4371 kPa in the Brookston soil at RC = 0.91. The corresponding soil resistance in the Conestogo soil was 874 kPa at RC = 0.91, respectively. The relatively large soil resistance in the finer textured soils at $\theta_a = 0.15$ could have had a negative impact on physiological processes in both roots and shoots (Passioura, 2002). A zero value of NLWR of these soils implies that limitations due to aeration may have been progressively replaced by limitations due to soil resistance as θ_a increased from 0.10 to 0.15 and limitations due to soil resistance and/or water supply became more severe as θ_a increased from 0.15 to 0.20.

Irrespective of the nature of limitations to root and shoot growth in the finer textured soils, it is obvious that caution should be exercised in using optimum water contents for a given soil to describe non-limiting water contents. Soils that have processes operating at less than the maximum rate at optimum water content must, by definition, have a NLWR of zero. Six of the eight-soil/RC combinations in this study had a NLWR of zero for root growth.

Further studies are necessary to determine the applicability of the results of this study to field conditions. Soil properties in the root zone, particularly compaction and water content, are more spatially variable in the field. This may lead to limiting conditions of different magnitude in different parts of the rooting system, resulting in multiple signaling (Tardieu, 1994) and modified shoot response (Masle, 1998; Montagu et al., 2001). In addition, light levels used in the controlled environment chambers were low compared to incident light levels in the field at noon during summer months. Although results of gas exchange measurements may have been influenced by the relatively low light levels, daily cumulative photosynthetic photon flux density was approximately 90% of that encountered under field conditions. Dry matter accumulation and grain yield of maize grown indoors under relatively low light levels can be greater than those grown under field conditions (Tollenaar and Migus, 1984). However, the interaction between light levels and shoot response, particularly to high soil resistance to root penetration has not been well defined.

4. Conclusions

Root and shoot characteristics varied with soil air content, soil and relative compaction. The optimum range in water contents encompassed the $\theta_a = 0.15$ treatment for both roots and shoots under the conditions of this study. However, gas exchange rates, biomass accumulation, root morphology and plant development varied with soil and RC at optimum water content. Soils with highest clay contents showed the greatest decrease in root and shoot characteristics relative to those in the Conestogo soil. Adverse soil conditions encountered by the roots resulted in concomitant changes in shoot characteristics, once a critical decrease in root characteristics had occurred. Causal mechanisms were not identified. However, the persistence of one or more limiting factors at optimum water content would, by definition, result in NLWR having a value of zero. Identification of the limiting factors and subsequent development of ways to remove these limitations have important ramifications for improving the physical quality of soils for crop production and thereby increasing productivity.

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