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DEPARTMENT OF HORTICULTURE

THE INFLUENCE OF ROOTING DEPTH ON NITROGEN UPTAKE IN ZEA MAYS L.  
UNDER OPTIMUM AND N-DEFICIENT CONDITIONS

CHELSEA A. SUTHERLAND  
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Reviewed and approved\* by the following:

Jonathan P. Lynch  
Professor of Plant Nutrition  
Thesis Supervisor

Kathleen Kelley  
Associate Professor of Horticulture  
Honors Adviser

\* Signatures are on file in the Schreyer Honors College.

### Abstract

A well developed root system is a necessity for the acquisition of nutrients. Nitrogen (N) is predominantly found in water soluble chemical compounds that are highly mobile and expected to leach to deeper soil layers in the course of the cropping season. The purpose of this study was to evaluate the importance of root architectural traits of maize genotypes (*Zea mays* L.) under optimum and N-deficient conditions. It was hypothesized that deep rooted plants would be better able to acquire N and thus have enhanced performance. Maize inbred lines with contrasting root architecture: three genotypes with a shallow rooting system and 4 with a deep rooting system were sown in a randomized complete split-plot design. Root systems were measured destructively at six weeks after planting, at flowering, and at physiological maturity. Nitrogen acquisition by the plant was monitored over time by measuring leaf nitrogen content and SPAD as a proxy-measure for leaf chlorophyll. Furthermore grain yield was measured. The results indicated that steeper root angles produce deeper roots, and root angles, depth and branching are negatively correlated. Performance of both shallow and steep genotypes was similar under both conditions, as shallow genotypes responded to N deficient conditions by producing steeper root angles over time. These structural alterations facilitated N acquisition and minimized the differences between rooting types.

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## Introduction

### *Nitrogen as a macronutrient*

Nitrogen (N) is arguably the most important macronutrient for plant growth and yield. It is a component of essential plant molecules, including amino acids and chlorophyll. Moreover, it also stimulates root growth and the uptake of other nutrients, and is required in high amounts (Hofman and Cleemput, 2004). Depending on the crop species and the N content of the soil, N requirements may vary from about 100-400 kg N ha<sup>-1</sup> between growing seasons (Hofman and Cleemput, 2004). N deficiency results in stunted plants that mature earlier, resulting in a truncated photosynthetic period and a decreased yield. (Hofman and Cleemput, 2004, Rajcan and Tollenaar, 1999a). It is estimated that the potential crop yield for a given piece of land has doubled in the past century due to overcoming N deficiencies with fertilizer (Erisman, et al., 2008). In Sub-Saharan Africa, N deficiency is common and fertilizers are rare and extremely expensive, both when compared to prices elsewhere in the world and in relation to the farmers' meager salaries. In these regions, maize yields are known to double or quadruple when adequate N supplies are available (Sanchez, 2002).

Nitrogen has a history of very intensive use in industrialized countries. Between 1,750 and 7,000 kg N ha<sup>-1</sup> is typically present in the plow layer, though it is typical for less than 5% to be actually available (Hofman and Cleemput, 2004). Industrial-scale production of usable N was made possible by the introduction of the Haber-Bosch process a century ago. The Haber-Bosch process was cheaper, easier, and more secure than other methods of N fixation or acquisition and quickly became popular (Erisman, et al., 2008). Anhydrous ammonia has been the dominant form of N fertilizer used since its commercial introduction in the 1950s (David, et al., 2009). Today, ammonium (NH<sub>4</sub><sup>+</sup>), nitrate (NO<sub>3</sub><sup>-</sup>), and urea (CO(NH<sub>2</sub>)<sub>2</sub>) are the most common forms of

inorganic N fertilizer, and their effectiveness is based on soil properties and ion exchange (Hofman and Cleemput, 2004). Worldwide production of N fertilizer has surpassed 108 million tonnes per year (*IFADATA*, 2010). Such a tremendous N output requires a huge monetary investment. Globally, fertilizer production consumes about 1.2% of the world's energy, 92.5% of which is linked solely to N (Kongshaug, 1998). In addition to this huge energy requirement, there are also costs for shipping raw materials, packaging the final product, safely shipping fertilizer from industrial sites to agricultural lands, and applying it to the fields. This is a tremendous cost for fertilizer that may later be lost from agricultural fields and pollute the environment, rather than get utilized by crops.

Fertilizer use has increased drastically since the mid twentieth century. Before 1945, fertilizer use was negligible, but it has nearly doubled every ten years since the then (McIsaac and Hu, 2004). This increased fertilizer use first brought incredible yield benefits. Today, incredible amounts of fertilizers are applied to agricultural fields each year, but less than half, perhaps no more than one third, of applied N is actually taken up and used by plants (Glass, 2003 and Tilman, et al., 2002). When initial N application sixty years ago resulted in drastic yield increases, excited farmers wished to maintain this trend. Rates of fertilizer application continue to rise as farmers wish to increase or at least ensure a decent harvest, at the expense of cheap fertilizers. As a result, historical increases in fertilizer application have not been met with comparable yield increases, and approximately \$15.9 billion is wasted each year as excess fertilizer (Raun and Johnson, 1999). Plants simply cannot acquire all of the N that is added to the soil.

*Adverse effects of nitrogen*

Instead of being used for additional food production, a significant amount of N now runs off of fields to pollute nearby ecosystems. During the past 50 years, the net N input to water sources draining from agricultural fields increased proportionately to the amount of fertilizer applied (McIsaac and Hu, 2004). High levels of N fertilizer use have led to the eutrophication and anoxia of downstream estuaries. Research has indicated that a reduction in the use of fertilizers on watershed agricultural lands must be accompanied by enhanced denitrification to repair these systems (Brush, 2009).

In addition to the disturbance of ecosystems through water pollution, N causes negative disruptions within the atmosphere. Unreactive  $N_2$  is a major constituent of atmospheric gas, but N forms used in fertilizer are reactive molecules. Only 10-40% of N inputs are denitrified back to atmospheric  $N_2$ , and nitric oxide (NO) and ammonia ( $NH_3$ ) emissions are now five times their pre-industrial rates (Galloway, et al., 2004). Atmospheric ammonia exists in equilibrium with the high volumes of applied ammonium fertilizer (Hofman and Cleemput, 2004). The fertilizer production process also causes 1.2% of total Greenhouse gas emissions (Kongshaug, 1998). All of these factors have potential negative impacts on the atmosphere, climate, environment, and human populations.

*Green Revolutions for increased yield*

A major Green Revolution took place in the mid twentieth century. During this time, a boom of agricultural advances allowed a drastic increase in the extensive production of cereal crops. Genetic improvements and new industrial production methods for mass quantities of mineral fertilizer enabled farmers to gather huge grain yields without much added effort. Sixty years later, starvation and malnourishment are still points of global distress, and new concerns

have emerged. There are currently over 870 million undernourished persons in the world, a number that has been increasing for decades, and the vast majority of these people are in the developing world (Number, 2009). Sub-Saharan Africa has remained unaffected by the Green Revolution, because mineral fertilizers there are significantly pricier than in other parts of the world (Sanchez, 2002). While poor farmers suffering from undernourishment generally cannot afford fertilizers to renew their depleted fields, the overuse of N fertilizers in wealthy societies has led to the pollution of ecosystems worldwide. Many are now calling for a “second Green Revolution” to adapt plants to better use the soil, rather than create soil that plants might better use (Lynch 2007).

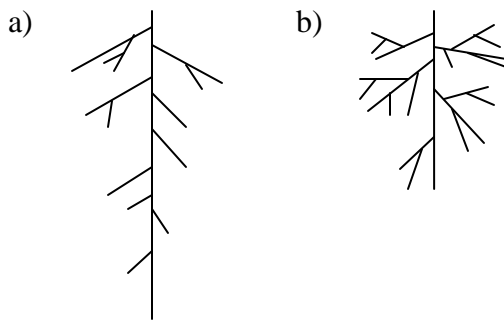
In past decades, increasing the amount of agricultural land in use was a popular method for increasing production. Unfortunately, the best land areas are now already in use for agricultural purposes, ecosystems are at risk at their continued expansion, and water has become a limiting factor (Tilman, et al., 2002). Extension education in the United States has promoted soil testing and proper timing of fertilizer application, resulting in more appropriate and tailored practices and better yields (Tilman, et al., 2002). While beneficial to more financially stable regions, these programs are not appropriate for poorer areas where education is limited and testing equipment is unattainable. To develop agricultural practices to meet the demands of the twenty first century, it has become necessary to study the precise impact of nutrients within the plant and the role of roots in nutrient acquisition. Plant effectiveness, rather than fertilizers, area, or education, must be increased.

### *Structure and function of roots*

Soil is highly temporally and spatially heterogeneous, and differences are greater between sites. Roots must be highly adaptive to survive in this broad range of conditions. Roots must



provide structural support and acquire water and nutrients, both requiring a very intricate and diversified association with the soil environment. Relationships have been found between different aspects of root architecture and nutrient cycling, sediment loss, nutrient runoff, and various aspects of nutrient acquisition (Henry, et al., 2010). The root structure of a plant can vary based on nutrient requirements and availability. Immobile nutrients are best acquired by thorough soil exploration by an extensive, dichotomous root system (Figure 1). Mobile nutrients, such as soluble nitrates, are better acquired by a herringbone topology (Dunbabin et al 2003). Herringbone structures can follow water deeper into the soil throughout the cropping season.



**Figure 1:** Herringbone (a) and dichotomous (b) root systems.

Several plant characteristics determine the form a root system will take on. The angle, rate, and duration of root growth, in addition to the pattern of root branching are the most commonly noted variables. Recent research has suggested developmental instability, or stochasticity in development, also plays a major role (Forde, 2009). This instability allows plants to adapt to soil variability throughout the growing period. In fact, plants often adapt their root system to match the current soil environment, including water and nutrient availability (Hodge, et al 2009). The root system of a maize plant consists of one embryonic primary root and later shoot-born and lateral roots. Shoot-born roots include six whorls of crown roots and two to three

whorls of brace roots (Hochholdinger 2009). The impact of differing root structures on yield and nutrient uptake has huge agricultural implications.

#### *Nitrogen and the root system*

The N-containing compounds used by plants are water soluble. Unlike insoluble nutrients such as phosphorus, N can be acquired easily with water uptake. These compounds are also known to leach out of top soil layers and deeper into the horizon throughout the season (Dunbabin et al 2003). Organic material and N are often most prevalent in the 50-100 cm depth (David, et al., 2009). In these cases, increased root length density and depth enhance N capture (Dunbabin et al 2003). As such, the differences between shallow and deep rooting structures are often attributed to the specialization of plants to different soils and stressors (Araki, 2000). While changes in the direction of elongation and timing throughout growth may have impacts on rooting depth, the main factor determining depth is the growth angle of a root (Araki, 2000). Therefore, the selection of deeper, herringbone root structures with steeper angles may increase the ability of maize plants to acquire N, particularly in N deficient soil or soils prone to N leaching.

#### *Methods of root assessment*

Many aspects of plant growth and fitness are easily studied, but the subterranean nature of the root system makes its evaluation difficult. Many methods have been developed to best circumvent this problem. Plants can be harvested, or simply dug out of the soil, then examined. This method is effective for viewing an entire root system, but harvesting, moving, cleaning, and analyzing dozens of plants becomes labor intensive. Removing the plants from their original locations may also damage roots or bend them out of their original shapes. Another invasive technique is excavation. Trenches are dug next to plants of interest and then slowly expanded

towards them. This method permits very precise information about the arrangement of roots within the soil layers, but is painstaking and extremely labor intensive. Soil cores may be used to assess plants at specific points in time throughout the cropping season. Repeated soil coring allows the estimation of root development over time and depth. Each method has benefits that are preferred by scientists depending on the aim of the study and time, monetary, and labor constraints.

The amount of chlorophyll produced by a plant depends on N uptake, as the molecule contains high amounts of N. This pigment is crucial for growth and yield, and the amount present can be used to estimate the success of a plant. SPAD meters are easily transportable and provide quick results, lending to their increasing popularity as a suggestive measure for chlorophyll content. Strong relationships have been found between chlorophyll content and SPAD values (Earl and Tollenaar, 1997, Xu, et al., 2000). Likewise, higher SPAD values, or more chlorophyll, are correlated with yield formation (Montemurro, et al., 2006).

### *Objectives*

The purpose of this experiment was to investigate the effect of N level on root architecture and the effects of root architecture and rooting depth on N acquisition and crop physiology under optimum and N deficient conditions at 45 days after emergence (DAE), 78 DAE, and 114 DAE.

## Methods

### *Experimental site*

Experiments were carried out in 2009 at the Russell Larson Research Station of the Pennsylvania State University in Rock Springs, Pa, USA (40°42'37".52N, 77°57'07".54W, 366 m.a.s.l.). The experiment was conducted on a Hagerstown soil (fine, mixed, semiactive, mesic Typic Hapludalf).

### *Experimental design and statistical analysis*

The experiment was set up as a split plot design replicated four times. Two N treatments (high/optimum, and low/deficient) were randomly assigned to two adjacent fields. Each field contained 40 plots, subdivided into four replications of ten plots. Ten maize genotypes were randomly assigned to the plots within each replication. Each plot consisted of five 6.6 m long rows spaced at 75 cm. Subplots were assigned to each half of rows two and four, with a total of four subplots. Rows one, three and five were kept as borders to separate data rows. Spacing between plants within rows was 23 cm. Plots within the high N field received conventional N fertilizer in the form of 40.8 kg/acre urea at planting, while the plots assigned to the N deficient treatment were left unfertilized. Potassium was also applied to the high N field, as 13.6 kg/acre of K<sub>2</sub>O, though none was required in the low N field. FORCE, a corn rootworm pesticide, was applied before planting at 0.14 kg per 304.8 m of corn row. Herbicide, Kerptone (1.89 L/ acre) and Callisto (88.7 mL/acre), was also applied before planting. Three different harvest times were assigned to each subplot.

Analysis of variance for root architectural traits and shoot parameters was conducted with the nlme package in R (Pinheiro et al., 2004). The statistical model applied was:

$$y = \alpha + \beta + \delta + \gamma + \rho + \delta:\gamma + \delta:\rho + \gamma:\rho$$

where  $\alpha$  stands for the number of replications nested within a treatment,  $\beta$  for the blocks in each treatment,  $\delta$  for the different harvest times,  $\gamma$  for the levels of N fertilization, and  $\rho$  for the genotype. The terms,  $\delta:\gamma$ ,  $\delta:\rho$  and  $\gamma:\rho$ , represented interactions between traits of interest.

Analysis of variance of root distribution in the soil was carried out using the nlme package in R applying the following statistical model:

Fixed effects:  $RWA \sim \delta + \gamma + \rho + \eta$ , random:  $\alpha / \beta / \gamma \rho$ , where  $\eta$  is the soil depth from which root samples were taken, fixed effects are represented in terms of non-random explanatory variables and random effects are explained as if arising from random causes.

### *Plant material*

Seven *Zea Mays* genotypes with varying root architecture were grown: Four genotypes with steep root structures, OHW21, OHW48, IBM79, and IBM368, and three genotypes with shallow structures, NYH180, NYH227, and NYH277. Steep genotypes OHW21 and OHW48 had shallow, low branching crown roots and steep, low branching brace roots, and IBM79 and IBM368 had steep, highly branched brace roots and intermediate branching and angled crown roots. Shallow genotypes NYH180, NYH227, and NYH277 all had highly branched, shallow crown and brace roots. Root structures were classified as deep or shallow based on root angles measured in preliminary experiments (Trachsel et al., 2010, in preparation).

### *Soil nitrogen analysis*

To ascertain differences in treatment, nitrate and ammonium concentrations within the soil were analyzed in two locations in each experimental field at each harvest stage. Soil cores

were taken with a 7/8" diameter soil probe in six 10 cm increments. Replicate cores were pooled, the water content was determined, and samples were frozen. Samples of 40 g were later combined with 100 ml of 1 M KCl solution, shaken at 150-200 rpm for one hour and filtered (Whatman 41). Filtrate subsamples were frozen until colorimetrically analyzed for nitrate and ammonium concentration (Multiskan Ex Primary EIA V. 2.3).

### *Measurements at harvest*

Planting took place on the first two days of June, 2009. Harvests were conducted 45 days after emergence (DAE), 78 DAE (flowering), and 114 DAE (physiological maturity). For each harvest, three representative plants from each subplot were excavated, soaked for 5 minutes, rinsed, and scored. Several aspects of each root structure were visually scored (Table 1). A chart was made to standardize the measurements between plants and harvests. All angles were measured, and the number of whorls and roots counted.

Table 1: Root Architecture Measurements. All factors were measured on standardized scales. Angles were estimated with the use of marked score cards.

Measurement	Abbreviation
Number of brace root whorls	BW
Number of total brace roots	BO
Angle of brace roots originating from the first whorl	BA1
Angle of brace roots originating from the second whorl	BA2
Degree of brace root branching	BB
Number of crown roots	CN
Angle of crown roots	CA
Degree of crown root branching	CB

At each harvest, three leaves were washed, pooled, bagged, and dried for analysis. At Harvest 1, the youngest fully developed leaves were selected, while ear-leaves were used for Harvests 2 and 3. Samples were later pulverized in plastic vials with Plexiglas ball pestles (0.95 cm diameter) in a SPEX SamplePrep Mixer/Mill (SPEX Industries Inc.). The N content of

subsamples was measured with a PerkinElmer 2400 Series II CHNS/O Elemental Analyzer (Shelton, CT, USA). The leaf N content and overall plant biomass were then used to quantify N uptake.

Several days prior to each harvest, the height of each genotype was assessed by averaging the heights of three representative plants within each subplot. SPAD readings were taken as a proxy-measure for leaf chlorophyll with a SPAD 502 Konica Minolta. (Konica Minolta Sensing, Inc., Sakai, Osaka, Japan) Again, the youngest fully developed leaves were selected at Harvest 1, while ear-leaves were chosen for Harvests 2 and 3. Each leaf sample was measured on the adaxial side near the center. Soil cores were also taken at each harvest, within rows and centered between two plants. Cores of 5 cm in diameter were taken with a Giddings Soil Coring Device and reached a depth of 60 cm. Root samples were extracted in 10 cm segments from each core and weighed. Weights were used to calculate the depths above which 50% and 95% of roots occur (D50 and D95, respectively) for genotypes of each rooting pattern.

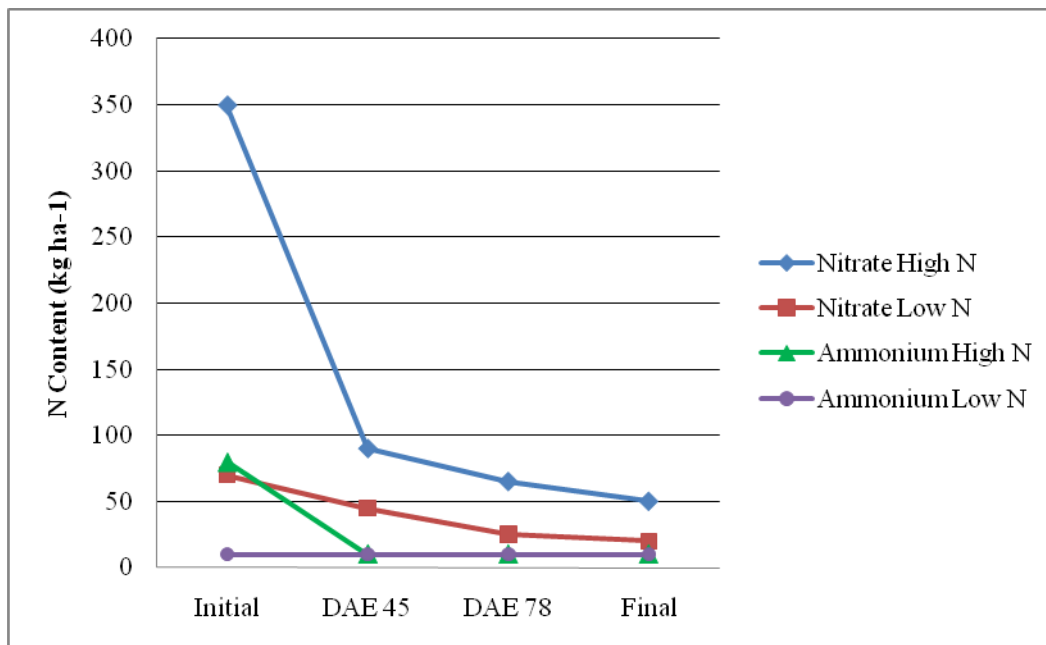
At the final harvest, the yield was also collected. Ears were collected from five representative plants in each plot. Ears were dried, and grain was removed and weighed.

## **Results**

Overall depth of the root system was calculated with measurements for the depth above which 50% and 95% of root mass is located. Differences between genotypes were noisy and not significant, so the analysis focuses upon differences between rooting patterns to allow an increased sample size. These values increased throughout the season as the roots grew deeper.

### Soil nitrogen

Nitrogen content of the soil was determined at each harvest stage. There was significantly more N in the high N condition, particularly in the top layers of the soil and in later harvest stages (Figure 2). In the high N treatment, nitrate concentrations decreased over the first 9 weeks of the growing season from 350 kg ha<sup>-1</sup> to about 50 kg ha<sup>-1</sup>, when it remained fairly stable. Ammonium concentrations in the high N field showed a great decrease during the first 5 weeks of the growing season, from approximately 80 kg ha<sup>-1</sup> to 10 kg ha<sup>-1</sup>. Nitrates in the low N field gradually decreased from approximately 70 kg ha<sup>-1</sup> to 20 kg ha<sup>-1</sup>. And ammonium concentrations remained fairly stable at 10 kg ha<sup>-1</sup>.

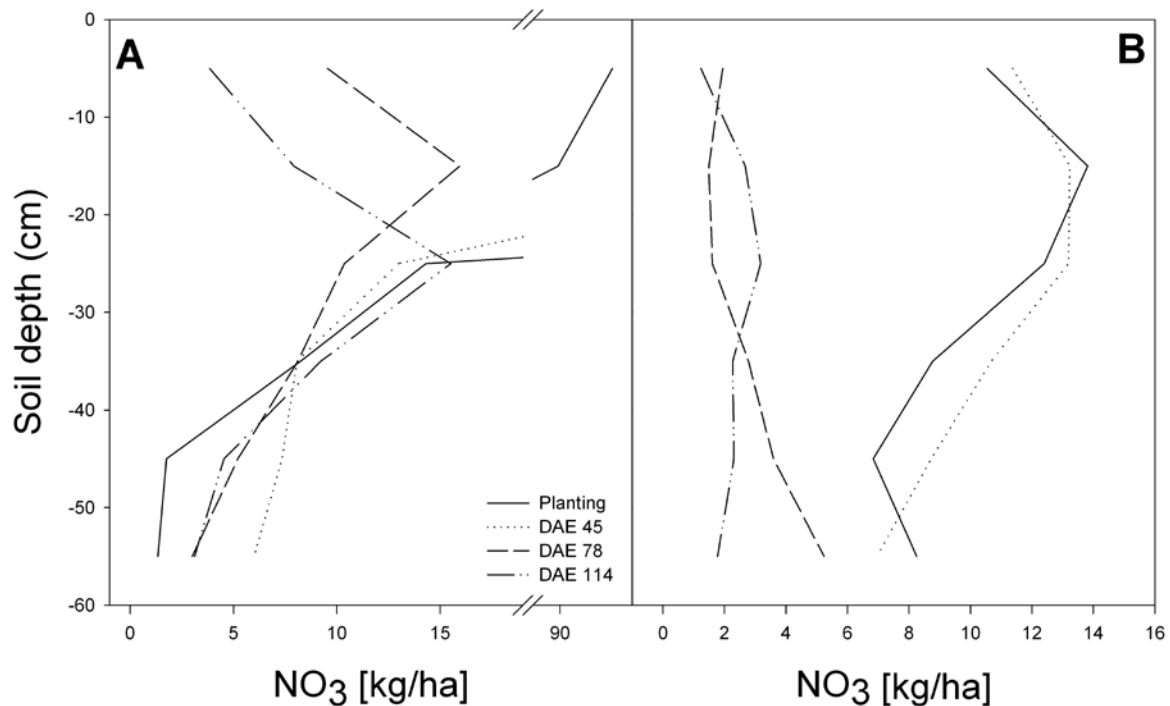


**Figure 2:**

Nitrate and ammonium concentrations in the high and low N treatments over the growing season. The initial nutrient concentrations were measured two days after planting. Final concentrations were stable levels reached approximately 9 weeks into the growing season for nitrates and 5 weeks into the season for ammonium.



Nitrogen concentrations between fields differed spatially as well as temporally (Figure 3). Nitrate concentrations in the high N field were greater in the upper soil layers until very late in the season, after the first harvest. In the N deficient field, nitrate concentrations were higher in the upper soil layers for the first 9 weeks of the season, then higher in the lower layers. In both fields and throughout the season, ammonium concentrations were higher in the top 40 cm of soil.



**Figure 3:** Shows the N content of the soil over various depths in the high (a) and low (b) N conditions.

#### *Differences between harvests*

Between the first (DAE 45) and second harvests (DAE 78), more differences were observed between genotypes of different rooting patterns than between N treatments. Trait values showing a greater change in steep than shallow genotypes between the first two harvests include plant height ( $p=0.01$ ), brace root branching ( $p=0.05$ ), crown root angle ( $p=0.05$ ), and D50 ( $p=0.01$ ) (Table 2). The only significant difference between treatments was the number of

brace roots, which was greater in the low N treatment ( $p < 0.001$ ). More differences between N treatments were observed between the second and third (DAE114) harvests than between the first and second. The number of brace roots ( $p=0.04$ ), brace root angle from the first whorl ( $p=0.05$ ), and crown root angle ( $p=0.03$ ) showed a stronger increase between the second and third harvests in the N deficient treatment. Up to the third harvest, the number of crown roots ( $p=0.01$ ) and root depth ( $p=0.05$  for D95 and  $0.03$  for D50) had also increased more for steeper genotypes.

#### *Shallow versus steep structures*

Data compiled from the soil cores were used to estimate root distribution at different depths. By 78 DAE, the depth above which 50% of the roots occur (D50) was significantly deeper for steep genotypes than for shallow genotypes ( $p=0.01$ ). The bottom half of the root distribution, was deeper for steep genotypes by 114 DAE (Table 3). This is reflected in significantly deeper D50 ( $p=0.03$ ) and D95 ( $p=0.05$ ). Rooting angles were positively correlated with D95, with the strongest correlations observed in the optimum N treatment. This was true for brace root angles from both whorls (BA1 and BA2,  $r=0.79$ ) and crown roots ( $r=0.85$ ) in high N.

Several constitutive differences between genotypes with shallow and steep root structures were observed. Up to DAE 78, steep genotypes increased in height more strongly than shallow genotypes ( $p=0.01$ ). Steep genotypes showed a smaller increase in brace root branching ( $p=0.05$ ) than shallow genotypes. Angles of crown roots increased more strongly for steep genotypes up to DAE 78 ( $p=0.05$ ). Under low N, the steep genotypes did not change crown root angles over time as much as the shallow genotypes. By both 78 and 114 DAE, steep genotypes show at least a trend towards a larger increase in crown root numbers than shallow genotypes (78 DAE;  $p=0.06$ , 114 DAE;  $p=0.01$ ). A few similarities also existed between the rooting patterns. The total

number of brace roots and the number of crown roots were positively correlated for both rooting patterns ( $r= 0.41$  in optimum N, but only  $0.29$  in low N). There was also a positive correlation between the branching of crown and brace roots ( $r= 0.36$ ).

**Table 2:** Anova summary table of root traits and other measurements over time and N treatment. The acronyms stand for traits and factors. Treat is the treatment (high or low N), Gen is the rooting pattern (steep or shallow genotype), TreatlowN is the low N treatment, and Gensteep are steep rooting patterns. DAE:Gen, Treat:Gen, and DAE:Treat are interactions of those factors.

	SPAD			PHT			SPADxPHT			SFW			Shoot N Content		
	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value
DAE			<.0001			<.0001			<.0001			<.0001			<.0001
Treat			0.1829			0.017			0.0586			0.1504			0.0328
Gen			0.8721			0.0002			0.0745			0.8609			0.5239
DAE:Gen			0.7861			0.0256			0.0708			0.9582			0.6179
Treat:Gen			0.5935			0.6803			0.5108			0.4593			0.4761
DAE:Treat			0.9715			0.4981			0.6084			0.1605			0.9598
DAE45	35.3	2.4	0.00	11.1	1.4	0.00	4.0	1.1	0.00	90.7	36.3	0.01			
DAE78	53.3	2.2	0.00	40.2	1.4	0.00	21.8	1.1	0.00	653.1	37.8	0.00	1.82	0.20	0.00
DAE114	56.9	2.2	0.00	42.9	1.4	0.00	48.7	1.2	0.00	596.6	37.8	0.00	2.15	0.17	0.00
TreatlowN	-0.4	2.9	0.90	-1.2	1.7	0.49	-1.2	1.5	0.42	-15.0	46.5	0.75	-0.18	0.24	0.43
Gensteep	0.4	2.7	0.89	1.1	1.6	0.48	0.2	1.4	0.86	-16.3	43.4	0.71	-0.05	0.23	0.82
DAE78:Gensteep	-0.3	3.3	0.94	4.8	1.9	0.01	2.4	1.4	0.10	-6.3	45.3	0.89			
DAE114:Gensteep	1.8	3.3	0.59	0.5	1.9	0.79	-0.7	1.5	0.64	-15.2	44.9	0.74	-0.18	0.23	0.45
TreatlowN:Gensteep	-1.5	2.7	0.59	0.6	1.6	0.69	1.0	1.6	0.54	39.8	50.6	0.44	0.05	0.27	0.86
DAE78:TreatlowN	-0.6	3.2	0.84	-1.0	1.9	0.61	-1.0	1.3	0.44	-82.2	44.0	0.07			
DAE114:TreatlowN	-0.7	3.2	0.83	-2.2	1.9	0.24	-1.3	1.4	0.34	-58.4	43.4	0.18	-0.01	0.20	0.96

**Table 2  
(continued)**

	BW			BO			BA1			BA2			BB		
	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value
DAE			<.0001			<.0001			<.0001			<.0001			<.0001
Treat			0.1092			0.0019			0.012			0.0001			0.4785
Gen			0.1632			0.3227			0.0002			<.0001			0.0242
DAE:Gen			0.4892			0.6853			0.1199			0.3933			0.1204
Treat:Gen			0.8845			0.9214			0.0106			0.001			0.1549
DAE:Treat			0.2673			0.0041			0.1174			0.707			0.5864
DAE45	1.0	0.1	0.00	2.1	0.4	0.00	4.8	0.4	0.00				1.3	0.4	0.01
DAE78	2.1	0.1	0.00	7.4	0.4	0.00	4.7	0.4	0.00	4.3	0.4	0.00	7.1	0.4	0.00
DAE114	2.1	0.1	0.00	6.5	0.4	0.00	4.9	0.5	0.00	4.3	0.5	0.00	5.6	0.5	0.00
TreatlowN	0.0	0.1	0.93	0.2	0.5	0.71	1.1	0.6	0.06	2.8	0.5	0.00	-0.5	0.5	0.35
Gensteep	0.0	0.1	0.94	-0.5	0.5	0.31	1.6	0.5	0.00	2.8	0.5	0.00	-0.4	0.5	0.45
DAE78:Gensteep	-0.2	0.2	0.22	0.4	0.6	0.48	0.9	0.6	0.12				-1.2	0.6	0.05
DAE114:Gensteep	-0.1	0.2	0.51	0.4	0.6	0.54	0.0	0.6	0.97	-0.4	0.6	0.53	-0.5	0.6	0.39
TreatlowN:Gensteep	0.0	0.1	0.89	0.0	0.5	0.94	-1.5	0.6	0.01	-2.1	0.6	0.00	0.7	0.5	0.15
DAE78:TreatlowN	-0.3	0.2	0.11	-1.9	0.6	0.00	0.9	0.6	0.13				0.0	0.6	0.98
DAE114:TreatlowN	-0.1	0.2	0.54	-1.1	0.5	0.04	1.1	0.6	0.05	-0.2	0.6	0.71	-0.5	0.6	0.36

Table 2 (continued)

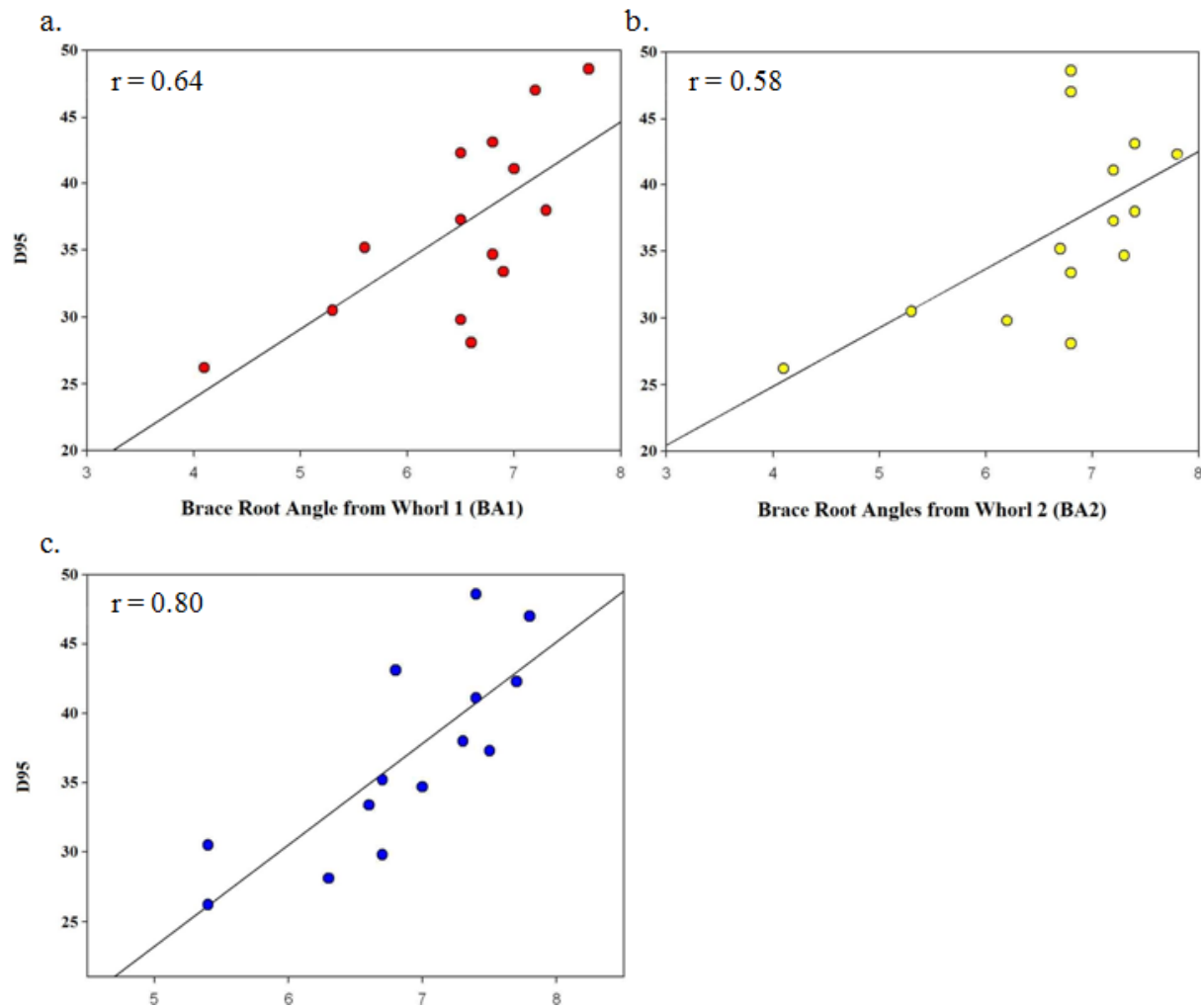
	CN			CA			CB			AD95			AD50		
	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value
DAE			<.0001			<.0001			<.0001			<.0001			<.0001
Treat			0.1673			0.2581			0.1593			0.0362			0.8629
Gen			0.0011			<.0001			<.0001			0.0021			0.0004
DAE:Gen			0.037			0.1405			0.2077			0.1342			0.0145
Treat:Gen			0.1508			0.3144			0.7567			0.6832			0.3466
DAE:Treat			0.2203			0.0832			0.3693			0.3746			0.5713
DAE45	5.4	0.5	0.00	6.1	0.4	0.00	7.2	0.5	0.00	21.0	4.1	0.00	13.9	2.6	0.00
DAE78	5.4	0.5	0.00	5.3	0.4	0.00	7.3	0.5	0.00	32.8	4.4	0.00	13.9	2.9	0.00
DAE114	5.5	0.5	0.00	5.2	0.4	0.00	7.4	0.6	0.00	33.5	4.1	0.00	15.2	2.6	0.00
TreatlowN	-0.7	0.6	0.25	0.0	0.4	0.95	0.2	0.6	0.77	2.8	4.2	0.51	-0.8	3.3	0.80
Gensteep	-0.4	0.6	0.52	1.3	0.4	0.00	-1.9	0.6	0.00	1.3	4.0	0.76	-1.5	3.2	0.64
DAE78:Gensteep	1.2	0.6	0.06	1.0	0.5	0.05	0.1	0.7	0.89	6.6	5.0	0.20	11.2	3.8	0.01
DAE114:Gensteep	1.7	0.6	0.01	0.5	0.5	0.34	-1.1	0.7	0.12	9.9	4.8	0.05	8.9	3.8	0.03
TreatlowN:Gensteep	0.9	0.6	0.16	-0.5	0.4	0.27	-0.2	0.6	0.77	1.0	4.0	0.81	3.0	3.1	0.35
DAE78:TreatlowN	0.7	0.6	0.27	0.8	0.5	0.13	0.9	0.7	0.21	4.0	4.7	0.40	-0.2	3.7	0.96
DAE114:TreatlowN	1.1	0.6	0.09	1.1	0.5	0.03	0.0	0.7	0.97	-2.3	4.7	0.63	-3.4	3.8	0.38

**Table 3:** Root depth distribution over time and across genotypes and treatments. TreatlowN relates to effects caused by the low N treatment. Dep refers to the soil depth from which root samples were taken.

	Root weight (g)	Std.Error	p-value
DAE45	0.0891	0.0518	0.0863
DAE78	0.2462	0.0505	0.0000
DAE114	0.2229	0.0494	0.0000
TreatlowN	0.0116	0.0378	0.7634
Gensteep	0.0201	0.0397	0.6182
Dep20	0.1706	0.0415	0.0001
Dep30	-0.0069	0.0425	0.8704
Dep40	-0.0752	0.0448	0.0947
Dep50	-0.1529	0.0503	0.0026
Dep60	-0.1787	0.0546	0.0012
DAE78:TreatlowN	0.0250	0.0744	0.737
DAE114:TreatlowN	0.1868	0.0742	0.013
DAE78:Gensteep	-0.0027	0.0787	0.972
DAE114:Gensteep	-0.0141	0.0770	0.855
TreatlowN:Gensteep	-0.0650	0.0825	0.442
Gensteep:Dep20	0.0883	0.0830	0.288
Gensteep:Dep30	0.2463	0.0849	0.004
Gensteep:Dep40	0.2753	0.0897	0.002
Gensteep:Dep50	0.2338	0.1047	0.026
Gensteep:Dep60	0.2480	0.1158	0.033

#### *Relationships between root traits*

There were several prominent relationships between root architectural traits. As already mentioned, brace root branching is negatively correlated with crown root angle and rooting depth. Root angles predicted rooting depth, as indicated by the high correlation between angles and depth. Brace root angle had a strong positive correlation with the depth above which 95% of the roots occurred for the first ( $r= 0.64$ ) and second whorls ( $r= 0.58$ ), but only a weak correlation with D50 (Figure 4, a-b). Crown root angle had a strong positive correlation with both D95 and D50 ( $r= 0.80$  and  $0.58$ , Figure 4c).



**Figure 4:** Root angles were correlated to the depth of the root system for brace roots in the first whorl (a), brace roots in the second whorl (b), and crown roots (c).

There may be a relationship between the number of roots and the average rooting depth. The number of crown roots had a strong correlation with the crown root angle ( $r = 0.76$ ) and moderate positive correlations with rooting depth. Conversely, the number of brace roots was not an indicator for any other root traits. There was no observed correlation between the number of brace roots and the extent of brace root branching, the number of crown roots, or D50. A weak negative correlation between the number of brace roots and D95 was observed.

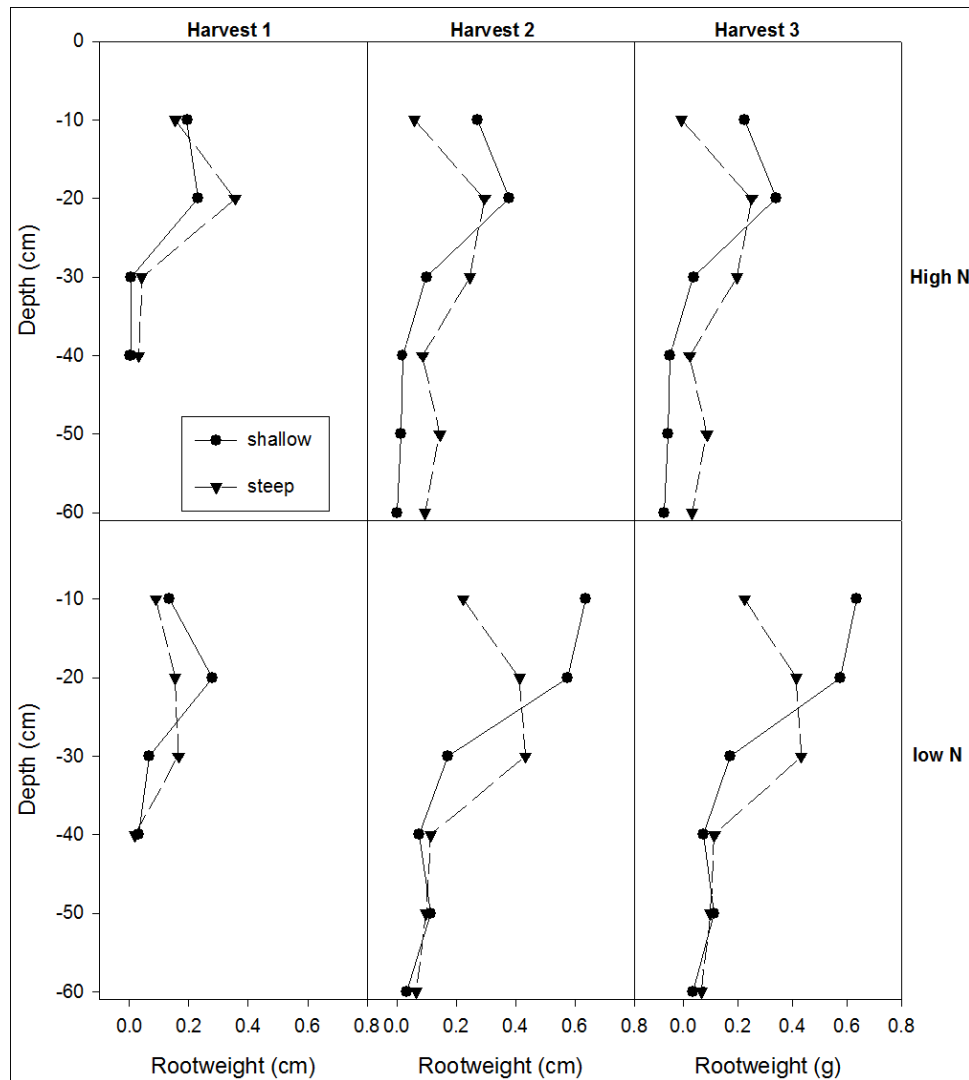


*High versus low nitrogen*

The amount of available N had several significant effects on the root structures of maize plants grown in high and low treatments. By 78 DAE, there is a trend towards a lower shoot fresh weight in the low N treatment ( $p= 0.07$ ). Compared with the low N treatment, the number of brace roots increased more strongly over time in the high N treatment for 78 and 114 DAE ( $p < 0.0001$  and  $p= 0.04$ ). Root angles were steeper in the N deficient condition. Between Harvests 2 and 3, brace root angles increased more in the low N treatment, but the increase was less accentuated for steep genotypes (BA1,  $p= 0.01$  and BA2,  $p < 0.0001$ ). The crown root angles were also steeper ( $p= 0.03$ ) and there was a trend towards more crown roots in the low N condition ( $p= 0.09$ ).

One relationship between root characteristics was specific to N level. Crown root angles have a strong positive correlation with brace root angles from the first and second whorls in high N ( $r= 0.95$  and  $0.87$ , respectively). Crown root angle explains less variation in brace root angle in low N ( $r= -0.33$  for BA1 and  $0.65$  for BA2). Differences between steep and shallow rooting patterns were also minimized in the low N treatment (Figure 5). Steep genotypes were significantly deeper under optimum conditions, but with N deficiency, both systems reached similar depths (Table 3). “Shallow” genotypes were no longer shallower, but had steep roots and a similar rooting pattern to steep genotypes.

Elemental analysis of leaf tissue indicated that steep genotypes may have performed better in low N conditions. There was a tendency for shallow genotypes to have lower shoot N under low N conditions, though this trend was not significant. Shoot N values tended to be reduced at DAE 114 compared to DAE 78 for both root patterns, but this was also not significant.



**Figure 5:** Root depths for shallow, medium, and steep rooting patterns in optimum (high) and low N conditions and over three harvests. Data were collected from soil cores and depths are shown in cm below the soil surface (0 cm).

*Nitrogen and Yield*

Grain yield was compared across genotypes and treatment with an ANOVA and a Tukey-Kramer Multiple Comparison Test. Nitrogen level has a significant impact on yield which was considerably higher in the high N treatment (Table 5). There was a trend towards an effect of rooting pattern as well, with a higher yield produced by shallow genotypes.

**Table 5:** Analysis of variance for yield across treatments and genotypes, and Tukey-Kramer Multiple Comparison Test for yield across treatments and genotypes (steep versus shallow).

Source	Prob
Term	Level
Treat	0.006354*
Gen	0.088363
* Term significant at alpha = 0.05	
	Grain
Treatment	yield
low N	236.2658 A
high N	314.1911 b
Genotype	Mean
<b>steep</b>	251.046
<b>shallow</b>	299.4109

The importance of root architecture for plant performance is highlighted by different degrees of correlation between root architectural traits with yield under optimum and N deficient conditions (Table 4). For both conditions, crown root traits explained little variation in yield. There was a weak negative correlation between crown root angle and yield, and a weak positive correlation between crown root branching and yield. Under N-deficient conditions, brace root angles had a strong influence on yield. This is indicated by a negative correlation of the angles of brace roots in the first whorl with yield under high N, while these angles are positively correlated with yield under N-deficient conditions ( $r = -0.36$  and  $0.61$ ). Brace root branching also had a larger impact on yield under N stress as seen in the stronger positive correlation ( $r = 0.73$  in low and  $0.25$  in high). Under optimum N conditions, deeper soil exploration was unnecessary and perhaps detrimental to the crops. All root angles and depth measurements were negatively correlated with yield.

**Table 4:** Correlations between root traits, root depth, and yield. Abbreviations are defined in Table 1.

a.	BW	BO	BA1	BA2	BB	CN	CA	CB	Yield	AD95
<b>BO</b>	0.47									
<b>BA1</b>	-0.49	-0.28								
<b>BA2</b>	-0.35	-0.19	0.45							
<b>BB</b>	0.37	-0.06	-0.64	-0.77						
<b>CN</b>	-0.06	0.08	0.29	0.43	-0.53					
<b>CA</b>	-0.43	-0.09	0.52	0.64	-0.78	0.76				
<b>CB</b>	0.36	-0.03	-0.31	-0.09	0.36	-0.22	-0.58			
<b>Yield</b>	0.08	0.34	-0.17	-0.62	0.35	-0.27	-0.34	0.02		
<b>AD95</b>	-0.59	-0.28	0.64	0.58	-0.70	0.44	0.80	-0.56	-0.42	
<b>AD50</b>	-0.35	0.01	0.25	-0.08	-0.18	0.41	0.58	-0.86	0.16	0.51

b.	BW	BO	BA1	BA2	BB	CN	CA	CB	Yield	AD95
<b>BO</b>	0.29									
<b>BA1</b>	-0.49	0.07								
<b>BA2</b>	-0.55	0.17	0.93							
<b>BB</b>	0.41	-0.26	-0.90	-0.77						
<b>CN</b>	0.11	0.41	0.71	0.50	-0.83					
<b>CA</b>	-0.56	0.15	0.95	0.87	-0.95	0.69				
<b>CB</b>	0.35	0.02	-0.38	-0.49	0.42	-0.05	-0.55			
<b>Yield</b>	0.05	-0.69	-0.36	-0.61	0.25	-0.18	-0.35	0.32		
<b>AD95</b>	-0.65	0.09	0.79	0.79	-0.68	0.39	0.85	-0.52	-0.46	
<b>AD50</b>	-0.18	-0.11	0.36	0.36	-0.41	0.18	0.53	-0.94	-0.14	0.50

c.	BW	BO	BA1	BA2	BB	CN	CA	CB	Yield	AD95
<b>BO</b>	0.82									
<b>BA1</b>	-0.28	-0.27								
<b>BA2</b>	0.07	0.27	-0.52							
<b>BB</b>	0.07	-0.06	0.25	-0.79						
<b>CN</b>	-0.24	0.29	-0.29	0.36	-0.20					
<b>CA</b>	-0.31	0.03	-0.33	0.65	-0.60	0.76				
<b>CB</b>	0.54	0.19	-0.26	-0.23	0.47	-0.63	-0.79			
<b>Yield</b>	-0.22	-0.23	0.61	-0.49	0.73	-0.25	-0.45	0.22		
<b>AD95</b>	-0.43	-0.29	0.36	0.39	-0.78	0.11	0.49	-0.74	-0.32	
<b>AD50</b>	-0.62	-0.29	0.45	0.07	-0.20	0.54	0.67	-0.93	0.14	0.61

## Discussion

The high N treatment received nitrogen fertilizer at the start of the season and, as a result, soil N concentrations were higher than in the low N treatment. There was roughly a five-fold difference in the initial N concentration between the fields. By harvest, this difference had decreased to about twice as much N in the high N treatment. The distinction was most obvious in the top 20 cm soil layer, which had the greatest concentration of N in the high N condition for both nitrate and ammonium.

Implementation of three harvest times spanning the maize growth cycle enabled the assessment of temporal differences in plant growth between genotypes. It was found that differences between genotypes, such as root angles and branching, were greater early in the season, while differences between the treatments, such as root number and angle, were greater later in the season. Differences between genotypes that were more accentuated earlier in the season include brace and crown root angles and brace root branching. These features likely developed early with the young root system, distinguishing the genotypes by structure.

Between the first two harvests, the plant height of steep genotypes increased significantly more than shallow genotypes. The steep genotypes selected may have been faster growing than the shallow genotypes, resulting in an early height difference that diminished as the shallow genotypes caught up.

Differences between plants growing in high and low N treatments, such as the number and angle of roots, became more prevalent up to the third harvest. This may indicate that N was not truly limiting in the low N condition until later in the season, that plants perceived N levels early in the season, but required time to adapt to the suboptimal conditions, or that plant responses and deficiency symptoms became more significant as time progressed. The severity of

N deficiency may have increased over the growing season, prompting the structural changes that were observed in later harvests.

Steep genotypes had deeper roots and steeper root angles, confirming a difference between “steep” and “shallow” genotypes. Rooting depth was found to correlate with crown and brace root angles, showing that steeper roots are able to proliferate deeper into the soil. Angles and depth were most closely related in the optimal nitrogen treatment and for D95 values. D50 values were significantly higher for deep rooting genotypes, but this value was only moderately correlated to root angles. It could be supposed that moderately deep roots are derived from moderate angles, while the deepest roots grow from the steepest angles.

The strongest correlations between rooting angles and depth were observed in the optimum N treatment, indicating that root systems in the low N treatment produced steep root angles without a comparable change in rooting depth. By DAE 114, crown roots and brace roots originating from the first whorl were significantly steeper in the low N treatment. Differences for D95 and D50 were not significant, though D95 tended to be slightly deeper and D50 slightly shallower for low N. This might indicate that plants formed more roots in the topsoil and also a few particularly deep roots, but further research would be needed to confirm this. As is, these data indicate comparable depths for high and low N, so it seems that the steeper angles utilized by plants in low N were employed to reach lower soils, all the while investing less in biomass.

Because the root angles in the low N treatment were consistently steeper, the lesser degree of correlation of angle to rooting depth might indicate a shallower root system or more random depths. This randomness might be the result of a more individualized response to the soil environment to maximize N capture. As soil is an extremely variable medium, each plant will not experience the same environment. When N is limiting, plants may have a heightened

sensitivity to this variation and react individually. Growth angles may have also altered as they grew away from the plant, resulting in an overall root angle that cannot be measured at the base of the root.

It has been suggested that root elongation is a major adaptive response of maize root systems to low N conditions (Tian, et al., 2005). The present data do not support such a conclusion, as greater depths in addition to the observed angle alterations would be expected. The Tian et al. (2005) conclusion may be limited to particular genotypes, including those investigated by the authors, as a specific adaptive response.

It was also found here that brace root branching is negatively correlated with brace root angles, crown root angles, and D95. More simply, steeper roots are less branched. This supports the conclusion that steep genotypes invest more energy and biomass in exploring deeper and away from the plant than in extensive soil exploration through a dichotomous structure. Lateral branching in the topsoil is reduced to optimize carbon allocation and avoid stress signaling of roots in dry surface soils under drought stress (Hund et al., 2009). As mobile nutrients, such as N, are located with the water reserves, plants seeking these nutrients would develop a root system similar to that which is optimal for water acquisition. Alternatively, the extent of branching may be an artifact due to genotype selection. The “steep” genotypes selected generally had lower levels of branching compared to shallow genotypes, which had highly branched, shallow brace and crown roots.

There was some commonality between genotypes with shallow and steep root structures as seen in the growth patterns of different root structures. The numbers and extent of branching of brace and crown roots were highly related, indicating that common schemes are used for the development of both root types. Plants with higher numbers of roots have higher numbers of

both types, and plants with greater branching had more extensive branching of each type. The angles of these roots were also highly correlated among each other, particularly in the high N treatment where the root systems were not altered due to deprivation.

As the only observed difference between experimental fields was the prevalence of nitrogen compounds, the differences between root structures in the high and low nitrogen treatments can be attributed to plant response to this deficiency. In the low N treatment, the N concentrations in the top soil layers were much lower than in the high N treatment. This presented a need for plants to seek N in lower soil layers. As mentioned above, plants in this N condition had steeper brace and crown root angles over time, presumably to compensate for limited N without additional biomass requirements.

Soil N concentrations were higher in the upper soil layers for about nine weeks after planting, thereafter concentrations in lower soil layers matched or surpassed those in the top 20 cm. This trend was observed in both conditions, though it was stronger in the high N treatment. Only by the third harvest were root angles significantly steeper in the low N condition. The observed data indicate that, when available, the upper soil N was utilized and diminished. Following was a plant response to this depletion, presenting itself in the steeper angles observed in the low N condition later in the season. Dunbabin (2003) suggested this as a potential plant strategy to minimize N limitation. Plants would prevent N losses from upper soil layers with high root density near the surface, then absorb N that leached into lower soil layers with deeper roots later in the season.

Crown and brace roots behave differently under low N conditions. It was found that brace root angles were significantly steeper for steep genotypes in all conditions, though increases in brace root angle were more accentuated for shallow than steep genotypes. While crown and



brace roots followed similar patterns under optimum N, brace root angle explained less variation in crown root angle in N deficient conditions. Crown root angles of steep genotypes were only greater with optimum nitrogen levels. Under low N, the difference between crown root angles of steep and shallow genotypes were not significant.

By the end of the season, shallow and steep genotypes had similar crown root patterns in the low N treatment, which were steeper with a trend towards more crown roots than in the high N treatment. Crown roots grow deepest when water and nitrogen are located in deeper soil layers (Araki, et al., 2000), so the plant may invest more in these root structures when nitrogen is lacking. Crown roots grew at steep angles for both rooting patterns to reach deeper soils where N sources might be located.

It was also found that, between harvests, the number of brace roots did not increase as much in the low N treatment as in the high N treatment. Chun et al. (2005) found that low N conditions typically resulted in a decreased number of axial roots produced by a given plant. In this study, brace roots appear to follow this trend, though the number and production of crown roots remained similar for both conditions.

The data indicate that maize yield was significantly lower in the low N treatment. This is consistent with previous research, which has seen as much as a 38% reduction from high to low N (Gallais and Hirel, 2004, Rajcan and Tollenaar, 1999a, Boomsma, et al., 2009). It appears that N deficiency was severe enough to cause a significant reduction in the production capacity of maize in that condition.

No differences were found between steep and shallow genotypes under low N conditions, likely because differences between the rooting patterns were not significant in this treatment. The low N levels led to many similarities between the root systems of the shallow and steep rooting

patterns. Root angles of shallow root structures were steeper in the low N treatment, resulting in a depth increase to match that of the steep genotypes. Benefits of a steep structure were not advantageous because the shallow structures gained access to these nutrients as well, with their increased angles and depth throughout the season.

The importance of root traits for N acquisition and yield may be gathered from correlation analysis of these factors. Root branching is positively associated with grain yield. Positive correlations were observed between root branching and yield under both high and low N, indicating the importance of lateral roots for the uptake of nutrients. Brace root branching explained considerably more variation in yield under N deficient conditions ( $r = 0.73$  versus  $0.25$ ), reflecting the plants' increased need for N and a closer relationship between lateral roots and the soil when N is limiting.

Previous research has also found a relationship between lateral roots and N uptake. Tian et al. (2005) suggested that limiting N concentrations stimulate lateral root elongation and that high nitrate supplies even inhibit growth. Results of root architecture modeling have proposed that high root density results in increased N uptake due to enhanced nitrate capture in spatially variable soils, rapid capture early in the season, and decreased N leaching (Dunbabin et al, 2003).

The importance of root angles for grain production varies based on the prevalence of nitrogen. Steep angles convey yield under low N conditions. In the high N treatment, N concentrations remained high in the surface soil layers well into the season. As such, root angles and D95 were all negatively correlated with yield under high N. Deep roots are unnecessary when there is high surface N. In nitrogen deficient conditions, however, brace root angles in the first whorl exhibited a strong positive correlation with yield. Despite the importance of brace

root angles under low N, D50 and D95 showed weak or negative correlations to yield under all conditions. This may be due to properties of the soil that limited N leaching, such as a hardpan. The deepest structures may not have been an advantage, as steeper angles allowed plants to invest less in achieving moderate depths. Particularly deep-rooting systems may have even been detrimental, as they passed N sources and wasted tissue, energy, and important nutrients in their growth. A hardpan might also limit rooting depth, as fewer roots would penetrate through it.

These results were in contrast to previous modeling efforts, which suggested deeper-rooted architectures enhance N acquisition later in the season because of enhanced access to deeper N stores and less depletion-zone overlap (Dunbabin, et al., 2003). Other studies (Chun, et al., 2005, Tian, et al., 2005) also found that root growth and elongation is enhanced under low N conditions.

The stronger relationship of brace roots than crown roots to yield indicates that brace roots may play a more important role later in the season and during grain filling. When nitrogen is limiting, root structures may be utilized differently and brace roots exploited for grain production. Previous studies have suggested that crown roots are more important for the acquisition of mobile nutrients and water, leading to a greater yield (Araki et al., 2000), though these data disagree. The negative correlation between crown root angles and yield is unclear. It may simply suggest that under the conditions the experiment was carried out crown roots played a less significant role at this point in the season for N acquisition. Alternatively, N concentrations in the upper soil levels may not have been low enough compared with lower soil layers to outweigh the costs of deeper crown roots.

Dunbabin, et al. (2003) found that highly dichotomous, very sparse, or particularly shallow plants performed poorly in models of soils where N stress was common due to high

leaching potential. That our results do not follow this pattern may indicate that plants do not retain one root architecture pattern. Instead, plants form a relationship with their environment that is capable of response and adaptation throughout the growth season.

## **Conclusion**

Crown and brace root angles can be used to predict rooting depth and branching. Steep angles result in deeper, less branched roots. Low N conditions also result in steeper root angles over time. Based on the results obtained here, it is not possible to say that “steep” genotypes performed better than “shallow” genotypes under low N conditions, because the differences between steep and shallow structures were minimized under low N. Under low N a reduction in yield was observed for steep or shallow genotypes, and in fact their performance was very similar. A steep structure with highly branched brace roots appears best for a good yield, however it seems that each rooting pattern responded to N deficiency by utilizing this structure. The similarity of root architectures between genotypes that contrast structures under optimal conditions may be the result of changes in root morphology to maximize N acquisition under low N conditions. These results highlight the importance of further research into this area to elucidate the causes and mechanisms of structural response to nitrogen status.

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## Academic Vita

### Chelsea Sutherland

**Local address:**

600 W. College Ave. Apt 106  
State College, PA 16801

**Permanent address:**

251 Tyro Road  
Baden, PA 15005

#### Education

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**The Pennsylvania State University,** Schreyer Honors College Scholar  
B.S. in Biology, May 2010 Dean's List  
Honors in Horticulture  
Minor in Psychology

**University of Leeds, England,** '08-'09 academic year  
Obtained academic credit in upper level biology, psychology, ethics, and business through direct enrolment in the university.  
Traveled through 10 European countries, gaining comfort with cross-cultural situations.

**Tropical Field Ecology in Costa Rica,** '09-'10 short term  
Teamed with students, local researchers, and international scientists studying tropical ecology.

#### Research Experience

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**Undergraduate Honors Thesis, Penn State College of Agricultural Sciences,** '09 – present  
Investigated the effects of maize root architecture on the uptake of nitrogen in both optimum and N-deficient soils. Various measurements taken and analyzed throughout the cropping season and after harvest.

**Children's Hospital of Pittsburgh Summer Research Internship,** '08  
Completed an independent project investigating the effect of the overexpression and knockdown of a particular gene on lymphatic development in zebrafish.  
*End of Summer Project Poster Session, First Place out of thirty student interns.*

**Penn State College of Health and Human Development,** '07-'08  
Subject dissection, tissue preparation, sample experimentation, and data collection and analysis to investigate the effect of iron on neural pathways.

**Penn State College of Science,** fall '07  
Assisted several graduate students in data collection, data entry, and experimental setup and design on experiments studying thistles as an invasive species.

**Penn State College of Agricultural Sciences,** spring '07  
Assisted a graduate student in data collection and plant care during his research on the interaction between atmospheric carbon dioxide, nutrient uptake, and plant growth.

#### Leadership and Volunteer Experience

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**Camp Lutherlyn,** '07 Staff Riding Instructor and Counselor. Designed and coordinated group riding instruction for various age groups, rotating leadership among equestrian staff.

**Program Ambassador**, informed and supported those investigating Education Abroad in Leeds.

**Global Programs Welcome Week Volunteer**, Helped process paperwork and provide a comfortable transition for international students studying at Penn State.

**PA Literacy Corps Tutor**, Tutored English as a second language in an adult literacy program.